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CICLO XXI

Separate Motion-detecting Mechanisms for First- and Second-order Motion revealed by Priming, Position Shift and Motion Aftereffect

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Abstract

A striking number of psychophysical, neuropsychological, and human neuroimaging studies suggest the presence of distinct mechanisms and neural substrates for the perception of motion defined by spatiotemporal variations of luminance (first-order motion) and the perception of motion defined by spatiotemporal variations of contrast (second-order motion) (Ledgeway & Smith, 1994a,b; Lu & Sperling, 1995, 2001). The experiments outlined in this Thesis aimed to investigate further the mechanisms underlying the perception of first- and second-order motion and how these two motion signals are integrated by the visual system. To this end, first-order, second-order and cross-order motion conditions were tested under different experimental paradigms such as *motion priming* (Chapter 2), *motion aftereffect* (MAE - Chapter 3) and *motion-induced position shift* (MIPS - Chapter 4). In particular, the experiments were designed to possibly tap low-levels, intermediate-levels and high-levels of motion processing, to understand better whether first- and second-order motion perception involve different and separate mechanisms from the lower level of motion analysis (e.g., V1, V2/V3) and whether these two kinds of motion signals are integrated at a higher level of motion analysis.

In the first experiment (Chapter 5) we investigated the implicit short-term memory mechanisms for first- and second-order moving stimuli. In particular, we used a repetition priming paradigm (Chapter 2) in order to test if priming for motion direction is sensitive to spatial position with both first- and second-order motion. We also used a cross-order condition in which first-order motion patterns primed second-order moving patterns and vice versa. Testing priming for motion direction and spatial position separately for first- and second-order motion allowed us to assess if these two motion cues are represented and stored in neural substrates with a retinotopical organization. The cross-order condition permitted us to assess whether the implicit short-term memory for first- and second-order motion relies on the same mechanism/s and neural

substrates; that is, if first-order primes second-order motion and vice versa, this would suggest a common locus of priming representation for first- and second-order motion. We found that priming for motion direction occurs both with first- and second-order motion. Moreover, priming for motion direction is position-sensitive both with first- and second-order motion, suggesting a neural locus of priming representation with a retinotopical organization. Previous findings of Campana et al. (2002, 2006) have shown the involvement of cortical area MT in priming for motion direction using first-order stimuli, based on the results of the first experiment we suggest that MT might be involved also in second-order motion priming. We found that cross-order motion priming also exists but it is weaker and not sensitive to spatial position. From these findings we hypothesize that first- and second-order motion cues remain distinct and separate at the level in which global motion is extracted (i.e., MT; Edwards & Badcock, 1995). However, the two types of motion could be integrated at a higher level of motion processing, where the retinotopic organization is either lost or at least very coarse (e.g., MST).

The findings of the first experiment showed both that, in the within-order conditions priming for motion direction is dependent on the repetition of the same target's position; and, in the cross-order condition, priming is not sensitive to spatial position. These findings suggest not only there are two independent pathways for first- and second-order motion, but also that these two motion processing streams seem to encode the spatial position of a moving pattern separately. In the second experiment (Chapter 6) we assessed more specifically the issue of whether first- and second-order motion encode and assign the position of a moving pattern by means of a single and common mechanism, or whether there are two distinct mechanisms for position assignment. To this purpose we measured the motion-induced position shift (MIPS) for first-order and second-order drifting Gabors (De Valois & De Valois, 1991; Durant & Johnston, 2004; Edwards & Badcock, 2003; Fang & He, 2004). We first measured the MIPS for first- and second-order moving patterns separately, then conducted another experiment in which first- and second-order

drifting Gabors were presented within the same trial, to see if cross-order motion shifts perceived position as well. If there is a common position assignment mechanism for both first- and second-order motion cues, one would expect an effect size of cross-order MIPS intermediate between that obtained with first- and second-order motion separately. On the other hand, the lack of an effect for cross-order stimuli would indicate the presence of independent position assignment mechanisms. We found that both first- and second-order motion, presented separately, shift the perceived position. We did not find any positional shift with cross-order stimuli. This implies the presence of separate mechanisms that encode and assign the spatial position for these two motion cues.

In the third experiment (Chapter 7), we used a paradigm developed by Kanai and Verstraten (2005) in order to tap the mechanisms of motion processing (of both first- and second-order motion) and their interaction with adaptation at low- (e.g., V1) and intermediate levels (e.g., MT) of motion processing. Kanai and Verstraten (2005) showed that depending both on the duration of the adapting stimulus and that of the adaptation-test blank interval (i.e., inter-stimulus intervals [ISI]), the perceived direction of an ambiguous test pattern can be biased towards the opposite direction of the adaptation pattern, or in the same direction. Specifically, at very short ISIs (below 120 ms), very short adaptation durations (below 100 ms) can produce a rapid form of priming (rapid visual motion priming [rVMP]), whereas slightly longer adaptation durations (e.g., 320 and 640 ms) can yield a rapid form of motion aftereffect (rapid motion aftereffect [rMAE]). Moreover, Kanai and Verstraten (2005) showed that using even longer adaptation durations and ISI longer than one second biases the perceived motion direction of the test pattern toward the same motion direction (i.e., motion priming), obtaining a kind of priming for motion direction similar to that obtained in our first experiment. This probably reflects the activity of intermediate-level areas (e.g., MT). Very brief adaptation durations could selectively tap the response of low-level first- and second-order motion detectors. In this experiment we assessed if

rVMP, rMAE, and the motion priming obtained with longer ISI also exist within the second-order motion domain. We found that the rapid effects (i.e., rVMP and rMAE) and motion priming had similar time courses for first- and second-order motions when presented separately. In a cross-order adaptation condition (i.e., adapting to first-order then testing with second-order, and vice versa) we found asymmetric transfers between first- and second-order motion cues. First-order motion influenced the processing of second-order motion but not vice versa (resulting only in rMAEs) (see Schofield et al., 2007).

Taken together, our findings support the notion that first- and second-order motion are encoded by separate mechanisms from the early stages of motion processing but could be integrated at higher levels of motion processing (as in the case of the cross-order priming condition). However, the last experiment showed a certain degree of asymmetric transfer between first- and second-order motions: indeed, we found rMAEs only when we adapted to first-order and tested with second-order. These results imply that, even in low-level processing, first-order motion can influence the perception of second-order motion but not vice versa, further implying a hierarchical organization to the early mechanisms responding to these two motion cues.

Chapter 1

Literature Review

1. Motion perception

When we look at a moving scene its image continuously changes over our retina. However, even when we look at a static scene our eye, head, and body movements produce continuous motion on the retina. This information is combined to create a complex visual pattern, which can be used in several ways: (i) To segregate figure from background. Objects that are invisible when static are detected when they start to move. (ii) To extract the 3-D structure of an object. (iii) To control actions. When we move in the real world a great deal of information can be extracted from optic flow, including the speed and the direction of self-motion. (iv) In addition, motion information is exploited by the oculomotor system to fixate moving objects and to stabilize the retina's image during autokinesis.

The above example reveals the role of motion perception as a fundamental process in everyday life. It highlights the importance of questions such as, 'How do we detect the motion of an object?' and 'Which processes, mechanisms and neural substrates are involved?'.

1.1 The space-time representation

Motion can be defined as a change in position over time. To perceive the movement of an object, we have to identify the object, note its spatial position, and identify it again after a period of time in a new location. The velocity of the movement is commonly calculated by dividing the change in position (δs) by the time interval (δt). This simple definition gave rise to a class of models of

motion detection known as correlation-type models. The most representative correlation-type model is the model developed by Reichardt (1961), which will be considered later in this chapter.

A different approach suggests that motion information can be extracted from space-time representations of a moving stimulus e.g., the Adelson and Bergen (1985), model (Figure 1.1).

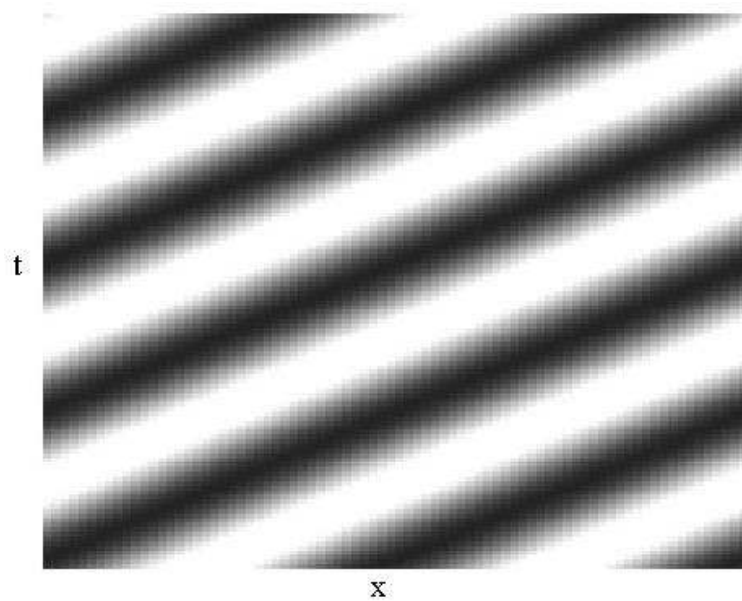


Figure 1.1. Space-time representation of a sine-wave grating drifting leftward. The abscissa represents the space, whilst the ordinate represents decreasing time. The orientation of the bars reflects the velocity (V).

Figure 1.1 shows a 2-D plot of a drifting sine-wave grating; the horizontal axis corresponds to space (x) and the vertical axis corresponds to time (t). It represents the distribution of luminance intensities over space and time. 1-D horizontal slices of this representation provide the description of the spatial pattern at one particular instant (t), whereas, vertical slices describe how the intensity of the image changes over time at one specific spatial position (x). The orientation of the white strips gives the velocity of the pattern. Thus, following this approach, motion can be considered as *orientation* in space and time. This kind of representation is very

useful since the velocity of the pattern can be obtained simply by recovering the orientation of the space-time image. Moreover, this approach treats the time dimension in a similar way to the spatial dimension, allowing the use of spatial filtering to extract information about motion direction and velocity.

In particular, the velocity (V) of a moving pattern can be extracted by measuring the local differences in intensity of the space-time image, that is, since velocity corresponds to orientation in space-time, it can be recovered by the ratio of the spatial and temporal intensity gradients (derivatives) (Figure 1.2).

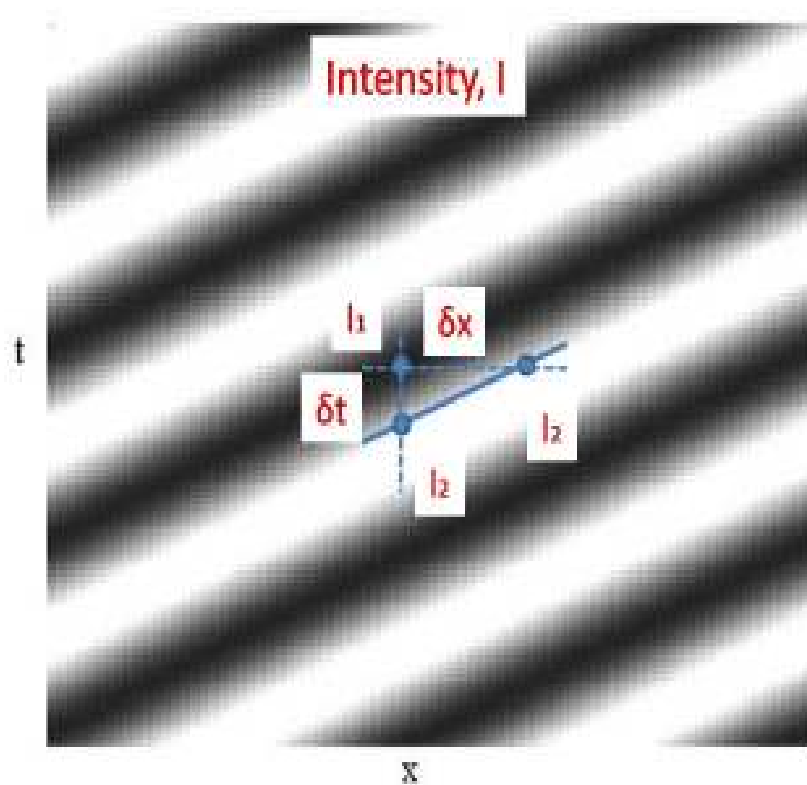


Figure 1.2. Velocity can be recovered from spatial and temporal gradients (or derivatives), and it is given by the ratio between the temporal and spatial gradients (see text for more details) (Adapted from Bruce et al., 2003).

To better understand the definition of velocity in terms of gradient, one should consider some basic concepts, in particular, some approximations.

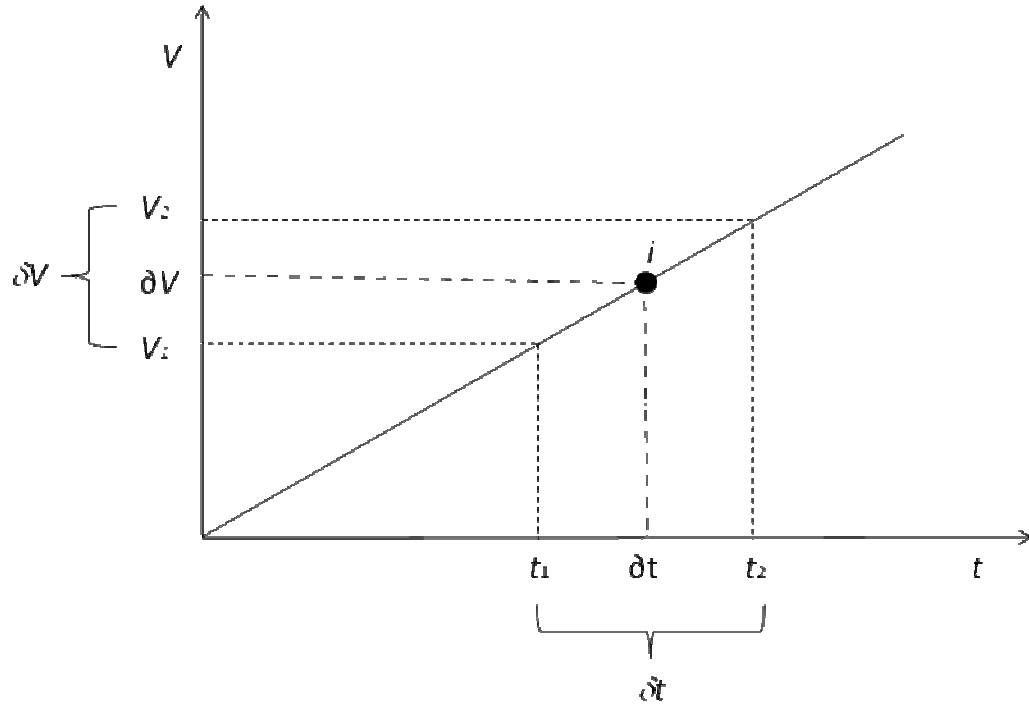


Figure 1.3. The plot represents the case in which an object moves by uniformly accelerated motion. Mean acceleration is given by the ratio $\delta V / \delta t$, whilst acceleration of the point 'i' (i.e., snap acceleration) is given by $\partial V / \partial t$.

In physics the acceleration of an object is defined as follows:

$$a = (V_2 - V_1) / (t_2 - t_1) = \delta V / \delta t \quad (\text{Eq.1})$$

As demonstrated in Figure 1.3, Equation 1 refers to a mean acceleration (i.e., calculated across a temporal interval). However, Equation 1 is not well suited if we have to calculate the snap acceleration of point 'i'. To calculate the snap velocity of point 'i' we have to shorten the

interval δV so that to match or approximate it to ∂V , the same thing should be done for δt ; in such case the interval δt must to be approximated to ∂t .

In our case the velocity of a moving pattern can be initially calculated in terms of the ratio between differences of intensity variations i.e.;

$$V = (\delta I / \delta t) / (\delta I / \delta x) \quad (\text{Eq.2})$$

where $\delta I = I_2 - I_1$ (see Figure 1.2).

Taking into account the previous considerations it is possible to extrapolate the following approximations:

$$\delta I / \delta t \approx \partial I / \partial t$$

$$\delta I / \delta x \approx \partial I / \partial x$$

Thus, the velocity of a moving pattern can be calculated in terms of the ratio between gradients:

$$V = (\partial I / \partial t) / (\partial I / \partial x) \quad (\text{Eq.3})$$

The spatial gradient of the intensity ($\partial I / \partial x$) is the ratio between spatial changes in intensity between consecutive points of the image, and the temporal gradient ($\partial I / \partial t$) is the ratio between temporal changes in intensity at a given position and the temporal interval (Figure 1.2). That is, the velocity of a moving pattern is expressed by the ratio between the temporal gradient and the spatial gradient. Evidence from computational and psychophysical studies suggests that

visual system incorporates and employs specific *filters* or *receptive fields* to detect spatial and temporal variations of the intensity of an image, whose ratio is proportional to velocity.

1.2 Motion detectors

Motion detectors respond to oriented structures in the space-time image (x, t). There are many ways to construct them, and a striking number of models have been proposed.

Early visual processing begins with local spatiotemporal filtering conducted by neuronal receptive fields. For instance, X-type retinal ganglion cells have a band-pass spatial response and a low-pass temporal response (Enroth-Cugell & Robson, 1966). Such receptive fields are symmetrical (e.g., receptive fields with centre ON and periphery OFF or vice versa) and are not oriented in space-time, so they cannot produce a directionally selective response to a moving stimulus. The general strategy shared by models of motion detectors is to combine the outputs of such local filters in order to obtain a *direction-selective* receptive field, which is elongated along a particular axis in space-time. The axis specifies both the preferred direction and the preferred velocity of the detector.

A spatiotemporal receptive field can be constructed from the input of two receptive fields having spatiotemporal weighting functions which are offset (i.e., shifted in space and time) relative to each other. When combined, they detect motion signals along a specific axis in space-time (Mather, 1994). The most common way to construct a spatiotemporal detector is make use of the relationship of quadrature that exists between receptive fields to introduce a spatiotemporal offset. It is well established that Gabor functions (a sine-wave or a cosine-wave multiplied by a Gaussian envelope) describe and characterize strictly the spatial structure of receptive fields (Marcelja, 1980; Pollen & Ronner, 1981). An offset in the spatial sensitivity profiles of two receptive fields centred on the same retinal location can be implemented by shifting the phase of the sine-wave carrier of one Gabor with respect to the other. For example, a phase shift of 90 deg

will convert an even-symmetric (cosine phase) receptive field into an odd-symmetric receptive field (sine phase). Assuming such relationship about the same spatial axis, the receptive fields are a quadrature pair.

Consider, a drifting sine-wave sampled by two receptive fields in quadrature. The image intensity corresponding to each receptive field will fluctuate sinusoidally over time as the sine-wave passes over and, due to the spatial offset, the temporal modulation at the two positions will be offset by a quarter of a temporal cycle. If the sine-wave drifts rightward, then the temporal modulation at the left-hand sampling position will influence and drive the modulation at the right-hand position. A directionally-selective response can be constructed by introducing a temporal delay between the responses of the two receptive fields. The net response of each receptive field is given by the product of its spatial response and its temporal response. If the temporal responses form a quadrature pair where the right-hand field's response leads the left-hand field's response by a quarter of a temporal cycle (i.e., the left-hand response is delayed), then the two responses will be temporally in phase for rightward motion. On the other hand, if the temporal response of the left-hand field leads the right, then the two responses will be in phase for leftward motion (Mather, 1994).

Thus, directionally-selective responses can be constructed by combining components which exhibit spatial and temporal quadrature. Figure 1.4 shows some basic detectors, each containing a spatial filter and a temporal filter in quadrature. The outputs of spatiotemporal filters from each path are combined to give a direction-selective response.

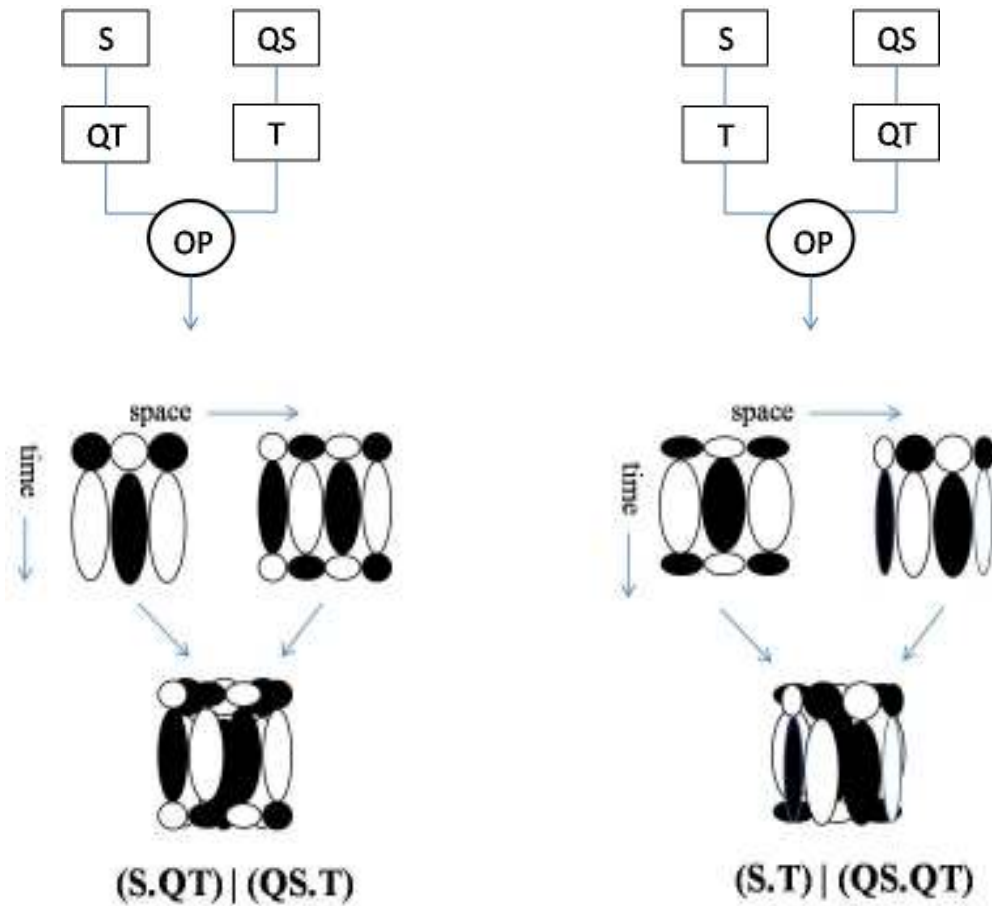


Figure 1.4. Basic motion detectors. Top: paths that form a basic motion detector. Each path contains a spatial and a temporal filter. The spatial and temporal filters of one path are in quadrature relationship with respect to the filters of the other path (S and QS , and T and QT). Responses from each path are combined to obtain a direction-selective response. The preferred direction depends on the form of the filters. Middle: spatiotemporal filters. From left to right: (i) filter $[S.QT]$ has an even-symmetrical spatial response and an odd-symmetrical temporal response; (ii) $[QS.T]$ has an odd-symmetrical spatial response and an even-symmetrical temporal response; (iii) $[S.T]$ has an even-symmetrical response over both space and time; (iv) $[QS.QT]$ has an odd-symmetrical response over both space and time. Bottom: when superimposed (i.e., summed) these spatiotemporal filters produce direction-selective filters. The filter on the left responds to leftward motion, whereas the filter on the right responds to rightward motion (Adapted from Mather, 1994).

2. Models of motion detection

Numerous models of motion detection have been developed employing the scheme outlined so far. However, they differ in their implementation of the scheme. This section provides a brief overview of the most important models of motion detection.

An early model of human motion perception was proposed by Hassenstein and Reichardt (1956) and Reichardt (1961). This is the most representative of the correlation-type models, in which motion detection is based upon the correlation of signals originating from two points in the retinal image. A motion detector based on the principle of correlation simply compares the same signal delayed over time and over two different spatial regions. Essentially, the Reichardt model contains two mirror-symmetrical subunits each consisting of a pair of receptors that respond to motion signals at two consecutive points in space (Figure 1.5). Each pair of receptors is spatially separated by a distance that determines the spatial sampling of the detector. Each subunit is direction-selective. Motion signal activates the first receptor and its output is delayed relative to the output of the second receptor. The delayed output from the first receptor is then correlated (i.e., multiplied) with the output from the second receptor and the product is integrated over time. Finally, the outputs of both directional subunits are subtracted to yield the detector's response. The Reichardt detector is a fully-opponent motion detection unit producing responses of the same amplitude but of different signs to motion in opposite directions (Figure 1.5).

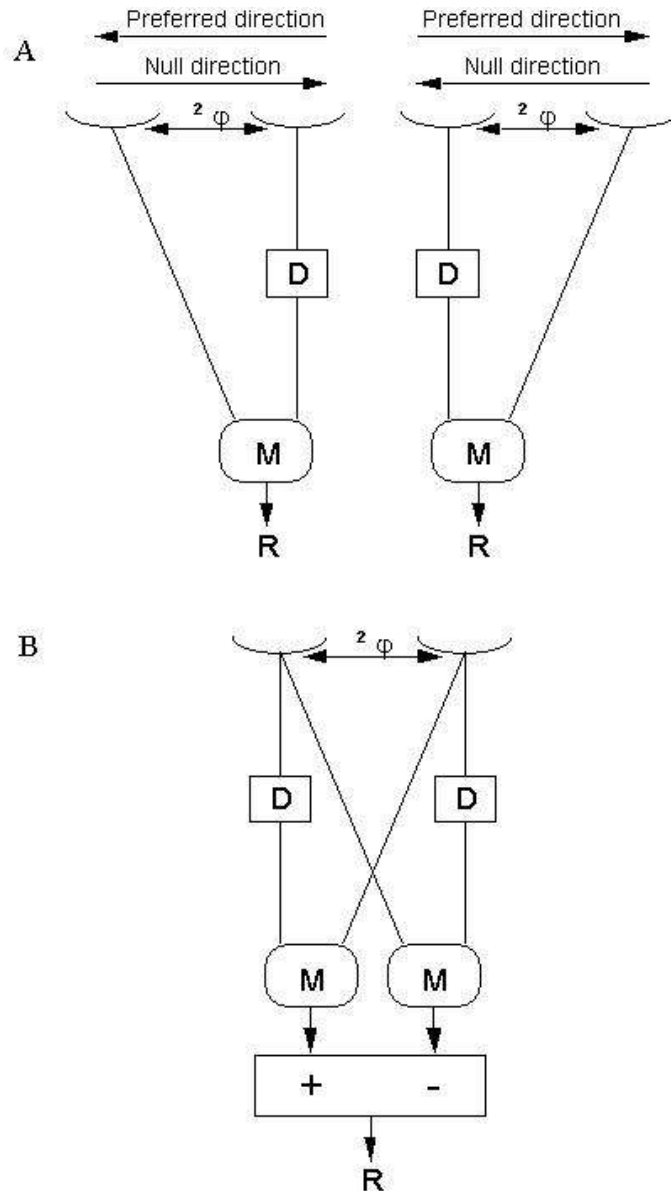


Figure 1.5. A. The Reichardt detector consists of two mirror-symmetrical subunits sensitive to movement in opposite directions. In each subunit, the signals from two neighboring receptors are multiplied (M) after a delay in time (D). B. The final detector response is given by the difference of the output signals from both subunits (Taken from Hutchinson, 2005).

Despite the fact that the Reichardt model provides a measure of the motion direction, it has a spatial aliasing problem strictly related to the spatial sampling (i.e., the distance between two subunits). The spatial sampling of the model influences both the spatial resolution of motion

detection and its dependence on the spatial frequency of the moving pattern. The smallest spatial frequency of a sinusoidal grating that is detected correctly equates to twice the spatial sampling of the model (Borst & Egelhaaf, 1989). For lower spatial frequencies the response may become inverted when the distance between input channels is between one-half and one spatial period. This aliasing problem has been overcome by replacing the receptors of the Reichardt detector with band-pass spatial filters. The elaborated Reichardt detector (ERD) model (van Santen & Sperling, 1985) uses local spatial frequency filters to extract motion signals from luminance variations. The receptive fields of the elaborated Reichardt detector are separated by one quarter of a cycle of their spatial frequency, and also the temporal filters are separated by a quarter of a cycle to prevent temporal aliasing. Thus, each subunit is essentially a pair of local spatial and temporal detectors in a quadrature relationship (Figure 1.6). The output of the local spatial and temporal filters is then multiplied and passed through a temporal integrator and the final motion direction is calculated by subtracting the outputs from the left and right filters (opponent motion). The ERD model is physiologically plausible as the multiplication stage is consistent with the finding that many forms of nonlinear physiological interaction are equivalent to multiplication (Torre & Poggio, 1978).

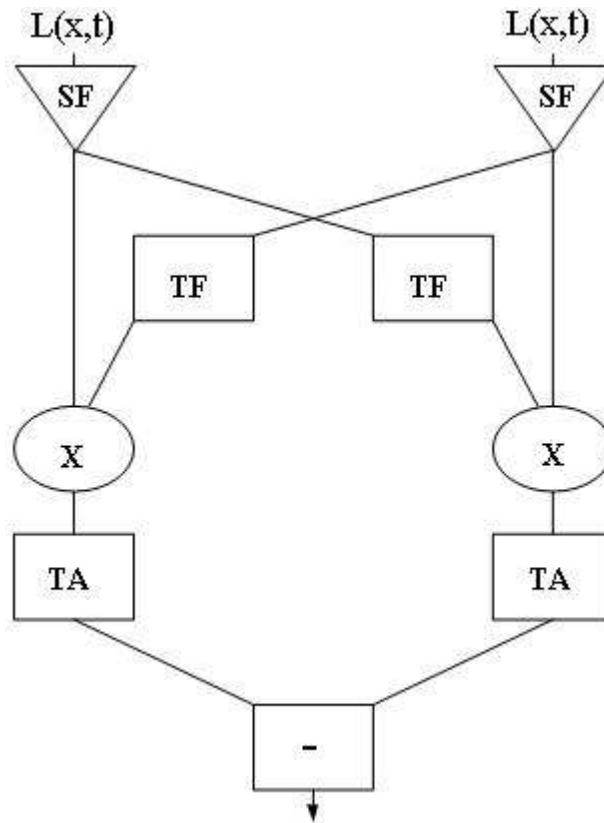


Figure 1.6. The elaborated Reichardt detector (ERD) consists of mirror-symmetrical subunits that operate as local spatial frequency filters to extract motion signals from spatiotemporal luminance variation $L(x, t)$. The luminance input is passed through left and right spatial and temporal filters in quadrature relationship. The output from these filters is then multiplied and passed through a temporal integration filter with infinite time averaging (TA). The output of these filters is subtracted to produce a signed output indicating the direction of motion (Taken from Hutchinson, 2005).

A similar model of motion detection has been proposed by Adelson and Bergen (1985). Adelson and Bergen's model is based on the assumption that motion detection is simply a detection of spatiotemporal orientation. Many cells in the visual system perform a weighted integration of the input signals. The positive and negative lobe structure of the receptive field defines the weighting function (i.e., spatial impulse response; Figure 1.7A). Since any spatial pattern can be

considered an ensemble of points of light, the spatial impulse response of a unit to a luminance pattern could be constituted by the sum of its responses to the local variations of intensities. A temporal impulse response is shown on the left in Figure 1.7A. It could be considered a temporal weighting function which describes how inputs are summed across time to produce a response. A separable spatiotemporal impulse response can be obtained combining spatial and temporal impulse responses. The output can be represented as depicted as three positive and three negative lobes as shown in the central part of Figure 1.7A. This configuration demonstrates how inputs at different locations and times are to be summed to give a certain output. Thus, if a cell weights all its spatial inputs by a spatial impulse response, and then the output is temporally filtered, the resulting spatiotemporal response will be separable. Alternatively, if the outputs of a large number of units are temporally filtered and then the filtered outputs are combined through a spatial weighting function, the response will be again separable. Separability is frequently observed in the early stages of cortical visual processing (Tolhurst & Movshon, 1975; Movshon et al., 1978a,b).

A spatiotemporally separable unit is not oriented in space and time and therefore it cannot detect the motion direction of a luminance pattern. However, if a unit is spatiotemporally oriented it becomes selective for direction of motion (Figure 1.7B).

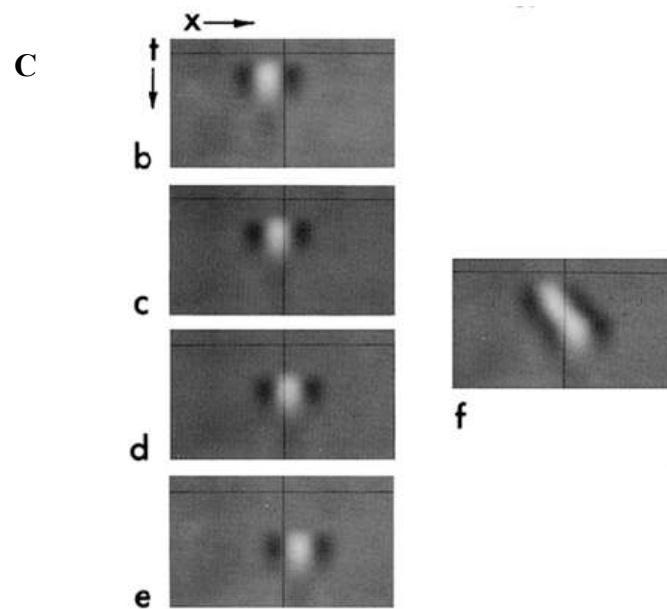
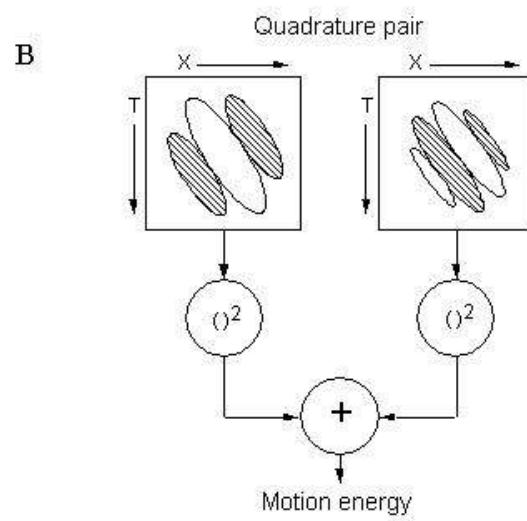
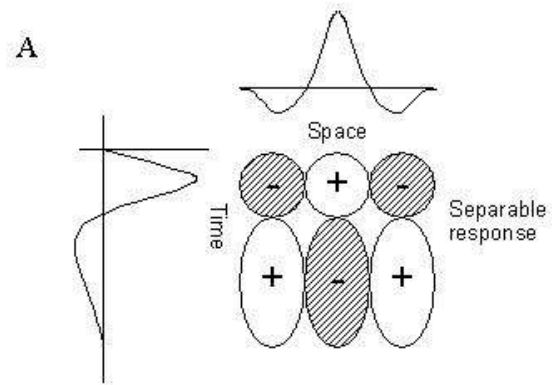


Figure 1.7. A. A separable impulse response that characterizes a spatiotemporally separable unit. The spatial and temporal impulse responses are shown along the horizontal and vertical axis, respectively. Output is determined by the spatiotemporal impulse response that sums inputs at various locations and times (Adelson & Bergen, 1985). B. A pair of spatiotemporally oriented filters in quadrature relationship (i.e., 90 deg out of phase). If their responses are squared and summed, the resulting output gives a phase-independent measure of local motion energy. The filters shown in panel B resemble spatiotemporally oriented Gabor functions. C. To approximate such functions, a number of separable filters b-e, which are shifted in phase and time, can be summed to form f. (Taken from Adelson & Bergen, 1985; Hutchinson, 2005).

Spatiotemporally oriented filters can be constructed by adding together the outputs of two separable filters with appropriate spatiotemporal characteristics (Watson & Ahumada, 1983).

Figures 1.7C (b-f) illustrates how a spatiotemporally oriented filter can be created by summing the outputs of four separable filters, which are equal except for a shift of their receptive field center and a temporal delay. An approximate quadrature partner for this filter can be constructed by using an odd-symmetric spatial Gabor function or simply shifting the filter spatially by 90 deg of phase. However, such procedures are quite coarse, and the resulting spatiotemporal oriented filters do not provide precise directional responses. Another, and more precise, way of using a separable pair of filters to construct quadrature pairs tuned for both leftward and rightward directions is shown in Figure 1.8. Initially, we can consider two spatial impulse responses (Figure 1.8A) and two temporal impulse responses (Figure 1.8B). In this case, the spatial impulse responses are second and third derivatives of Gaussians and the temporal impulse responses are based on linear filters of the following form:

$$f(t) = (kt)^n \exp(-ktt) \left[1/n! - (kt)^2 / (n+2)! \right] \quad (\text{Eq.4})$$

where n takes the values of 3 and 5 (Adelson & Bergen, 1985). Adelson and Bergen (1985) argued that such spatial and temporal functions are plausible approximations to filters inferred psychophysically (Robson, 1966).

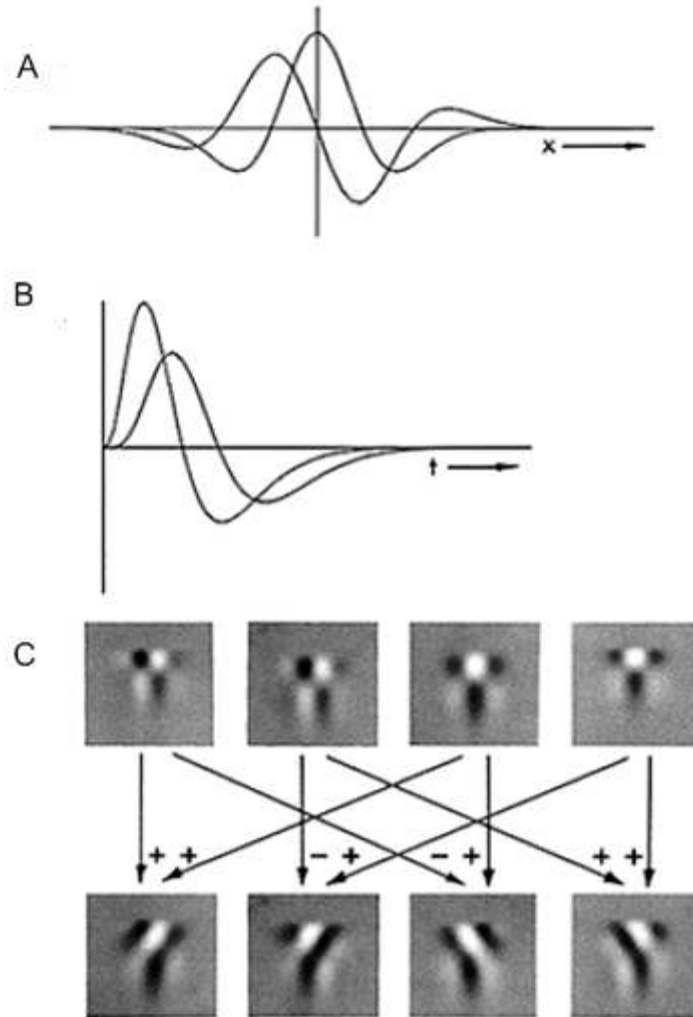


Figure 1.8. A method for constructing spatiotemporally oriented responses from pairs of separable filters (Watson & Ahumada, 1983). Two spatial and two temporal impulse responses are shown in panels A and B. The four spatiotemporal impulse responses shown on the top of panel C are the products of two spatial and two temporal impulse responses. Taking the sum and difference between these four spatiotemporal impulse responses it is possible to obtain four spatiotemporal oriented filters. The bottom row of panel C shows a pair of leftward- and a pair of rightward-selective filters. Members of a pair are approximately in quadrature (Adelson & Bergen, 1985).

There are four possible ways to combine the two spatial and two temporal filters into separable spatiotemporal filters. These possible combinations are shown on the top of Figure 1.8C. By taking appropriate sums and differences, we can construct the four spatiotemporal oriented filters (bottom of Figure 1.8C). Two are selective for leftward motion and two for rightward motion. The two members of each pair are approximately 90 deg out of phase with each other, thus are in quadrature relationship. To extract a measure of local motion energy the output of filters must be phase independent. Since spatiotemporally oriented filters are phase dependent, further elaborations are necessary. Adelson and Bergen (1985) achieved this requirement by squaring and summing the outputs of the two units resulting in phase-independent motion energy. The difference between the leftward and rightward responses gives a positive response when there is rightward motion, a negative response when there is leftward motion and no response for stationary or flickering patterns (Figure 1.7B). However, leftward and rightward energy detectors can be combined to produce a fully-opponent motion energy detector (Figure 1.9). The Adelson and Bergen (1985) model of motion is both psychophysically and physiologically plausible and can account for a range of phenomena. For example, it can predict the perceived direction of continuous and sampled displays (Anstis & Rogers, 1975). Moreover, from a physiological perspective, Pollen and Ronner (1981) have shown that simple cells in the striate cortex of the cat operate in approximate quadrature spatial phase. Furthermore, complex cells have been characterized as energy mechanisms that compute the sum of the squared outputs of quadrature pair of spatiotemporally oriented detectors (Pollen & Ronner, 1983; Emerson et al., 1986; Emerson, Bergen, & Adelson, 1992).

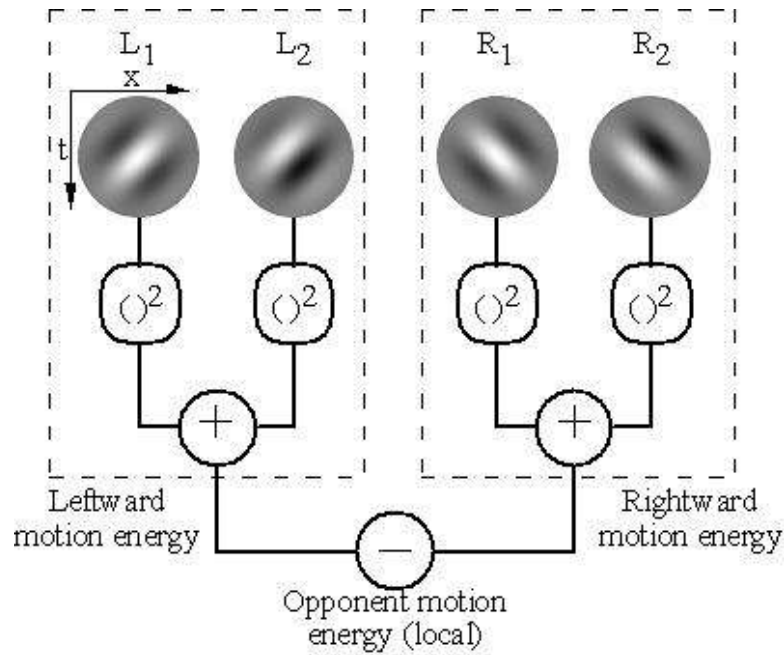


Figure 1.9. The motion-energy model of Adelson and Bergen (1985). The model employs two pairs of spatiotemporally oriented Gabor filters in quadrature relationship. The two pairs respond to motion in opposing directions (i.e., L_1 and L_2 respond to leftward motion, whereas R_1 and R_2 respond to rightward motion) and the outputs of each quadrature pair are squared and added to give a directionally phase invariant measure of local motion energy. The responses for each direction are subtracted to obtain the resultant opponent motion energy (Taken from Hutchinson, 2005).

Despite the fact that the models outlined above adequately encode the motion direction, they cannot encode the speed of a moving pattern, since other factors such as stimulus contrast, spatial frequency, and temporal frequency confound the magnitude of the output. However, a plausible model of motion detection should be able to encode both motion direction and velocity. To encode speed, the outputs of multiple detectors could be compared or combined by some later processing stage. Such a model has been proposed by Heeger (1987) in which the outputs of a set of linear, motion energy detectors (similar to Adelson and Bergen's detectors) with different

spatiotemporal tuning are combined to estimate the slope of the motion energy. The resultant velocity is the peak in the distribution of outputs from a population of detectors. It has been suggested that this function might be implemented in area MT (Heeger, 1987). Indeed recent electrophysiological evidence suggests that populations of neurons in MT show selectivity for different speeds, rather than to specific spatial and temporal frequencies (Perrone & Thiele, 2001) (see section 3 for further details).

A different class of models employs gradient detectors, and assumes the use of spatial and temporal gradients to encode direction and speed of a moving pattern. The most important gradient-type model is that outlined by Marr and Ullman (1981). Marr and Ullman (1981) exploited the fact that a moving edge having certain intensity produces spatial and temporal changes in image intensity, thus combining these signals it is possible to get information about motion direction and speed. Marr and Ullman proposed that a gradient detector contains two channels, namely S and T. The S channel computes the spatial gradient whereas T channel computes the temporal gradient. Motion information can be extracted from a comparison between the two gradients. The sign of the gradients specify the direction, whilst the magnitude specifies the velocity. Assuming that both S and T channels contain spatiotemporal filters, thus the spatial response in channel S is the spatial derivative of the spatial response in channel T, and the temporal response in the channel T is the temporal derivative of the temporal response in channel S. Marr and Ullmann (1981) proposed that the direction of a moving pattern is extracted by taking the product of channels S and T responses, although other non-linear operations are possible. Moreover, gradient detectors also exploit spatial and temporal quadrature relationships between the filters in the two channels. Consider the spatial response in channel S and T. If channel T has an even-symmetrical spatial response, its spatial derivative in channel S will have an odd-symmetrical spatial response, that is, the two responses are in spatial quadrature. Similarly to other models which use Gabor functions, a phase shift of 90 deg from cosine phase

to a sine phase is equivalent to spatial derivative, since the derivative of a cosine is a sine and vice versa. Furthermore, such a model does not incorporate a non linear-stage (e.g., squaring) to achieve a phase-independent response of the channel rendering these detectors suitable to model polarity sensitive filters. Thus the basic motion detector depicted on the top of Figure 1.4 can be considered as a gradient detector if we consider the QS component to be the spatial derivative of the S component, and QT component to be the temporal derivative of the T component. Marr and Ullman (1981) argued that the behavior of the X-type ganglion cells of the retina can approximate the S channel, whilst the Y-type ganglion cells could approximate the T channel.

All models of motion perception presented so far share some relevant features (Mather, 1994): (i) All motion detector models incorporate a process of band-pass filtering. (ii) Use paired input channels in quadrature relationships to achieve a spatiotemporal offset. There is psychophysical and physiological evidence to support some of the underlying attributes of all of the models outlined above. However, some of these models are more plausible than others. For example, Mather (1994) outlined that motion energy detectors (Adelson & Bergen, 1985) and the gradient detectors (Marr & Ullman, 1981) offer a more plausible approach to study motion detection. Indeed, he proposed that whilst Adelson and Bergen's (1985) motion energy model may be useful for understanding motion phenomena in the frequency domain, Marr and Ullman's (1981) gradient detector may map onto the family of polarity (i.e. phase) sensitive neurons in the middle stage of the motion energy model (i.e., the stage before rectification) and therefore is useful for understanding polarity-specific effects in human vision.

3. The neural basis of motion perception

A number of electrophysiological, neuroimaging and psychophysical studies in primates and humans have shown the existence of multiple cerebral areas that encode and process visual motion signals. These areas seem to form a complex interconnected network (Figure 1.10) that provides the neural substrate for many aspects of motion perception. Below follows a brief review of the most important findings on primates' visual pathway.

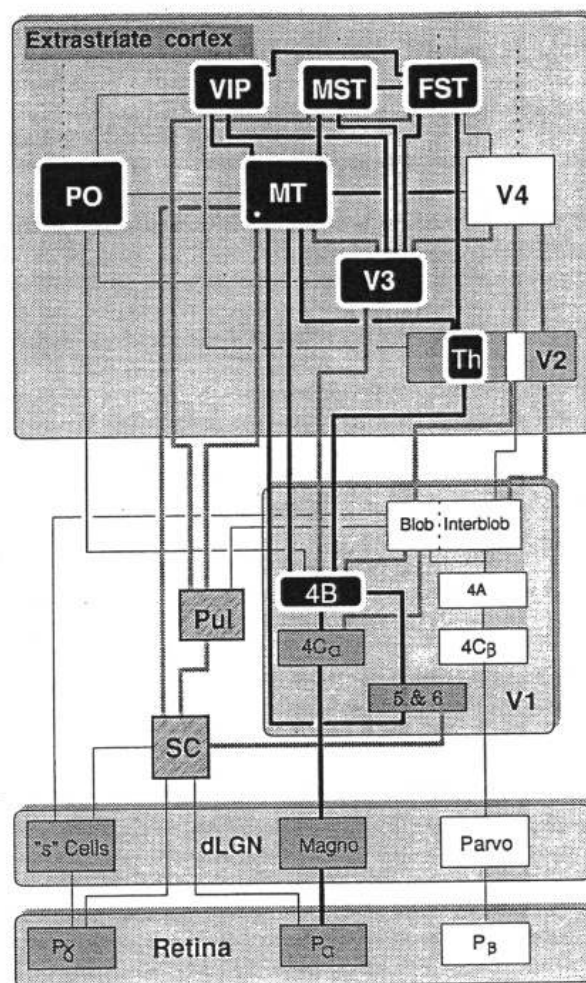


Figure 1.10. The network of the main areas involved in motion processing. Black boxes correspond to areas and layers with a high percentage of direction-selective neurons. White boxes correspond to areas and layers mainly involved in shape and color processing. Black thick lines show the connection between areas mainly involved in motion processing, gray thick lines

show some alternative connection between motion processing areas and dashed thin lines indicate projection to other areas not represented here (Adapted from Logothetis, 1994).

3.1 The retino-geniculo-striate pathway

3.1.1 Retina

The ganglion cell layer in the retina contains cells that differ in their morphology, type of connections and in their physiological properties (Gouras, 1969; De Monasterio & Gouras, 1975; Schiller & Malpeli, 1977; Kaplan & Shapley, 1986; Purpura, Kaplan, & Shapley, 1988). In primates three main categories of ganglion cells have been described (Boycott & Waessle, 1974; Leventhal, Rodieck, & Dreher, 1981): (i) Type P_{α} . These large cells comprise about 10% of the ganglion cells population. They have high contrast sensitivity, transient responses and conduct signals with high velocities. (ii) Type P_{β} cells are small-sized cells and make up about 80% of the ganglion cells. This class of cells present color opponency, sustained response, low contrast sensitivity and conduct signals at low velocities. (iii) Type P_{γ} cells, a heterogeneous group of small cells that represent about 10% of the ganglion cells (Schiller & Malpeli, 1977; Perry & Cowey, 1984; Perry, Oehler, & cowey, 1984) (Figure 1.10). It has been shown that primates' ganglion cells respond quite well to drifting gratings, but respond equally well for all directions. Moreover, it has been shown that in the human retina there are ganglion cells that send dendrites into the inner plexiform layer, where the cells receive bipolar input from ON and OFF bipolar cells (Figure 1.11) (Barlow & Levick, 1965; Wyatt & Daw, 1975; Amthor et al., 1984).

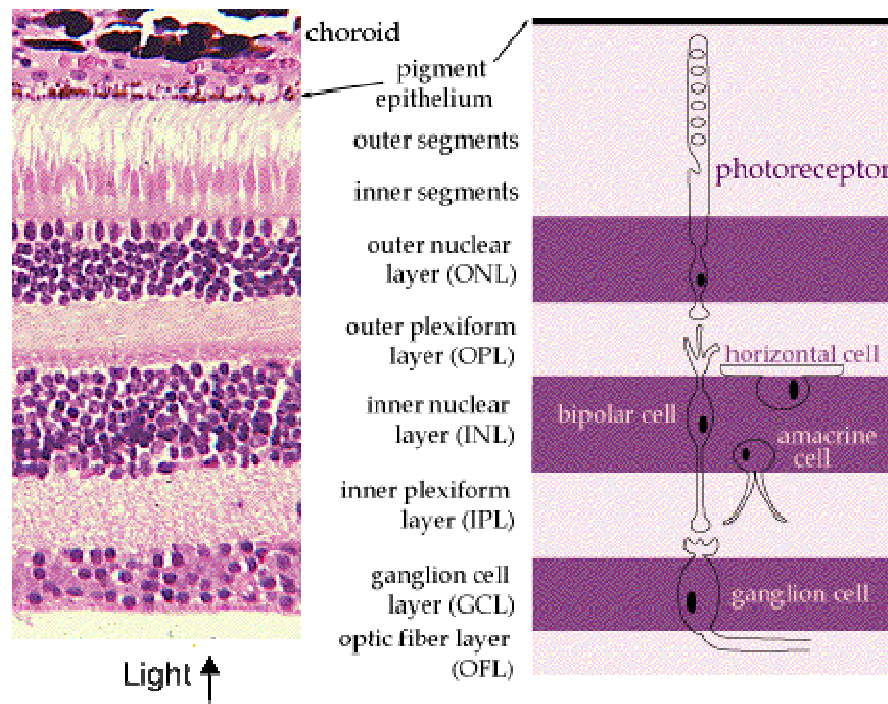


Figure 1.11. Diagram showing the layers of the retina.

3.1.2 The lateral geniculate nucleus

Approximately 90% of ganglion cells project to the lateral geniculate nucleus (LGN), which in turn projects to striate cortex (V1). The LGN is a stratified thalamic nucleus consisting of six layers. The first two layers (beginning from the ventromedial region) are classified as magnocellular layers, whereas layers from 3 to 6 are classified as parvocellular layers. Interleaved between the magnocellular and parvocellular layers are layers of small neurons (konio cells) that receive input from P_γ ganglion retinal cells and from the superior colliculus (Campos-Ortega & Hayhow, 1970; Giolli & Tigges, 1970, Kaas et al., 1978, Itoh et al., 1982). Magnocellular layers receive input from the P_α , whilst the parvocellular layers receive input from P_β cells (Leventhal et al., 1981; Perry et al., 1984). Magnocellular cells have large receptive field and show transient responses, high contrast sensitivity, no color opponency, high temporal

resolution and high conduction velocity. On the other hand, parvocellular cells have smaller receptive fields, and show sustained responses, color opponency, low contrast sensitivity, high spatial resolution, low temporal resolution and low velocity of conduction. Mangocellular and parvocellular cells respond to moving gratings, but only a small fraction of them show weak direction selectivity (Lee, Creutzfeldt, & Elepfandt, 1979), which in the case of parvocellular neurons depends on the wavelength of the stimulus (Lee, Creutzfeldt, & Elepfandt, 1979).

3.1.3 The Striate cortex

The topographical organization of the LGN is maintained in striate cortex. The magnocellular cells project to layer $4C_{\alpha}$, whereas the parvocellular cells project to layer $4C_{\beta}$ of the striate cortex. The cells of the layer $4C_{\beta}$ send projections to the layer 2 and 3 of the striate cortex corresponding with blobs. Blobs are structures of cells that respond to color and project in a specific manner to extrastriate areas (Livingstone & Hubel, 1982, 1988) and interblob regions (Lund, 1973; Lund & Boothe, 1975), whereas neurons of the layer $4C_{\alpha}$ project to layer 4B. In addition, koniocellular cells of the LGN project to layers 2 and 3 of the striate cortex, in correspondence with blobs (Figure 1.10) (Livingstone & Hubel, 1982). Electrophysiological studies on primates' striate cortex have shown that at least one-third of the striate cells, in particular the complex cells, are direction selective, and have been found overall in layers $4C_{\alpha}$, 4B, 4A and 6 of the striate cortex. Moreover, further studies have pointed out the presence of rapidly adapting units, with a broad speed tuning and a strong directional selectivity (Wurtz, 1969).

3.2 The tectopulvinar pathway

3.2.1 Superior colliculus

In primates, about 10% of ganglion cells project in the upper half of the gray layer of the superior colliculus (SC) (Hubel et al., 1975). The most prominent retinal input to the SC comes from P_γ ganglion cells. Collicular cells that receive retinal input have small response latencies and are almost completely independent on the activity of the striate cortex and LGN (Schiller et al., 1979). The SC receives input from striate cortex (V1) and from extrastriate areas such as V2, V3, V4 and the middle temporal area (MT) (Maunsell & Van Essen, 1983). Direction selective units in SC have been reported, though in primates the percentage of these cells is small. Nevertheless, they respond preferentially to one direction, but they do not show inhibition when stimulated with motion in non-preferred direction (Goldberg & Wuntz, 1972). Additionally, SC cells have a broad speed tuning and respond better to stimuli oriented perpendicularly to their motion direction.

3.2.2 Pulvinar

Pulvinar is the most caudal portion of the thalamus. It is divided into three nuclei, the inferior, the lateral and the medial nucleus. The pulvinar receives input from the retina, SC, LGN, striate cortex and from extrastriate cortices. Area MT, for example, is strictly connected to the inferior and lateral nuclei of the pulvinar, in turn the inferior nucleus is connected to the striate cortex, whilst the lateral nucleus sends projections mainly to extrastriate areas (Ogren & Hendrickson, 1976). The medial pulvinar receives input from the frontal and temporal cortices and, in turn, sends projections to the same regions and also to area 7a of the parietal lobe (Asanuma et al., 1985). It has been shown that the anterior pulvinar contains many retinotopically organized regions, whilst the lateral pulvinar contains both retinotopically and non-retinotopically organized regions. The retinotopically organized regions receive input from SC and cortex, and

sends projections to cortex. Many pulvinar neurons have quite large receptive fields, are binocular and respond either to static or moving stimuli (Bender, 1982). The cells in the inferior pulvinar are direction selective and respond to a broad range of speeds (Bender, 1982).

3.3 Extrastriate areas

3.3.1 Areas V2, V3 and V4

Cells in the thick stripes of area V2 are selective for orientation and motion direction, though only a small percentage (from 8% to 16%) are direction selective (Zeki, 1978). In particular, direction selective cells tend to respond better to slow movement. Interestingly, they seem to be selectively activated by moving stimuli rather than by motion produced simply moving eyes across a static retinal image (Galletti et al., 1988).

At least 40% of V3 cells are orientation or direction selective (Felleman & Van Essen, 1987). Some of these cells show a complex pattern of direction selectivity, responding to many different directions. What is more, 90% of V3 motion cells are speed tuned. Both V3 cells and V2 cells from thick stripes project to MT area, to the medial superior temporal area (MST), to the floor of the superior temporal sulcus (FST) and to the ventral intraparietal area (VIP). These areas have a high percentage of direction selective neurons.

Area V4 was initially considered to specialize in colour analysis. However, more recently it has been shown that neurons respond to different attributes of a stimulus such as colour, orientation and direction (Desimone & Schein, 1987). Indeed, Desimone and Schein (1987) and also Ferrera et al. (1994) have shown that at least the 13% of V4 cells respond at least three times as well and 24% at least two times as well to stimulus movement in the preferred direction, if compared to a stimulus moving in the null direction. Notably, after reversible inactivation of either the magnocellular or parvocellular pathways, the direction selectivity of V4 neurons is unimpaired, suggesting that direction selectivity in V4 does not necessarily require the integrity of the

magnocellular pathway. Contrarily, MT cells' responses were consistently reduced after the inactivation of the magnocellular pathway. Moreover, area V4 is strongly interconnected with MT. It has been suggested that such interconnections between V4 and MT could mediate competitive interactions between these areas (Walsh, Ellison, Battelli, & Cowey, 1998).

3.3.2 Middle temporal area

In macaque monkeys the middle temporal area (MT) is placed approximately in the caudal part of the superior temporal sulcus. Anatomical and physiological studies have shown that MT is characterized by a zone of dense myelination in the lower layers. This highly myelinated area has a retinotopic organization of the central and the mid-peripheral part of the visual field (about 30 deg), with the peripheral part represented outside this zone (Ungerleider & Mishkin, 1979). Crossing the medial border of the myelinated zone, area MTp (Figure 1.12C), coarsely represents the visual field. In addition, it has been shown that both MT and MTp process the output of V1 and V2.

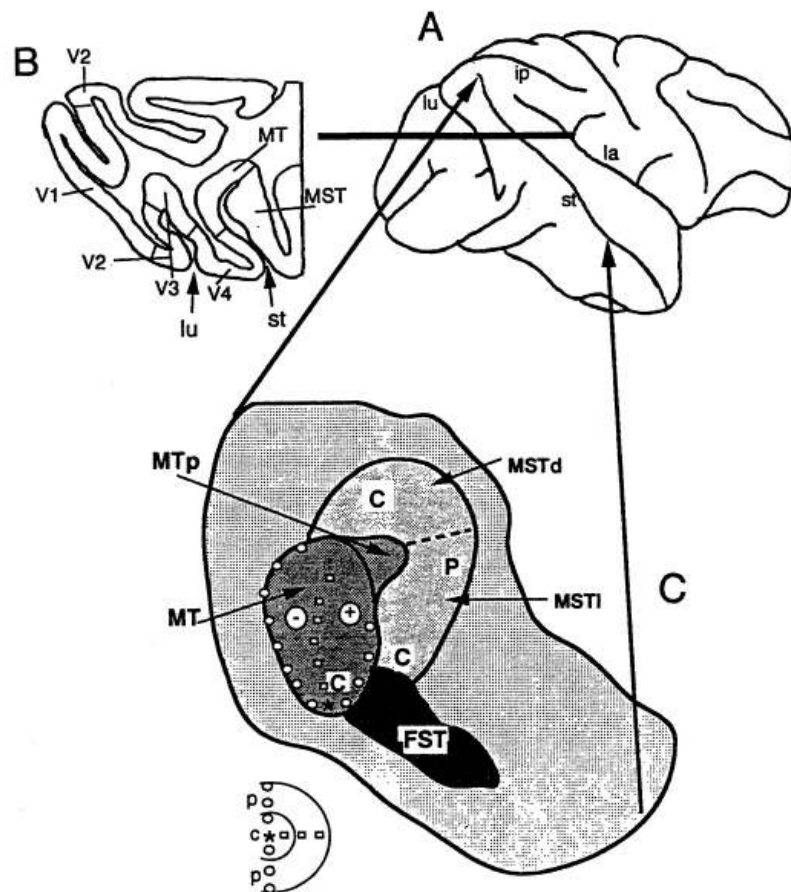


Figure 1.12. Location of visual motion areas in macaque cortex. A. The position of the lunate sulcus (lu), the intraparietal sulcus (ip), the superior temporal sulcus (st) and the lateral sulcus (la). B. A horizontal section through the thick black line showing the arrangement of the most important motion areas. C. An unfolded representation of st (between arrows) showing areas MT, MST and FST (see text for more details); “C”: central visual field, “P” peripheral visual field (Taken from Snowden, 1994).

The receptive fields of MT neurons are approximately 10 times the size of those in striate cortex; this ratio is maintained for a wide range of eccentricities (Gattass & Gross, 1981). However, such a relationship exists only for the non-direction selective neurons in V1. Indeed the receptive

fields of MT cells are about 3 times of those present in layers 4 and 6 of the striate cortex, in which the neurons are direction selective.

One of the most important properties of area MT is the high presence (about 84%) of directionally selective neurons (Dubner & Zeki, 1971). Some studies support the hypothesis that the direction selectivity of MT neurons could be inherited by a sub-population of V1 cells with directionally selective properties that projects to MT. Thus, MT neurons could merely inherit the direction selectivity and not create it by themselves (Movshon & Newsome, 1984; Shipp & Zeki, 1985). However, other findings do not support this hypothesis. Firstly, it has been shown that when the activity of V1 is eliminated the response properties of MT neurons change very little (Rodman et al., 1989). Secondly, MT neurons give a directionally selective response to rapid presented stationary frames (apparent motion) over a wider range of displacements than those supported by V1 cells (Mikami et al., 1986). Taken together these findings suggest that MT neurons both inherit and create by themselves directional selectivity.

However, MT neurons are sensitive not only to motion direction but also to the speed of the stimulus. Rodman and Albright (1987) using moving slits identified three types of MT neurons, namely S1, S2 and NT cells. S1 neurons have a speed tuning in the preferred direction that is mirrored in the antipreferred direction. S2 neurons have a speed tuning in the preferred direction but have a reciprocal tuning in the antipreferred direction. Finally, NT cells give a strong response in the preferred direction dependently on the speed of the pattern, but they are not tuned for speed in the antipreferred direction (Figure 1.13).

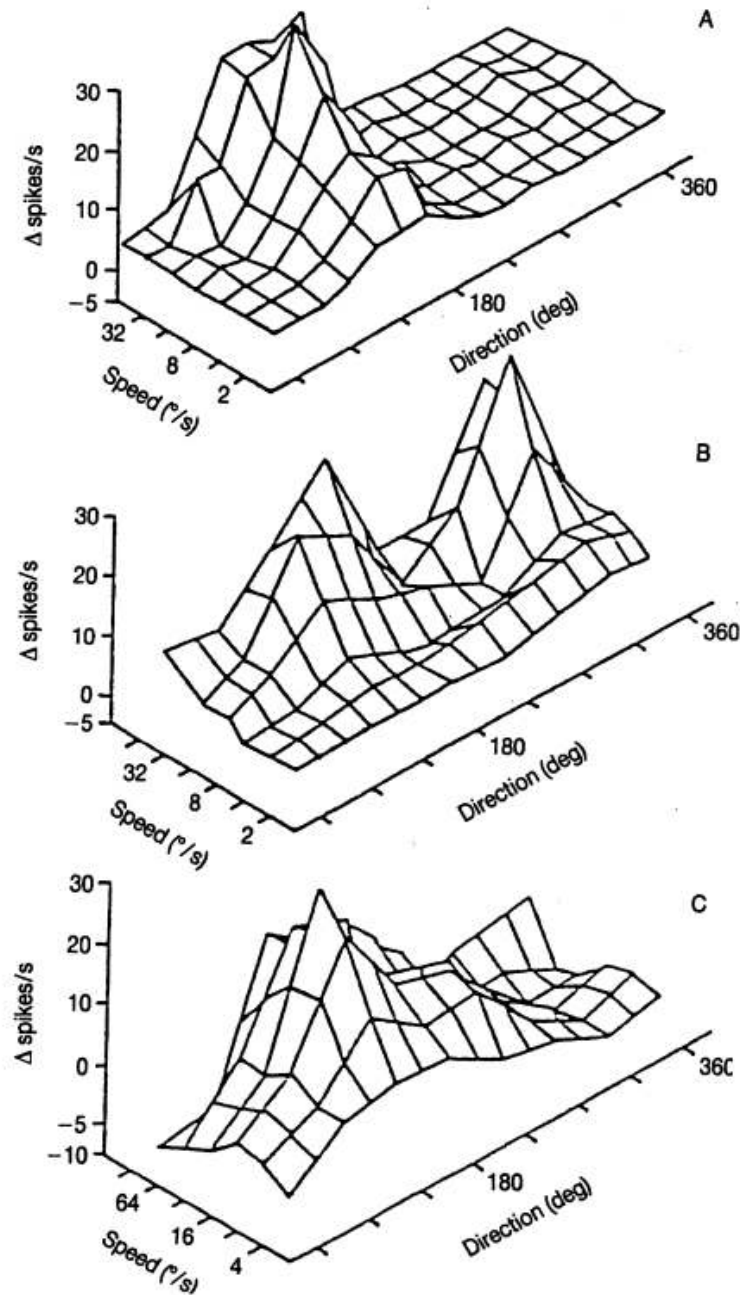


Figure 1.13. Three dimensional plot showing the response of three different types of MT cells. A. This cell give a strong response which is dependent on speed in the preferred direction, but it does not show any speed tuning in the antipreferred direction (NT type). B. This cell gives a strong response in the preferred direction and a also a strong response in the antipreferred direction (i.e., the response to the preferred is mirrored in the antipreferred direction) (S1 type). C. This cell is speed tuned in the preferred direction but has reciprocal tuning in the antipreferred direction (S2 type) (Taken from Snowden, 1994).

Then again, the stimuli employed by Rodman and Albright (1987) are not really suitable to study the speed tuning of MT neurons. This is because a slit has specific spatial and temporal frequency. As a slit changes speed the temporal frequency changes as well, thus the change in response of a neuron could be due to temporal frequency rather than speed. However, MT neurons might perform a transformation from a temporal frequency code into a speed code. To test this hypothesis it is necessary to obtain strong activity employing the same speed regardless of changes in the spatial frequency of the moving pattern. Newsome et al. (1983) and Movshon et al. (1988) described some MT cells that show selectivity for a certain speed rather than temporal frequency over a small range of spatial frequencies. These findings support the hypothesis that some MT neurons are selectively tuned for speed and transform a temporal frequency code into a speed code. Contrarily, it has been shown that directionally selective neurons in V1 are tuned for temporal frequency but not for speed (Tolhurst & Movshon, 1975). Moreover, Rodman and Albright (1987) explored the directional tuning of the MT cells as a function of the speed and found that changes in speed varied only the level of activity of the cells rather than their direction selectivity (Figure 1.14). This finding suggests that the functional properties of MT cells remain quite stable in front of changes in other features of the stimulus, such as contrast, speed, density, polarity.

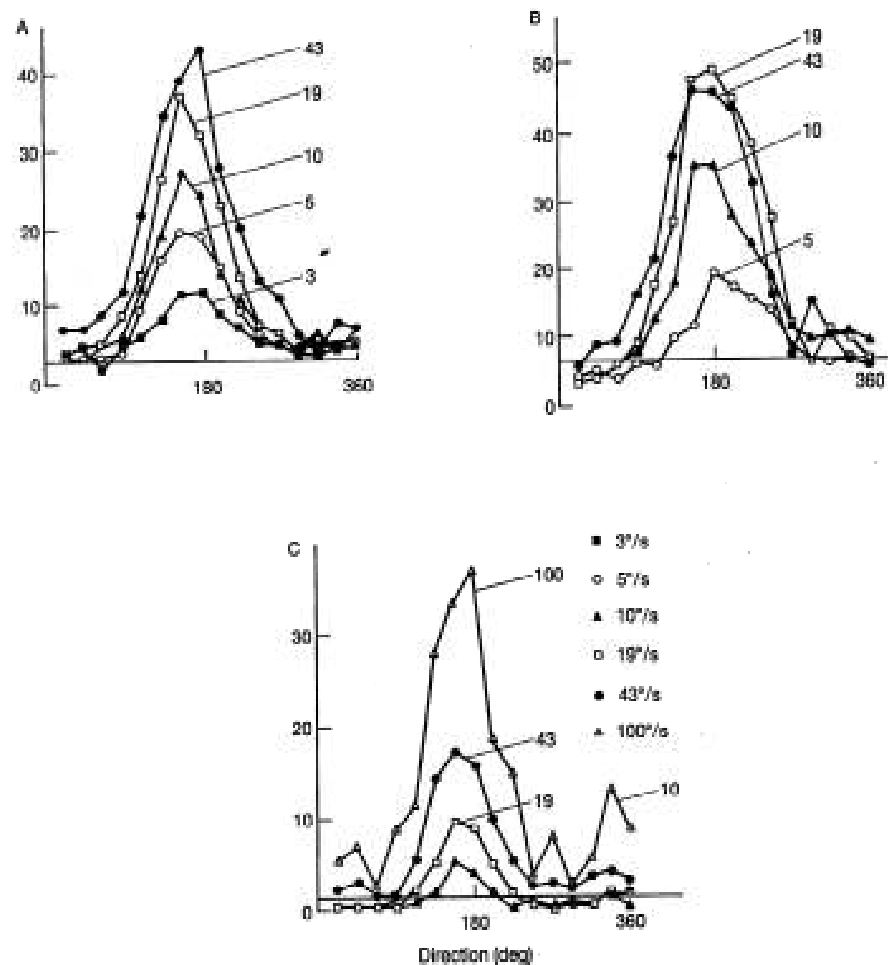


Figure 1.14. Directional tuning of three MT cells for different speeds. Variations in speed seem only to modulate the magnitude of the activity rather than alter the directional selectivity (Taken from Snowden, 1994).

In addition, a number of studies have shown that if a bar or a small patch of dots moves across the receptive field of a MT neuron, its response is weakened if it is presented a background moving in the same direction and with the same speed. However, if the background changes in speed or direction such suppression is reduced (Tanaka et al., 1986; Tootell & Born, 1990). On the other hand, if the bar or the small patch of dots is not presented, the background alone cannot modulate the response of the neuron. From these findings it emerges that MT neurons can

perform a match between the stimulus in its receptive field and the stimuli presented in other parts of the visual field. Likewise, it seems that the surround modulates the activity of a neuron by suppressing or enhancing it. Born and Tootell (1992) presented a large field of moving dots after injecting an activity marker. They found that MT was not uniformly stained, but there were patches of bright and dark tissue. Subsequent cell recordings pointed out that patches of bright tissue contained cells with antagonistic surround (involved in the processing of small moving patterns), whereas patches of dark tissue contained cells with either no antagonistic surround or surround that increased the response of the cell as the stimulus increased its size. Thus, cells that respond to small patterns could be involved in figure/ground segregation, whilst neurons responding to larger moving patterns could process information about an animal's movement such as optic flow.

3.3.3 Medial temporal superior area

Situated anterior to MT is the medial temporal superior (MST) area. It is closely connected to MT and presents neurons with very large receptive fields.

Electrophysiological studies (Komatsu & Wurtz, 1988) on macaque cortex have pointed out the existence of regions within MST with neurons having distinct response properties. In particular, the distinction is made between the dorsal portion of MST (MSTd) and the lateral portion of MST (MSTl).

Neurons in MSTd (Figure 1.12C) respond to complex moving patterns. Some cells show selectivity for patterns rotating in a particular direction (e.g., clockwise or anticlockwise), some respond to expanding or contracting patterns (Tanaka & Saito, 1989; Duffy & Wurtz, 1991a,b) and others respond to translational motion. Such movements occur, for example, when an animal moves in its environment, and this leads to the hypothesis that MSTd neurons are involved in processing optic flow. Moreover, it has been shown that MSTd neurons have very large

receptive fields, and respond better to large fields of moving dots, further suggesting their role in optic flow (Komatsu & Wurtz, 1988; Tanaka & Saito, 1989; Duffy & Wurtz, 1991a). Graziano et al., (1994) further investigated the selectivity of MSTd neurons, and found that MSTd cells do not split the response to a spiral pattern into different basic function. They do not break, for example, the spiral movement into a rotational and contracting components, but they show strong activity when presented with a spiral pattern, and give a non-optimal response to the rotation and the contraction when presented separately, showing a selectivity for complex moving patterns. It remains unclear how MSTd cells produce such selectivity. Neurons in MSTl (Figure 1.12C) appear to have different response properties to those of MSTd. In particular, they respond strongly to small moving patterns and decrease their response as the size of the stimulus increases (Tanaka et al., 1993). This opposite behaviour with respect to that of the neurons in MSTd leads to the hypothesis that neurons in MSTl perform the complementary activity of processing and analysing the movements of objects relative to their surround, operating figure/ground segmentation (Tanaka et al., 1993). Indeed, Tanaka and colleagues found that MSTl cells that are directionally selective for small moving patterns lose their selectivity when large moving stimuli are displayed in their receptive fields. Yet, their direction selectivity can be recovered by placing an occluding stationary stimulus in the centre of the large moving pattern, although the preferred direction for the pattern is now opposite to the preferred direction shown for the small moving pattern. Thus, MSTl neurons seem to signal a “relativistic motion”. Indeed a stationary object over a leftward moving background has a rightward component relative to its background.

3.4. The effects of lesions and “virtual lesions” on motion processing

Previous sections have pointed out the existence of many interconnected brain areas and structures involved in the analysis of motion. Therefore, one would expect that selective lesions

or ablations to particular structures might have dramatic effects on motion processing. It has been shown that the disruption of the parvocellular channel impairs the perception of high spatial frequency shapes and impairs colour vision, whilst sparing the perception of motion. On the other hand, magnocellular lesions impair the perception of moving stimuli and flickering patterns, but only for particular spatiotemporal characteristics. After magnocellular lesions there is a loss of contrast sensitivity for drifting gratings and the perception of drifting gratings is affected for high temporal frequencies and low spatial frequencies (Schiller et al., 1990a,b). However, it has been shown that increasing the contrast of the stimulus and its size, improves the performance. The magnocellular pathway appears to also be involved in mediating the visibility of a moving stimulus as lesions to the magnocellular channel do not completely abolish the ability to discriminate motion direction and speed. These findings suggest that the motion system needs to integrate the information from both visual pathways, and seems to weight the contribution of each pathway on the basis of the features of the stimulus.

Studies involving lesions in monkey area MT have demonstrated that the activity of MT cells may directly underlie motion perception (Logothetis & Schall, 1989). Newsome and Paré (1988) using a random dot kinematogram stimulus found that, after the MT lesion, motion detection thresholds were much higher than those measured before the lesion. However, the lesion did not affect the contrast sensitivity, suggesting a specific impairment of motion perception rather than a more general visual impairment. Moreover, bilateral lesion to MT, MST and FST impaired permanently the ability of the monkeys to use a kinetic boundary to perform shape discrimination, whilst their ability to segregate a shape using luminance cues was unaffected (Marcar & Cowey, 1992). Pasternak and Merigan (1994) made extensive lesions to area MT and MST, and tested both local and global motion sensitivity using drifting gratings with different spatiotemporal frequencies, and dynamic random dot patterns. Using drifting luminance gratings they found no impairment in contrast sensitivity for both detection and direction discrimination.

However, they found threshold elevations for speed discrimination, though the ability to discriminate the speed of the pattern was not abolished at all. In fact, monkeys could still discriminate speed differences of less than 40%. Weak deficits were also found when testing global motion with a dynamic random dots pattern. In particular, mild deficits were found when the dynamic random dot pattern had a strong motion signal. The authors varied both the direction of the dots and the percentage of noise. Setting the noise at zero whilst varying the direction of the dots revealed weak deficits for small differences in direction or speed. But, severe and permanent deficit was found when the signal-to-noise ratio was reduced.

All these studies also reported fast recovery of visual motion functions following partial lesions to MT, probably because in areas where neurons have large receptive fields the reorganization is faster. Then again, it has also been shown that the complete ablation of MT/MST area only weakly affects basic visual motion tasks such as direction or speed discrimination, suggesting that area MT and MST alone are not sufficient for motion perception. Despite this, these areas appear to play an important role in integrating neural inputs from other visual areas.

This notion is supported also from studies that used Transcranial Magnetic Stimulation (TMS) technique do interfere with the normal activity of motion areas. TMS is a noninvasive method that permits interference with the activity of neurons. Through a weak magnetic impulse, or a series of magnetic impulses, (i.e., repetitive transcranial magnetic stimulation - rTMS), the electric activity of the underlying nervous tissue is altered. Such a technique is well suited to trigger and study the brain activity, the functionality of the circuitry and the connectivity of the brain. For example, in agreement with the electrophysiological data reported so far, a study of McKeefry et al. (2008) pointed out that motion perception does not depend only on the activity of area MT. In particular, after having identified the location of visual areas V1, V3A and MT in participants, they explored the role of such areas in the perception of stimulus speed. To this purpose rTMS was used to interfere with the normal activity of the visual areas of concern. The

observers were required to discriminate the speed of drifting gratings (i.e., if a reference grating or a test grating presented after an inter-stimulus interval of 1250 ms was faster) or perform spatial frequency discrimination of static gratings. rTMS could be delivered at any time between the reference pattern and the test pattern. The results showed that delivering rTMS to areas MT and V3A induced a subjective slowing of visual stimuli and caused increases in speed discrimination thresholds. rTMS did not influence spatial frequency discrimination when delivered over V3A or MT. Moreover, the application of TMS to regions of the cortex adjacent but outside to V1, V3A and MT, did not influence speed perception. These results suggest that, in addition to area MT, other visual motion areas (in this case V3A) play an important role in the cortical network underlying the perception of stimulus speed in the human brain, and that MT is not the solely visual area involved in motion perception.

4. Second-Order Motion

4.1 Introduction to first- and second-order motion

The computational models of low-level motion perception outlined so far take into account only spatiotemporal variations in luminance. However, objects differ from their surroundings not only in terms of differences in the intensity of light, but also in terms of the textural properties of their surface. When these objects move, the luminance and textural information present in the retinal image also move and usually give rise to vivid perceptions of motion (Cavanagh & Mather, 1989).

Chubb and Sperling (1988) made a distinction between these two types of motion referring to them as Fourier and non-Fourier motion. Although non-Fourier motion provides convincing impressions of movement, it does not provide a consistent signal for conventional low-level

motion detectors (i.e. detectors that encode spatiotemporal variations in luminance). This is due to the fact that models of human motion perception usually involve some degree of Fourier decomposition (band-pass filtering) of the input signals. However, since non-Fourier moving stimuli contain equal luminance energy at all spatial and temporal scales (i.e., they are micro-balanced) they are not explicit in the Fourier domain.

Cavanagh and Mather (1989) redefined Fourier and non-Fourier motion as first-order and second-order motion, based on the statistical properties of these two classes of motion stimuli. A first-order motion process responds to differences in luminance, in particular, first-order statistics specify the frequency with which individual points in an image have specified intensity values. Second-order motion refers to patterns which two areas have the same mean luminance but are differentiated by other cues such as texture, relative motion, orientation, binocular disparity etc. Therefore second-order statistics define the frequency with which specific combinations of intensity values occur for pairs of points (Figure 1.15). Thus a second-order process, if such a mechanism exists, would respond to second-order differences in luminance even in the absence of first-order differences. So a standard directionally selective unit would detect no net directional motion in the displacement of the border separating two such regions, however, as outlined above, these stimuli produce clear impressions of motion (Julesz, 1971; Ramachandran et al., 1973; Pantle, et al., 1978; Anstis, 1980; Chubb & Sperling, 1988; Turano & Pantle, 1989; Cavanagh & Mather, 1989).

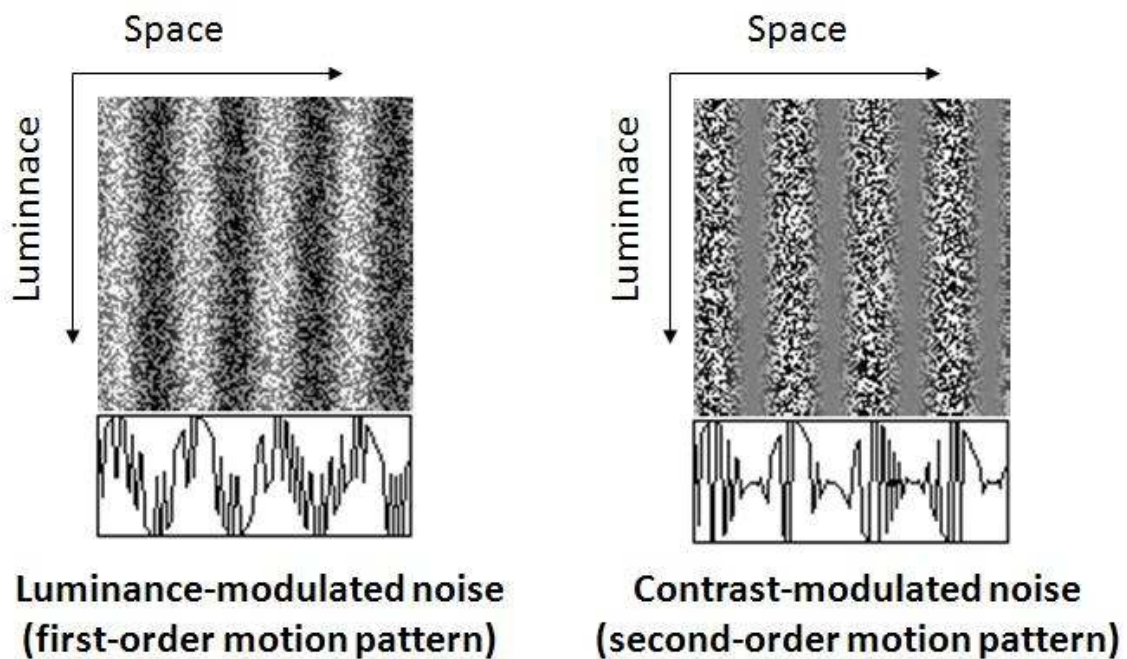


Figure 1.15. The mechanism/s by which first-order motion is processed respond to the displacement of first-order differences in luminance, specifying the frequency with which individual points in an image have designated intensity values. Second-order image statistics define the frequency with which specific combinations occur for pairs of points. This is demonstrated by the luminance profiles corresponding to the first-order (left panel) and second-order (right panel) motion patterns shown above (Adapted from Chubb & Sperling, 1988).

Luminance-defined, drifting, sinusoidal gratings and luminance-modulated noise patterns (Figure 1.16) have been extensively employed to probe the spatial and temporal properties of the visual mechanisms that respond to first-order motion. In a similar manner, the properties of the mechanisms that possibly encode second-order motion have been studied using patterns that have only second-order motion (e.g., contrast-modulated noise, see Figure 1.15) but no consistent first-order motion. Contrast-modulated noise patterns (i.e., second-order motion patterns) are typically obtained by modulating the contrast of a noise pattern, the carrier, by a drifting sinusoidal grating known as the envelope, while the noise itself either remains static or is

dynamic such that any luminance changes carry no net movement information (Chubb & Sperling, 1988) (Figure 1.16).

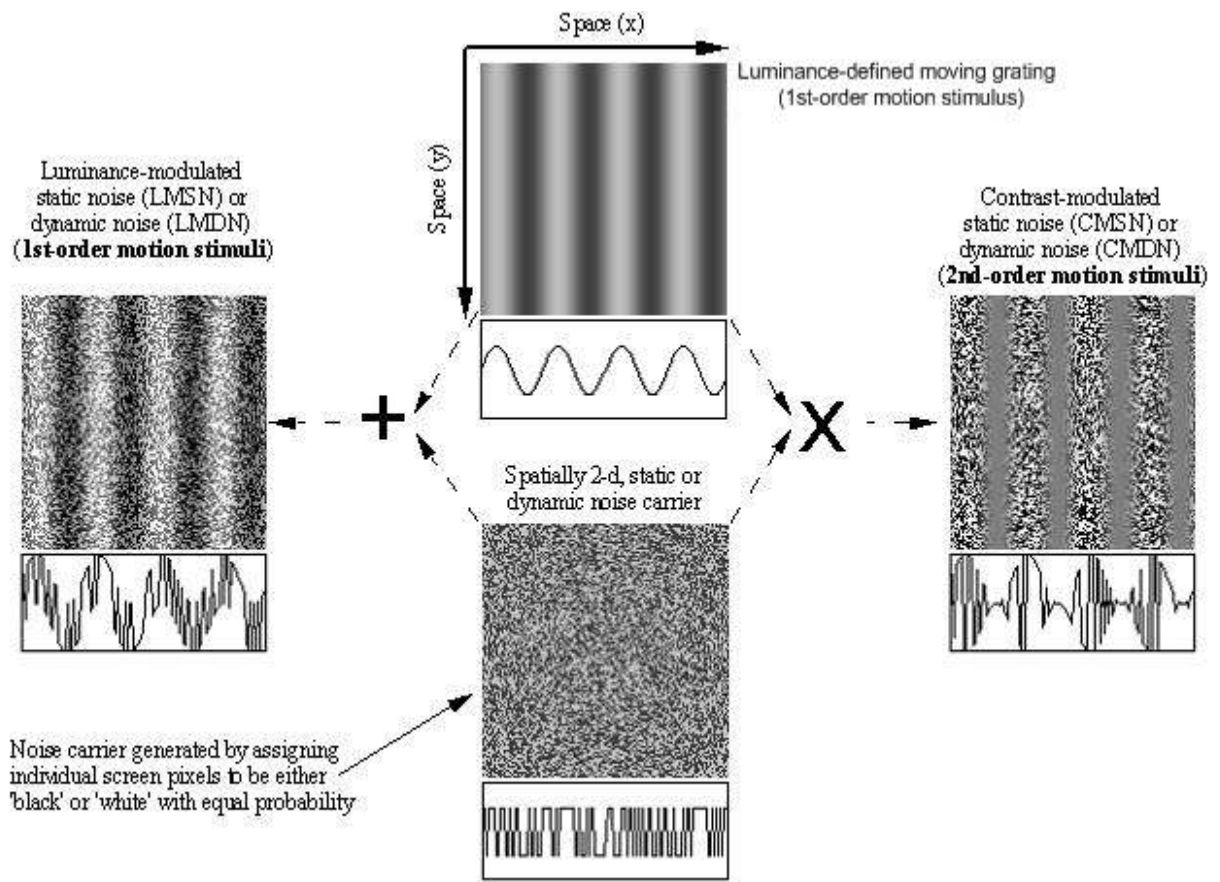


Figure 1.16. Composition of first-order and second-order stimuli. First-order stimuli are either luminance-defined gratings or luminance-modulated noise. Luminance-modulated noise patterns are produced by summing a luminance-defined grating with a spatially 2-d noise carrier. To produce a second-order stimulus, a luminance-defined grating is *multiplied* by a noise carrier, resulting in a contrast-modulated noise pattern (Taken from Hutchinson, 2005).

4.2 Models of second-order motion detection

Second-order motion perception has been modeled in two ways. Firstly, it has been suggested that first- and second-order motion are encoded by a single mechanism (e.g. Johnston, McOwan & Buxton, 1992; Taub, Victor, & Conte, 1997; Benton, et al., 2001; Benton, 2002). Secondly,

both first-order and second-order motion have been modeled implementing two separate and parallel motion-processing systems (e.g. Chubb & Sperling, 1988, 1989; Cavanagh & Mather, 1989; Wilson, Ferrera & Yo, 1992; Baker, 1999).

Many authors (Johnston, McOwan, & Buxton, 1992; Taub, Victor, & Conte, 1997; Benton, et al., 2001; Benton, 2002; Baloch, et al., 1999) suggest that from a theoretical perspective it is not necessary to postulate the existence of two separate mechanisms for encoding first-order and second-order motion. This single mechanism model is based on the spatiotemporal gradient model of Marr and Ullman (1981) (see Chapter 1 - Section 3 for more details) in which the ratio between a temporal luminance gradient and a spatial luminance gradient at a given point in space, gives an estimation of local motion speed and direction.

Despite the fact that the single mechanism approach is plausible from a theoretical point of view, the majority of computational models are based on the assumption that the two classes of motion are detected separately, at least in the early stages of visual processing.

The first models of second-order motion detection implemented two parallel energy-detecting pathways. One of these two pathways involves a non-linear processing stage for detecting second-order motion. For example, in Wilson et al's (1992) model (Figure 1.17), the image is passed through an orientation-selective filtering at a given spatial scale, after which two parallel pathways emerge, one deputed to the elaboration of first-order, Fourier, motion and the other for encoding second-order, non-Fourier, motion.

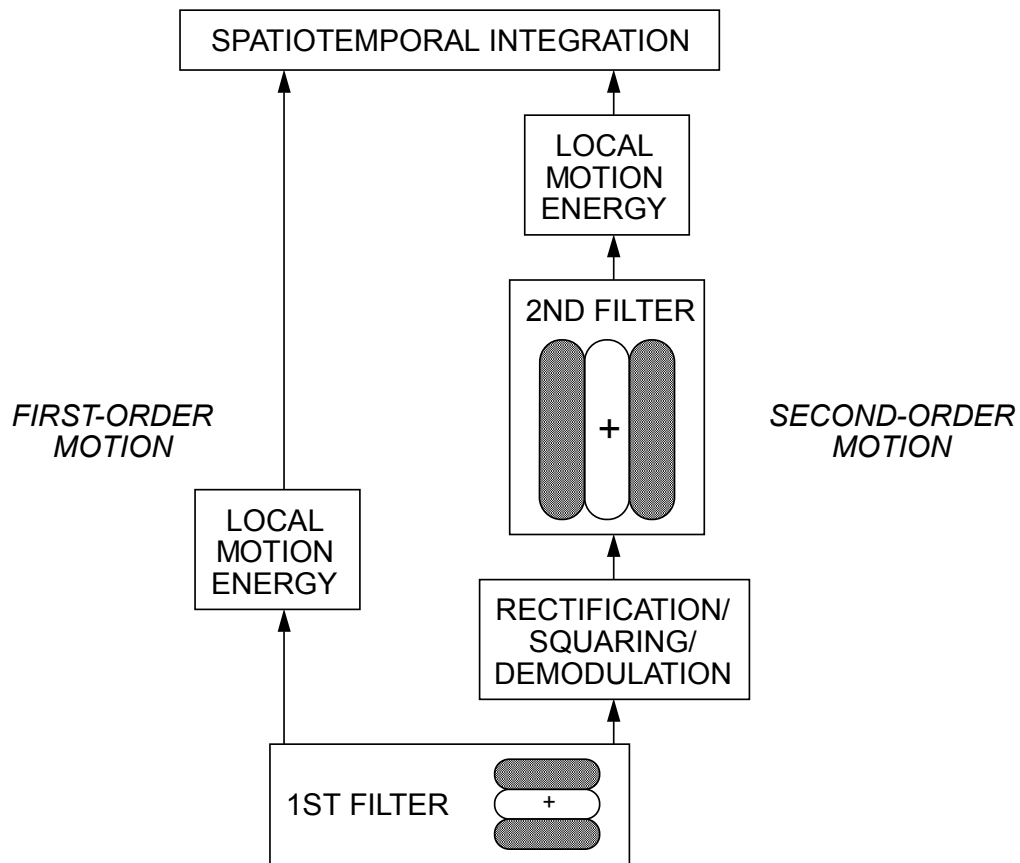


Figure 1.17. Generic model of first-order and second-order motion processing outlined by Wilson et al. (1992). The image first undergoes orientation-selective and spatial frequency-selective filtering before branching off into two separate streams or pathways. Where first-order information is concerned, the local motion energy contained within the image is simply extracted using Reichardt-like detection units. For second-order motion, a rectification stage follows the initial filtering of the image. The rectification stage turns second-order information into first-order information and is followed by a second stage of orientation-selective filtering at a different spatial scale, before the local motion energy is finally extracted. The local first-order and second-order motion information is then pooled for spatiotemporal integration (Chubb & Sperling, 1988; Wilson, Ferrera, & Yo, 1992; Baker, 1999) (Taken from Hutchinson, 2005).

After the initial filtering stage one pathway simply extracts the first-order motion energy, whereas the other pathway incorporates rectification (or response squaring) followed by an additional orientation-selective filtering stage in order to make the second-order information visible to conventional Energy-like motion detectors or Reichardt motion detectors. The second set of filters are very similar to the initial filters except that filtering generally occurs at a different orientation and about one octave lower in spatial frequency and seems to be more broadly tuned to spatial frequency than the first-stage filters (Sutter, Sperling, & Chubb, 1995). After the “filter-rectify-filter” process is complete, motion-energy is extracted. The outputs of the two pathways are then combined to provide some measure of the net direction and speed of motion.

4.3 Neuropsychological and Neurophysiological studies

4.3.1 Brain lesions studies

First- and second-order motion perception has been investigated using a number of different techniques including neuropsychology, neuroimaging, single cell recordings and psychophysics. The findings suggest that the two types of motion are encoded, at least initially, by distinct and separate mechanisms.

Vaina and colleagues (Vaina, LeMay, & Gryzwacz, 1993; Vaina & Cowey, 1996; Vaina, et al., 1998; Vaina, Cowey, & Kennedy, 1999; Vaina, et al., 2000; Vaina & Soloviev, 2004) have shown a double dissociation between first-order and second-order motion processing for four neuropsychological patients. In particular, they have discovered two neuropsychological patients who exhibit impaired performance on tests of first-order motion but intact performance on tests of second-order motion, and another two patients that showed the opposite performance. Patient RA (Vaina et al., 1993; Vaina & Cowey, 1996; Vaina et al., 1999) suffered a restricted unilateral lesion close to the medial surface of the occipital lobe, including parts of the extrastriate cortex

(i.e., involving areas V2 and V3). RA's lesion also involved white matter and, therefore, could have disrupted connections between V1 and the extrastriate visual areas. Patient JV (Vaina & Soloviev, 2004) suffered small unilateral infarcts centered on the ventral occipital region, in particular in areas V2 and VP. When tested on a range of psychophysical tasks involving the perception of local and global first-order and second-order motion, both patients demonstrated a selective impairment on tests of first-order motion but intact performance on tests of second-order motion. On the other hand, Vaina and colleagues have also shown evidence from other two patients who exhibit impaired performance on tests of second-order motion but intact performance on tests of first-order motion. In particular, patient FD (Vaina et al., 1998; Vaina et al., 1999) suffered a small cortical lesion in his left hemisphere, just dorsal to area MT. Patient TF (Vaina et al., 2000; Vaina & Soloviev, 2004) suffered small unilateral infarcts centered in the dorsal regions on areas V2 and V3. When tested, both patients demonstrated a selective deficit for second-order motion but showed normal performance on tests involving first-order motion. This double dissociation suggests that two separate and parallel mechanisms may be involved in first- and second-order motion processing. Moreover, first- and second-order mechanisms seem to use different neural substrates.

4.3.2 Human neuroimaging

Only a few neuroimaging studies have compared regions of cortical activation in response to first- and second-order moving patterns. However, these studies produce conflicting results. Smith et al. (1998) used fMRI to measure cortical activation in response to first-order and second-order motion patterns and found that areas V3 and VP showed a greater activation in response to second-order than to first-order motion stimuli. Dumoulin et al. (2003) have identified areas in the occipital and parietal lobes that respond preferentially to the two types of motion. In particular, they found preferential activations for first-order motion in the left

precuneus and the right medial occipital lobe. For second-order motion, the bilateral occipital lobe and the bilateral anterior superior parietal lobule were activated. In contrast, other studies have found no distinction between cortical activations for first-order and second-order motion. For example, Nishida et al. (2003) and Seiffert et al. (2003) found similar activations in response to both first-order and second-order motion in areas V1, V2, V3, V3A, VP, V4v and MT. However, it is also possible that in these last studies the authors did not completely remove residual luminance artifacts in second-order patterns (in section 4.4 we will discuss this important issue more in detail), so first-order cues in second-order pattern might have concurred in the cortical activation of low-level visual areas such as V1 and V2.

4.3.3 Electrophysiological studies

A number of single cell recordings have revealed cells that respond to both first-order and second-order motion in both the simple and complex cells of visual areas V1, V2, MT and MSTd of the monkey and A17 and A18 of the cat (e.g. Albright, 1992; Chaudhuri & Albright, 1997; O'Keefe & Movshon, 1998; Zhou & Baker, 1993, 1994, 1996; Mareschal & Baker, 1998a, b, 1999), though a very small number of V1 and V2 cells respond selectively to second-order motion or both to first- and second-order motion.

Albright (1992) found that 87% of the cells that he studied in the macaque area MT exhibited similar direction tuning for both first-order (luminance-defined stimuli) and second-order stimuli (contrast-defined textures). O'Keefe and Movshon (1998) measured the responses of the macaque MT neurons to first-order and second-order motion stimuli, and found cells that responded to both stimulus types. However, responses to second-order motion were generally weaker than responses to first-order motion. Although cell responses to first-order and second-order motion were highly correlated in terms of their preferred direction, they found weak correlations for preferred spatial frequency. Moreover, the cells preferred lower temporal

frequencies for second-order motion than for first-order motion. Leventhal et al. (1998) have measured the responses of neurons in areas V1 and V2 of rhesus monkeys and A17 and A18 of the cat to stimuli defined by luminance, contrast and texture. They found very few cells in V1/A18 that respond to all types of stimuli. On the other hand, many of the cells in area V2/A18 responded to all stimuli, showing also a directional selectivity.

Zhou and Baker (1993, 1994, 1996) and Mareschal and Baker (1998a, 1998b, 1999) have provided evidence that cells in areas A17 and A18 of the cat respond to both first-order and second-order motion stimuli. In particular, they found that only few neurons of those tested in A17 and at least half of those tested in A18 responded significantly to both first- and second-order stimuli (Zhou & Baker, 1993). According to the results of Leventhal et al. (1998) responses to second-order patterns were weaker than to first-order stimuli but exhibited a consistent directional and orientation selectivity for both stimulus types (Zhou & Baker, 1993, 1996; Mareschal & Baker, 1998a, 1998b, 1999). In addition, A18 cells preferred lower spatial and temporal frequencies for second-order than to first-order (Mareschal & Baker, 1998b), which is consistent with psychophysical evidence. Based on the findings outlined above, Baker (1999) has proposed a physiologically motivated model of the response of a cortical neuron to first-order and second-order motion (Figure 1.18). The model is very similar to that of Wilson et al. (1992).

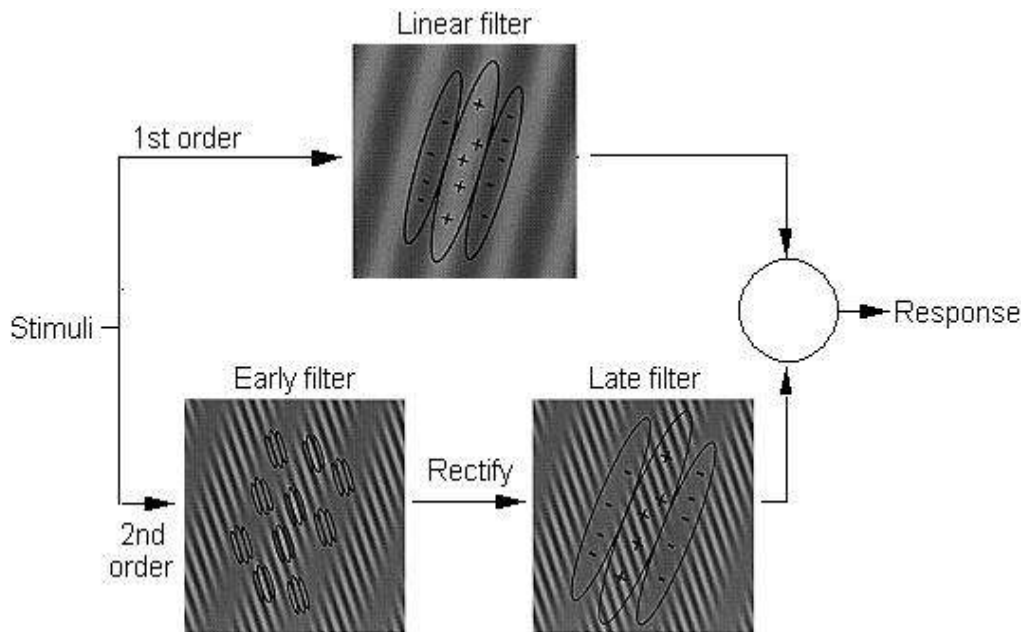


Figure 1.18. Model of a neuron that respond to both first- and second-order motion. First-order stimuli are encoded by linear spatiotemporal filters (top pathway) whereas second-order stimuli are encoded by a serial “filter-rectify-filter” mechanisms consisting of early linear subunits, a rectification stage and a late spatiotemporal filtering (bottom pathway) (Taken from Hutchinson, 2005).

Further evidence regarding neurons that encode both first- and second-order motion comes from a recent study of Barraclough et al. (2006). They measured the responses of single neurons in monkey’s visual cortex (V1, V2 and the third visual complex) to moving first-order stimuli and to combined first- and second-order stimuli, beat stimuli, in order to assess whether first-order motion was influenced by second-order motion. Thus, to distinguish first-order and second-order direction-selective responses the authors compared responses to moving first-order gratings alone with responses to beat patterns with first-order and second-order components moving in the same or in opposite directions. A beat pattern is obtained by multiplying a drifting sinusoidal carrier, first-order component, and a drifting contrast envelope, second-order component. In the

majority of the cells measured in V1, V2 and the third complex, responses to first-order motion were significantly influenced by the presence of a second-order signal. In particular, second-order interfered more when moving in the opposite direction to that of the first-order stimulus, reducing first-order direction sensitivity. These results are compatible with a unique motion system that process first- and second-order stimuli. However, it should be noted that: (i) There are relatively a poor number of cells whose activity is modulated by both first- and second-order motion, although Albright et al. (1992) found about 87% of the cells that he studied to respond to both these motion cues. (ii) No cells have been identified that respond solely to second-order motion. This is perhaps because neurons that respond to second-order motion have traditionally been probed using first-order drifting gratings. Thus, it would be worthwhile investigating the mechanisms that encode second-order motion using exclusively second-order motion patterns (i.e., contrast-modulated or flicker patterns).

4.4 Psychophysical studies

A number of psychophysical studies have investigated the perception of second-order motion. The research reveals that the perception of first- and second-order motion is a complex process, but overall the evidence suggests that these two motion types are processed by separate and distinct motion systems.

Initially, the mechanisms underlying the perception of first-order and second-order motion have been extensively studied using motion adaptation paradigms. After prolonged exposure to first-order, luminance-defined, motion, a subsequently viewed stationary test pattern is seen to move in the opposite direction to that of the adaptation pattern. This phenomenon is known as the motion aftereffect (MAE) (see Chapter 3). The first MAE studies concerning second-order motion employed static test stimuli and did not obtain reliable MAEs. However, adaptation to second-order motion results in a substantial MAE when test stimuli are dynamic (i.e.,

counterphase flicker or dynamic visual noise [see Chapter 3 – Section 2]). Ledgeway (1994) measured the magnitude of the motion aftereffect obtained following adaptation to both first-order (luminance-modulated noise) and second-order (contrast-modulated noise) drifting patterns. The test pattern was a counterphase grating which was either first-order or second-order, resulting in a directionally ambiguous stimulus. Adaptation to either first-order or second-order motion produced a substantial MAE in that after adaptation the perceived motion direction of the ambiguous test pattern was biased toward the opposite direction to that of the adaptation pattern. This was true in both same-adaptation (e.g. first-order adaptation and first-order test pattern or second-order adaptation and second-order test pattern) and cross-adaptation (e.g. first-order adaptation pattern and second-order test pattern or vice versa) conditions.

Ledgeway (1994) also manipulated the relative amplitudes (modulation depths) of the counterphase test pattern which was composed of two sinusoidal gratings drifting in opposite direction and with the same spatial and temporal frequencies until the MAE was nulled. The modulation depth ratios needed to null the MAE were very similar for first- and second-order motion. The component moving in the same direction as adaptation needed to be approximately twice that of the component drifting in the opposite direction. Furthermore, Ledgeway and Smith (1994b) have shown that the duration of the MAE in counterphasing test patterns is also similar for first- and second-order motion. In all conditions, same-adaptation and cross-adaptation, the directionally ambiguous test stimuli appeared to drift coherently in the direction opposite to the adaptation pattern for approximately 5 seconds.

It has also been shown that prolonged exposure to first-order motion can alter the perceived speed of subsequently viewed test patterns. Ledgeway and Smith (1997) have shown the existence of a similar effect also within the second-order domain. To measure the effects of adaptation on perceived speed the authors presented an adaptation stimulus which was either a luminance-modulated noise pattern, a contrast-modulated noise pattern or, in control conditions,

an un-modulated noise field. Stimuli were presented in one half of the observer's visual field, either to the left or right of a central fixation point. Following adaptation, speed matches were measured using a two-alternative forced choice (2AFC) procedure involving the simultaneous presentation of a test motion stimulus (either luminance-modulated noise or contrast-modulated noise) and a reference motion stimulus (always luminance-modulated noise) to different parts of the observer's field of view. The test motion stimulus was always presented in the adapted part of the visual field and the reference motion stimulus was presented in the other (unadapted) half of the visual field. The adaptation and test motion stimuli always had the same direction of drift but the test and comparison motion stimuli always drifted in opposite directions towards the fixation point in order to facilitate fixation. The observer's task was to indicate which of the two motion stimuli presented during the test phase appeared to be drifting faster. The results were similar for first- and second-order motion. Adaptation reduced perceived speed, particularly when the adaptation speed was faster than the test speed. However, when the adaptation speed was lower than the test speed, increases in perceived speed were found. What is more, the authors found also cross-order adaptation effects between first-order and second-order motion. These underlying similarities between first-and second-order motion shown in the adaptation studies support the notion that first-order and second-order motion are encoded by mechanisms that operate using similar underlying computational principles.

Nevertheless, many other psychophysical studies seem to suggest that the two types of motion are processed by distinct motion-detecting mechanisms with different computational principles. For example, Mather and West (1993) presented two-frame random dot kinematograms in which the dots were defined either by first-order (luminance-defined) or second-order (contrast-defined) characteristics. They measured the ability to discriminate the motion direction as a function of the size of dot displacement between frames. The direction was accurately detected over a wide range of displacements when the frames were both first-order or both second-order. However,

when the frames alternated between first-order and second-order motion, performance fell to chance level. In addition, performance was at chance even for small displacements further suggesting that the two frames could not be integrated. Kristjánsson (2001) found that sensitivity to increases or decreases in the speed of the first-order motion pattern increased as adaptation time increased, but sensitivity to speed changes of the second-order pattern remained unchanged throughout the adaptation time. These results on motion adaptation are in agreement with models of motion perception that assert distinct-detecting mechanisms for first- and second-order motion. Nishida, Ledgeway and Edwards (1997) found that adaptation to either first-order or second-order motion produced MAEs that were selective for motion direction and spatial frequency. They obtained MAEs selective for motion direction when adaptation and test patterns had the same direction, obtaining a net adaptation effect. However, spatial frequency selectivity was not found in a cross-adaptation conditions (i.e., when the adaptation and test patterns were different types of motion). Since this selectivity was found for both types of motion, it provides further evidence that, like first-order motion, second-order motion is detected by bandpass multiple-scale channels. Thus these findings support models of second-order motion which use similar computational principles to those that process first-order motion. However, these selective adaptation effects were not found under cross-adaptation conditions, further supporting the notion that first-order and second-order motion are detected by different pathways, with each consisting of multiple bandpass spatial frequency channels.

Similar results were obtained by Schofield et al. (2007) by testing the transfer of the MAE between first-order and second-order motion stimuli. They found strong MAEs when the adaptation and test patterns were of the same type. In addition, these MAEs were tuned to spatial frequency. There was also a partial transfer of the 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. On the other hand, there was little or no transfer from second-order to first-

order patterns. This asymmetric transfer of the MAE between first- and second-order motion suggests some degree of separation between the underlying mechanisms that encode them.

Taken together these results suggest that there are two pathways each encoding a type of motion. These two paths seem to be essentially independent, at least until the directions of each variety of motion have been extracted.

Other psychophysical studies have pointed out a distinction between first- and second-order motion systems in terms of the differences between the temporal frequency tunings of the mechanisms that encode the two types of motion. For example, Pantle (1992) found that the direction of contrast-modulated gratings could not be identified at 8 degrees of eccentricity; in this case the second-order patterns appeared stationary. Yet other studies have shown that second-order motion is clearly visible in peripheral vision (e.g. Smith, Hess & Baker, 1994; Solomon & Sperling, 1995; Wang, Hess & Baker, 1997, Bressler & Whitney, 2006; Harp, Bressler, & Whitney, 2007). These different results are due to the different temporal frequency employed. Whereas Pantle (1992) used contrast-modulated gratings with a temporal frequency of 0.5 Hz, the other studies employed much higher temporal frequencies (e.g. 4 Hz). Therefore, it seems that the mechanism that encodes second-order motion is heavily influenced by the magnitude of temporal frequency when the stimuli are presented in periphery.

Moreover, it has been shown that first- and second-order motions differ in terms of their temporal acuity. For example, Derrington, Badcock, & Henning (1993) have shown that observers are unable to discriminate the direction of second-order motion (contrast-modulations and spatial beat patterns) at stimulus exposure durations of ≤ 200 ms. Similar results were obtained by Ledgeway and Hess (2002). Observers were required to identify the orientation and drift direction of first-order, luminance-defined, and second-order, contrast-defined, motion patterns. Whilst first-order motion direction was easily identifiable even at very brief durations (e.g., 26.49 ms), observers were unable to identify the drift direction of the second-order patterns

at exposure durations of ≤ 200 ms. On the other hand, observers were very accurate in discriminating the orientation for both first-order and second-order motion patterns at all stimulus durations tested. Therefore, it seems that the ability to judge the motion direction of first- and second-order stimuli depends merely on mechanisms that encode drift direction and such mechanisms are different to those involved in orientation discrimination. These results further suggest the presence of separate and distinct mechanisms for first- and second-order motion, since second-order mechanism is more sluggish than the mechanism that encode the motion direction of first-order patterns.

Smith and Ledgeway (1997) measured orientation discrimination and direction discrimination thresholds of contrast-modulated static noise and contrast-modulated dynamic noise patterns and found that thresholds for identifying drift direction were consistently higher than those for identifying the orientation for both types of stimuli. However, when they varied the size of the pixels of the noise carrier namely the pixels with the same luminance polarity were grouped to form a raster of variable dimension, they found that when a dynamic noise carrier was present, pixel size had no effect on threshold separation for orientation and direction discrimination, whereas when a static noise carrier was used, thresholds converged when noise pixels were quite large (≥ 4 arcmin). This convergence was taken as evidence that first-order, luminance-based, artifacts introduced by modifying the size of the pixels of the noise carrier may contaminate second-order stimuli (see also Gurnsey, Fleet, & Potvin, 1998) and influence the perceived motion direction of second-order patterns. These results suggest the presence of a mechanism that is specialized for the detection of second-order motion. In principle it is possible that second-order form perception (i.e., the orientation of the patterns) and second-order motion direction are based on separate processes. However, this is unlikely since the thresholds for identifying motion direction and orientation co-vary as a function of temporal frequency (Smith & Ledgeway, 1998), thus it seems that they share a common basis. The authors concluded

that, as in the case of first-order, second-order form and motion are based on a common initial filtering stage that feeds both processes, the only difference being that motion direction is extracted less efficiently (Smith & Ledgeway, 1997).

Thus, thresholds for identifying the direction of contrast-modulated dynamic noise (second-order) are consistently higher than those for identifying the spatial orientation of the pattern, unlike first-order gratings for which the two thresholds are typically the same. Ledgeway and Hutchinson (2005) proposed two explanations: (i) First- and second-order patterns are encoded by separate mechanisms with different properties. (ii) Dynamic noise selectively impairs sensitivity to second-order motion direction but not to orientation. The first hypothesis predicts that the two thresholds should remain distinct for second-order patterns, regardless of the temporal characteristics of the noise carrier (i.e., static vs. dynamic). The second hypothesis predicts that motion direction thresholds should be higher than orientation thresholds for both second-order and first-order motion patterns, when dynamic noise is present. The authors measured motion direction and orientation discrimination thresholds for luminance (first-order) and contrast (second-order) modulations of static or dynamic noise. The results showed that the two thresholds were exactly the same for first-order stimuli but very different for second-order stimuli. They found direction thresholds that were about 50% higher than orientation thresholds. These results were obtained independently of the kind of noise carrier used (static or dynamic); the overall contrast of the noise; and the temporal frequency of the envelope. These results further suggest that first- and second-order motion are encoded by distinct and separate mechanisms and that the mechanism encoding second-order stimuli cannot determine motion direction at the absolute orientation threshold (Ledgeway & Hutchinson, 2005).

In addition, Hutchinson and Ledgeway (2006) explored the spatiotemporal “window of visibility” for first-order motion (luminance-modulated noise) (Figure 1.19A) and for a variety of second-order motion patterns, such as contrast-modulated noise (Figure 1.19B) and polarity

(flicker)-modulated noise (i.e., the luminance polarity of individual pixel within the noise carrier was varied sinusoidally) (Figure 1.19C). For polarity-modulated noise the probability that a ‘black’ pixel would flip to ‘white’ or that a ‘white’ pixel would flip to ‘black’ was varied following a sinusoidal function. The resultant pattern was a drifting wave of flicker that produced a moving grating of smoothly drifting bars composed of more or less flickering dots and spatial length-modulated noise (i.e., the pattern was determined by the vertical length of flickering bars) (Figure 1.19D). The length of the bars varied sinusoidally as they moved and a new random sample of noise was used every time the sinusoidal wave was shifted in phase.

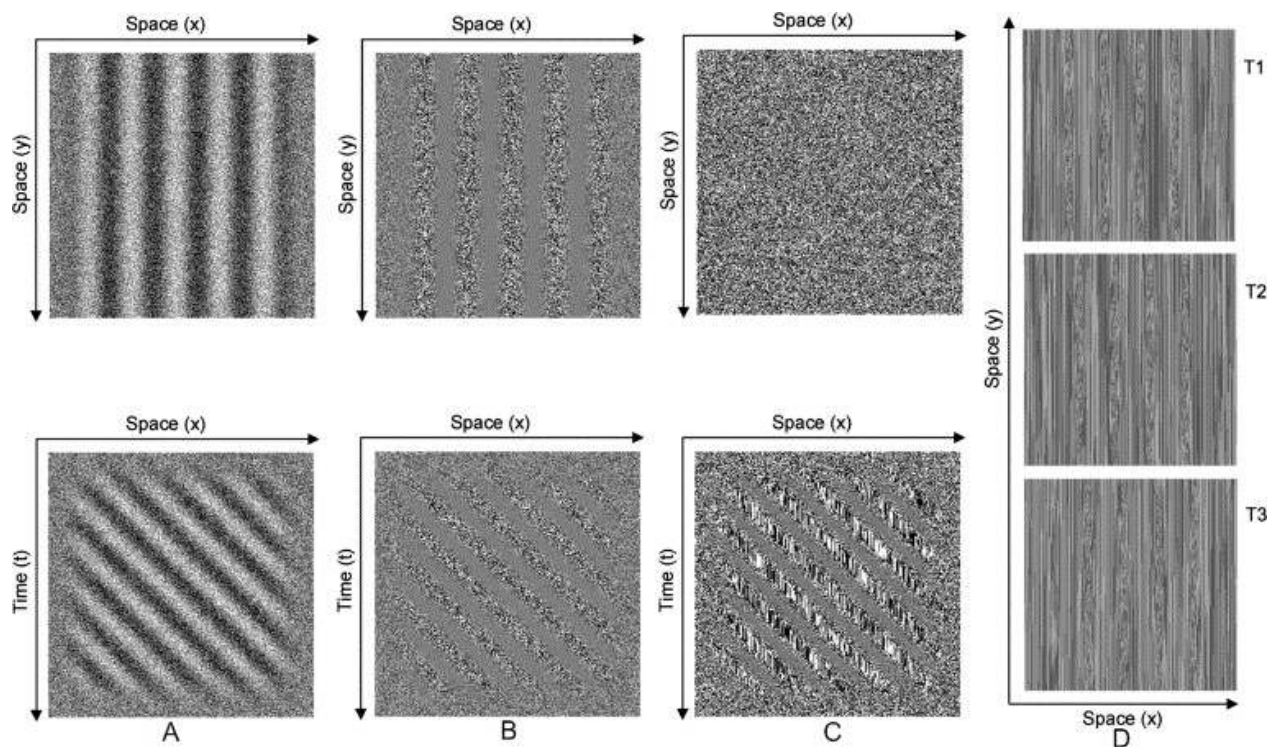


Figure 1.19. Representation of the motion patterns used in the study of Hutchinson and Ledgeway (2006). A. Space-space and space-time representation of a luminance-modulated dynamic noise pattern. B. Contrast-modulated dynamic noise pattern. C. Polarity (flicker)-modulated dynamic noise pattern. D. A space-space representation of a spatial length-modulated motion pattern. T1, T2 and T3 represent three different times of three consecutive frames of a rightward motion sequence (Adapted from Hutchinson & Ledgeway, 2006).

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, for each kind of pattern. Thresholds were converted into modulation sensitivity ($1/\text{threshold}$). 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. Moreover, the authors found that the functions of the contrast-modulated and polarity-modulated noise were very similar in terms of both shape and sensitivity. On the other hand, sensitivity to modulations of spatial length was very poor and a great deal more lowpass with respect to the second-order patterns, suggesting that a feature tracking mechanism may be required in order to discriminate the motion direction of such patterns.

The studies revised above demonstrate that second-order motion exhibits poorer temporal acuity than first-order motion, and sensitivity to second-order motion declines to a larger extent with increasing the temporal frequency than for first-order motion (Derrington, 1994; Holliday & Anderson, 1994; Smith & Ledgeway, 1998). On the basis of these results Derrington et al. (1993) proposed that second-order motion cannot be identified when stimulus exposure is brief because it is subjected to more severe lowpass temporal filtering than first-order motion. In addition, it is worth noting that these differences provide strong evidence against the hypothesis that first- and second-order motion are encoded by a unique system, though there are some common spatiotemporal characteristics between these two types of motion.

Most of the psychophysical studies reviewed thus far indicate that second-order motion is extracted primarily by low-level motion detectors, and that such low-level second-order detectors are sufficient to extract information about motion direction of second-order patterns. In spite of this, there is also some psychophysical evidence suggesting that second-order motion

perception, at least sometimes, may be mediated by high-level, attentive, feature-tracking mechanism. For example, Ashida, Seiffert and Osaka (2001) used visual search rate to assess the attentional resources required for detecting opposing motion defined by either first-order (luminance) or second-order (contrast, flicker or size) modulations. The results showed that first-order motion was quickly detected, whereas second-order motion was detected much slower. Moreover, search times increased as the number of distractors increased and this effect was most pronounced at low drift temporal frequencies and only for second-order motion patterns. These results suggest that in this case second-order motion could be processed by a capacity-limited and late mechanism compatible with a feature-tracking mechanism. Moreover, Allen and Ledgeway (2003) investigated the effects of attention instructions on the ability of observers to identify the directions of pair of luminance-defined and contrast-defined moving stimuli. They found that direction discrimination thresholds for attended moving stimuli were lower than those for unattended stimuli, and this was true for both types of motion. However, while direction discrimination for first-order patterns was similarly affected at all temporal frequencies and durations, for second-order motion the effects of attention was strictly dependent on the temporal frequency and stimulus duration of the pattern, that is, the attention decreased direction threshold only for specific temporal frequencies and stimulus duration. Thus, Allen and Ledgeway (2003) showed that attention can influence the processing of second-order motion, but in this case the stimulus parameters seem to be crucial. In addition, the authors showed that, under appropriate conditions, the processing of first-order motion is also influenced by attention, though lesser than second-order motion.

Ukkonen and Derrington (2000) used a pedestal test to determine whether motion discrimination of contrast-modulated gratings has different properties for different levels of contrast. The pedestal technique consists on a stationary replica of the moving stimulus added to the moving stimulus itself. The rationale behind the pedestal test is that tracking features over time is

prevented by the pedestal because it produces an oscillation of the features without motion in any consistent direction (Lu & Sperling, 1995).

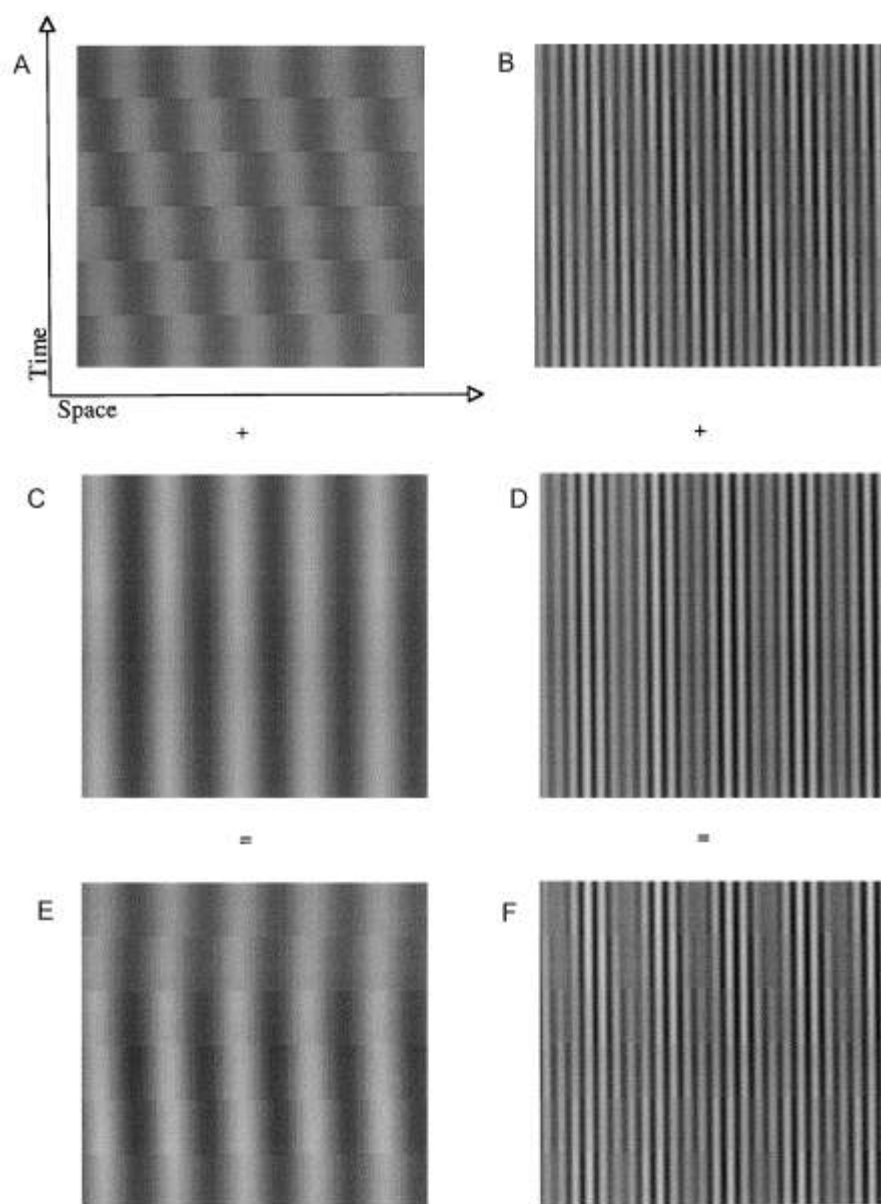


Figure 1.20. Space–time plots of the stimuli used in the experiment of Ukkonen and Derrington (2000). A. Sinusoidal moving grating with five phase shifts are represented. B. A contrast-modulated grating where the low frequency contrast envelope (1 c/deg) moves, while the high frequency carrier (5 c/deg) is stationary. C–D. Pedestals that are static replicas of the moving gratings. E–F. Patterns resulting from the sum of the moving gratings and their pedestals. Adding the pedestal to the moving grating prevents features moving consistently in any one direction (Adapted from Ukkonen & Derrington, 2000).

Ukkonen and Derrington (2000) used pedestals at both low and high contrast levels (i.e., 4.5% and 45% respectively). The pedestal consisted of stationary luminance gratings of 5 c/deg modulated by a moving 1 c/deg contrast envelope (Figure 1.20). Ukkonen and Derrington (2000) found that when contrast is low direction discrimination for contrast-modulated gratings is influenced by pedestals and became very hard or impossible to discriminate at about 4 Hz. On the other hand, at high contrasts, contrast-modulated gratings are unaffected by pedestals and the performance remained high up to 12 Hz. The authors conclude that these results are consistent with the hypothesis that separate mechanisms analyze the motion of contrast-modulated gratings at low and high contrasts. At low contrast a feature tracking mechanism is required to permit motion analysis, whereas at high contrast, contrast-modulated gratings are analyzed by low-level spatiotemporal filters.

Taken together these findings suggest that second-order motion perception, in the first instance, relies on the activity of low-level motion detectors which, in most cases, are able to extract motion information. However, under certain conditions, it may also be necessary for the visual system to recruit higher-level strategies such as feature-tracking in order to extract information about the direction of second-order motion.

Another interesting issue concerning first- and second-order motion perception remains unclear. Some psychophysical evidence suggests that, at some stage, first-order and second-order motion signals are integrated. Unfortunately, the stage at which first-order and second-order motion signals are pooled is not yet apparent. For example, in Wilson et al.'s (1992) model first- and second-order local motion signals are pooled in the last stage of the model in order to extract global motion information. Wilson et al. (1992) argued that this integration occurs in visual area MT. Although, it has been suggested that first- and second-order motion remain separate up to and including the level at which global motion is extracted. Edwards and Badcock (1995) provided psychophysical evidence regarding the independence of first- and second-order motion

systems at the level of MT in relation to global-motion pooling. They showed that adding a second-order motion signal (consisting of contrast-modulated dots) equal in strength and moving in an opposite direction (i.e. transparent motion) to a first-order global-motion signal (consisting of luminance-defined dots) had no effect on the extraction of the first-order global-motion signal, while adding a first-order motion signal to a second-order global-motion signal had an effect on extracting the second-order global-motion signal. These results suggest the presence of a system that responds only to first-order motion, and an independent system that encodes both first- and second-order motion. Moreover, these motion systems seem to remain separate up to and including the level at which global-motion signals are extracted. In order to measure interactions between first-order and second-order Mather and Murdoch (1998) used two kinds of motion that are indicative of interactions during global motion extraction, namely mutual repulsion and motion capture. The mutual repulsion stimulus contained two random-block patterns superimposed and drifting in different directions (i.e., transparent motion), and the motion capture stimulus contained square-wave gratings superimposed on an incoherent random block pattern. Repulsion and capture effects were measured when both stimulus components were of the same order (i.e. both first-order or both second-order) and when one component was first-order and the other was second-order. Both repulsion and capture effects were obtained regardless of the order of the two components in each display. This strongly suggests that the mechanisms that encode first-order and second-order motion interact during global motion analysis. In addition, Cavanagh and Mather (1989) found that when the subjective motion strengths of a luminance-defined and dynamic-texture-defined motion pattern were matched, the two motions nulled each other and observers perceived a flickering pattern reflecting a local interaction between first- and second-order local detectors. However, it is still not clear where first- and second-order signals are combined. It could be worthwhile to further investigate this issue by combining psychophysical and neurophysiological techniques, such as fMRI or

transcranial magnetic stimulation (TMS), in order to localize the site at which such integration occurs.

In summary, the evidence outlined in this section has demonstrated that the majority of psychophysical evidence indicates that first- and second-order motion are encoded by separate and distinct mechanisms from the early stages of motion processing.

5. Purpose of the Thesis

As pointed out in the previous session, second-order motion perception has received a considerable amount of interest in recent years. The experiments outlined in the following Thesis aimed to further investigate the perception of first-order and second-order motion and how these two motion signals are integrated by the visual system. In particular, first-order, second-order and cross-order motion conditions were tested by employing different experimental paradigms: (i) Motion Priming (Chapter 2), (ii) Motion Aftereffect (Chapter 3) and (iii) Motion-induced Position Shift (Chapter 4). As already outlined, a number of studies support the notion that first-order and second-order motion are encoded by distinct motion-detecting mechanisms and separate neural substrates. The psychophysical experiments outlined in this Thesis aim to tap low-level (V1), intermediate-level (V2/V3 - MT) and possibly high-level (MT complex) areas of motion processing. In essence, this Thesis investigated if the perception of first-order and second-order motions is mediated by distinct and separate motion-detecting mechanisms, moreover, we asked if first- and second-order systems are separated from the lower levels of motion analysis and at which stage first- and second-order motion signals are integrated. For this purpose we run three experiments:

(i) In the first experiment (Chapter 5) we explored implicit short-term memory mechanisms for

first- and second-order moving stimuli. In particular, we used a repetition priming paradigm, similar to that used by Campana and colleagues (2002, 2006) (see Chapter 2 for details). Priming for luminance defined, first-order motion has been shown to rely on the functional integrity of visual area MT (Campana et al., 2002, 2006). The retinotopical organization of this area predicts that priming for motion direction is sensitive to spatial position. In order to test this hypothesis, and to see whether a similar priming mechanism also exists within the second-order motion domain, we tested the presence of priming on motion direction and its interaction with spatial position for both first- and second-order motion. Whereas a number of studies have explored the mechanisms and the neural substrates for these two kinds of motion perception, the mechanisms and neural substrates mediating the implicit short-term memory for first- and second-order motion are still unknown. Moreover, we also used a cross-order condition in which first-order motion patterns primed second-order moving patterns and vice versa. Also in this condition we explored the existence of priming for motion direction and its interaction with spatial position. Such a cross-order condition is important since it allows one to assess if the implicit short-term memory for first- and second-order motion patterns relies on the same mechanism/s and neural substrates. Our results indicate that priming for motion direction occurs both with first-order and second-order motion. Additionally, priming for motion direction is position-sensitive for both first- and second-order motion, suggesting a neural locus of representation of priming with a retinotopical organization. Considering that a number of electrophysiological studies have shown the presence of neurons that respond to second-order motion in area MT, and in concurrence with the previous findings on first-order motion priming (Campana et al., 2002, 2006), we propose area MT as the neural locus of representation of priming for both types of motion. Though we found an effect of cross-order motion priming, it is not sensitive to spatial position. From these findings we hypothesized that first- and second-order motion cues remain distinct and separate at the level where global motion is extracted, MT (Edwards & Badcock, 1995), thus

the two types of motion could be integrated at a high level of motion processing, where the retinotopic organization is lost or is very coarse, say for instance, MST.

(ii) The first experiment showed that, whereas for within-order conditions motion priming is dependent on the repetition of the same target's position, in the cross-order condition, priming is not sensitive to spatial position. These findings further suggest the presence of two independent pathways, one processing mainly first-order motion and the other mainly processing second-order motion. In addition, these two motion pathways seem to encode separately the spatial position of a moving pattern. In the second experiment (Chapter 6), we assessed whether first- and second-order motion encode and assign the position of a moving pattern using a single and common mechanism, or whether there are two distinct mechanisms for position assignment. For this purpose we measured the shift in the perceived position induced by drifting first- and second-order Gabors (De Valois & De Valois, 1991; Durant & Johnston, 2004; Edwards & Badcock, 2003; Fang & He, 2004). We first measured separately the motion-induced position shift for first- and second-order moving patterns. Then, we conducted an experiment in which first- and second-order drifting Gabors were presented within the same trial to assess if cross-order motion shifts perceived position as well. The rationale was that if there is a common position assignment mechanism for both first- and second-order motion one would expect an effect size of cross-order motion-induced position shift that is intermediate between that obtained with first-order, and the second-order motion separately. On the other hand, a lack of an effect for cross-order stimuli would indicate the presence of separate and independent position assignment mechanisms. We found that both first- and second-order motion, when presented separately, shift the perceived position. However, we did not find any positional shift with cross-order stimuli. This result clearly implies the presence of separate mechanisms that encode and assign the spatial position for these two motion cues.

(iii) In the third experiment (Chapter 7) we used a paradigm developed by Kanai and Verstraten (2005) in order to tap low(e.g., V1) and intermediate levels (e.g., MT) of motion processing. In particular, the authors showed that fast adaptations bias the perceived motion direction of a subsequently presented ambiguous test pattern (Kanai & Verstraten, 2005). Depending on both the duration of the adapting stimulus and the durations of the adaptation-test blank interval, the perceived direction of an ambiguous test pattern is biased towards the opposite direction of the adaptation pattern (rapid motion aftereffect - rMAE), or in the same direction (rapid visual motion priming - rVMP). Moreover, they showed that using longer adaptation durations and adaptation-test blank intervals (i.e., inter-stimulus intervals - ISI) longer than 1 second the perceived motion direction of the test pattern is biased toward the same motion direction. This latter effect arises gradually over time and seems to reflect facilitation at intermediate-level of motion analysis. Such gradual effect is very similar to the Motion Priming obtained in the first experiment. Instead, very brief adaptation durations could selectively tap the response of low-level first- and second-order motion detectors. In the third experiment we assessed if rVMP, rMAE and the Motion Priming obtained for longer ISIs also exists within the second-order motion domain. We found that rVMP, rMAE and Motion Priming had similar time courses for first- and second-order motion patterns when presented separately. Subsequently, we run a cross-order adaptation condition (i.e., adapting to first-order and testing with second-order and vice versa) in order to assess if a single mechanism could explain the results obtained presenting first- and second-order motion separately. In the cross-order adaptation condition we found asymmetric transfers, that is, first-order motion influenced the processing of second-order motion (see Schofield et al., 2007). Indeed, we found that some rMAEs induced by first-order adaptation transferred to second-order stimuli, whereas second-order motion did not influence the processing of first-order motion. Indeed, we did not observe any rVMP and rMAE when adapting to second-order and testing with first-order.

In summary, the psychophysical evidence that we provide further supports the notion that first- and second-order motion are encoded by separate and distinct mechanisms from the early stages of motion processing (see Chapter 8). Additionally, we argued that first- and second-order motion signals could be integrated at high level of motion processing. Indeed, in the first experiments we found that cross-order priming for motion direction exists but it is not sensitive to spatial position, suggesting that first- and second-order motion signals are integrated at high-level of motion analysis in which the retinotopical organization is not maintained (e.g., MST). However, the last experiment showed that there seems a certain degree of asymmetric ‘cross-talk’ between first-order and second-order motion signals. Indeed, we found some rapid forms of motion aftereffect only when we adapted to first-order and tested with second-order. These results imply that, even at low-levels of processing, under certain circumstances first-order motion can influence the perception of second-order motion but not vice versa, in agreement with Edwards & Badcock (1995), suggesting a hierarchical organization of the early mechanisms responding to these two kinds of motion. However, the cross-order effects were weaker than that obtained in the within-order conditions. This supports the view that our visual system cannot easily integrate and combine these two classes of motion.

The following Chapters (2, 3 and 4) will review the most recent studies in the literature regarding Priming, the Motion Aftereffect and Motion-induced Position Shift. These Chapters constitute the theoretical fundamentals on which our experiments rely.

Chapter 2

Visual Priming

1. Introduction

Previous exposure to a visual stimulus or to a feature (i.e., color, shape, motion direction, spatial position etc.) facilitates its successive detection or discrimination. Such perceptual phenomenon is called visual priming. Recent studies have shed light on how our attention appears to be automatically captured by stimuli or features that have been recently attended. Recent research on visual priming in visual search tasks suggests that we possess a primitive memory system that draws our attention to features or objects that we have recently attended and are important to our goals or to the task we are performing. Moreover, it seems that we have little or no voluntary control over the workings of this primitive memory system. Since the pioneering studies of Maljkovic & Nakayama (1994, 1996) and Treisman (1992) a number of other studies have investigated priming effects in visual search tasks. Generally, these studies have shown that detection or discrimination of a visual stimulus or feature becomes easier if we have seen it in the past. Such an effect suggests the involvement of an implicit memory system that strongly influences how we subsequently allocate our visual attention. Priming can be defined as an altered activation state of particular representations or associations in memory which influences the responses of observers. It can also be described as an experimental procedure by which a stimulus is used to sensitize the subject to a later presentation of the same or a similar stimulus. Since it can be dissociated from declarative memory, priming is usually considered to be an example of implicit memory (Schacter & Buckner, 1998). For example, Warrington and

Weiskrantz (1968) tested Korsakoff patients, who are a class of patients who have lost the ability to retain new memories. They presented the patients with fragmented pictures of stimuli. Despite having no recollection of performing the task previously, recognition of the fragmented pictures increased with number of stimulus presentations. Gabrieli et al. (1995) studied a patient with right occipital cortex removed because of epilepsy. This patient had a normal declarative memory, but showed no perceptual priming since his identification of briefly presented stimuli did not improve with repetition. Interestingly this pattern of results is opposite the effects observed by Warrington & Weiskrantz (1968), and shows how priming can be dissociated from conscious awareness.

Perceptual priming is based on features such as color, orientation, shape, position, motion direction etc. (Becker, 2008a; Fecteau, 2007; Geyer, Muller, & Krummenacher, 2007; Goolsby & Suzuki 2001; Kristjánsson, 2006a; Lamy, Carmel, Egeth, & Leber, 2006; Magnussen & Greenlee, 1999; Maljkovic & Nakayama, 1994, 1996; Olivers & Meeter, 2006; Wolfe et al. 2003; see e.g. Kristjánsson, 2006b for review). More complex forms of priming have also been found in visual search tasks, such as priming for whole stimulus configurations (Chun & Jiang, 1998) or distractor set identity (Kristjánsson, Wang & Nakayama, 2002; Wang, Kristjánsson, & Nakayama, 2005; Saevarsson et al., 2008; Geyer, Muller, & Krummenacher, 2006). The fact that priming is seen for such different forms of stimulus characteristics presents a challenge for any theory of priming where a single mechanism is assumed to be involved in priming, and indicates that priming may reflect modulations of neural activity at a number of different processing levels in the nervous system.

2. Visual search

In a typical visual search experiment, repeating the same target feature or spatial position across trials results in better performance than if the target or feature changes from trial to trial. For example, if the target color on the present trial is red, as on the previous trial, search is facilitated, while if the present target color is green, search is slowed (Figure 2.1). Note however, that priming usually occurs more easily for features that are not directly associated with the motor response. For example, to maximize color priming, observers should be requested to respond to some other feature of the target, such as its orientation, spatial frequency or spatial position (see Olivers & Meeter, 2006).

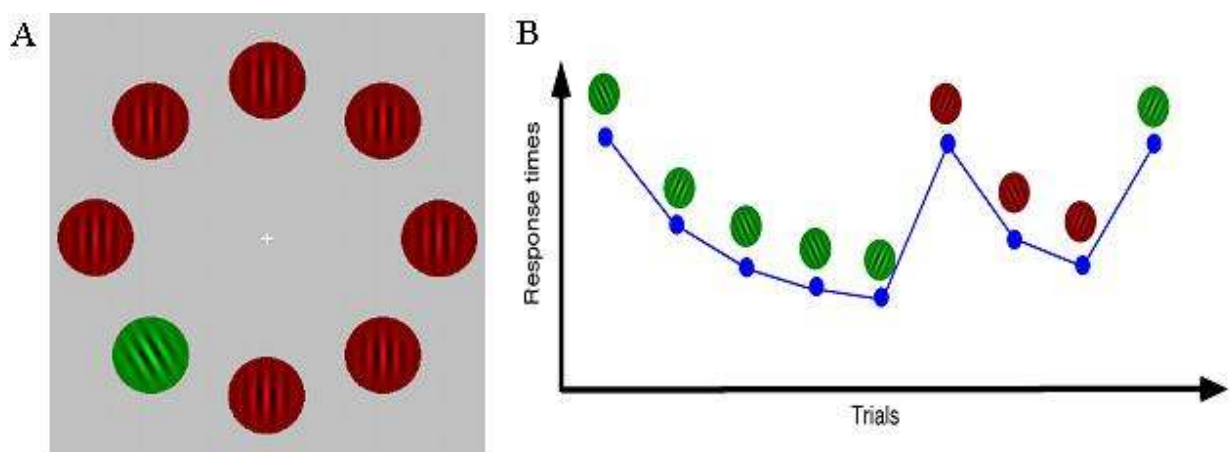


Figure 2.1. An example of priming in visual search. Panel A shows a visual search task where the oddly colored Gabor patch is to be found, and the task is to indicate whether it is tilted towards the left or right from vertical (paradigm based on Kristjánsson, 2006). Panel B then shows how response times change as the target color is repeated across consecutive trials (shown from left to right), or when the target color changes (simulated data) (Adapted from Kristjánsson, 2006).

Maljkovic & Nakayama (1994, 1996; see also Treisman, 1992) revealed the characteristics of priming in pop-out visual search. Their observers searched for a diamond of odd color relative to two distractor diamonds and judged whether the target had a notch on the right or on the left. Thus the response feature was different to the color of the target so that effects of repetition of a target color could be dissociated from effects of response repetition. They found that search was significantly faster if the target color was repeated from one trial to the next. Their results showed that even when search is easy and effortless as in a pop-out paradigm, perceptual priming can strongly influence the speed of the search. Moreover, Maljkovic and Nakayama (1994, 1996) showed also that priming between trials for features such as color or spatial frequency and spatial position was due to an implicit short-term memory mechanism, and not to stimulus expectancy (see also Sigurðardóttir, Kristjánsson, & Driver, 2008). Indeed, the authors found that even when the feature change was completely predictable and occurred on successive trials, response times were significantly slower than when the feature was also completely predictable but remained constant across trials. This result shows how conscious knowledge of task statistics has little or no effect on the performance. Another pertinent result of Maljkovic and Nakayama (1994, 1996) was that the priming effect from repetition of a particular feature was not confined to the subsequent trial, but continued to influence performance on at least seven subsequent trials. Finally, they also found that the effect of priming is cumulative, such that increasing repetitions of the same feature improves performance (Figure 2.1B). Perceptual priming has been found not only in easy pop-out search, but also in more difficult conjunction search tasks (Kristjánsson et al. 2002; Hillstrom, 2000; Wang et al., 2005). These findings show how the presentation of certain stimulus characteristics improves detection or discrimination of subsequent stimuli sharing the same characteristics. Stimulus selection is thus not only based on the current stimulus in its current context, but also on implicit influences from previous trials.

What we have recently attended can strongly influence how we subsequently allocate our attention.

Priming in visual search may reflect facilitated perceptual processing of previously attended objects or features, or even processing of whole displays that share properties with previously attended ones. Another possibility is that priming influences attention shifts. In fact, recent results of Sigurðardóttir et al. (2008) & Becker (2008b), indicate that priming affects attention shifts rather than perceptual performance directly, since while priming resulted in improved detection of a target, it did not facilitate acuity judgments on that particular target. Furthermore, it is also theoretically possible that priming affects response selection. However, Sigurðardóttir et al. (2008) have strongly argued against this because they found that the repetition of a target feature increased sensitivity (d') to a briefly presented target in a visual search task while having only a minuscule effect upon decision criteria (c) (see also Becker, 2008b). Another possibility has been provided by Maljkovic and Nakayama (1994, 1996). They argued that the priming patterns observed in their experiments reflected altered activation states to the recently attended and behaviorally important feature (i.e., the odd color on the preceding trial) so that the primed feature is more likely to grab attention than otherwise. Huang, Holcombe & Pashler (2004) see also Hillstrom (2000), proposed a rather different explanation. In their study observers searched for a bar tilted either 45 or -45° from vertical that was an odd size compared to randomly oriented distractors, that is, either a large target among small distractors, or vice versa. They observed an interaction between repetition of size, and brightness (black or white) such that repetition of both brightness and size assisted visual search, but when the target was a different size to the previous one, repeating the brightness of the target slowed the search. Since the feature repetition effect did not appear to be independent of the repetition of other features on the target, Huang et al. (2004) concluded that priming does not affect processing of single features. They argue that priming occurs at a later stage in the perceptual process, reflecting an episodic

memory representation of the preceding trial, and that the behavioral pattern following repetition reflects the priming of assembled objects rather than features. On the other hand, these results do not rule out the possibility of feature-based priming relying on low-level stage in the perceptual process. Indeed, Kristjánsson, Ingvarsdóttir, & Teitsdóttir (2008) found that depending on the type of stimulus tested the priming can be object-based or feature based. They contrasted search for stimuli that have been shown in previous studies to be processed differently in visual search tasks, either as whole objects or separate parts (Wolfe, Friedman-Hill, & Bilsky, 1994), as well as in visual short-term memory tasks (Vogel, Woodman & Luck, 2001). In particular, Kristjánsson et al. (2008) found that stimuli that the visual system seems more inclined to treat as objects tend to result in object-based priming patterns, while stimuli less conducive to object-based processing resulted in feature-based priming patterns (see Figure 2.2). In this light it seems quite likely that both the object-based and the feature-based views of priming may be true, but the stimuli and the circumstances of the task in each case dictate what sort of priming is seen. Taken together these results suggest that priming reflects modulations of neural activity at multiple levels of visual processing. Indeed, as we will see in the next section, neurophysiological findings on priming support the notion that it may be problematic to think of behavioral priming effects as reflecting a single perceptual process. The neurophysiological findings plus the findings that promote multiple mechanisms have supported conceptions of priming in visual search where priming reflects modulation of activity at several different levels of the perceptual process.

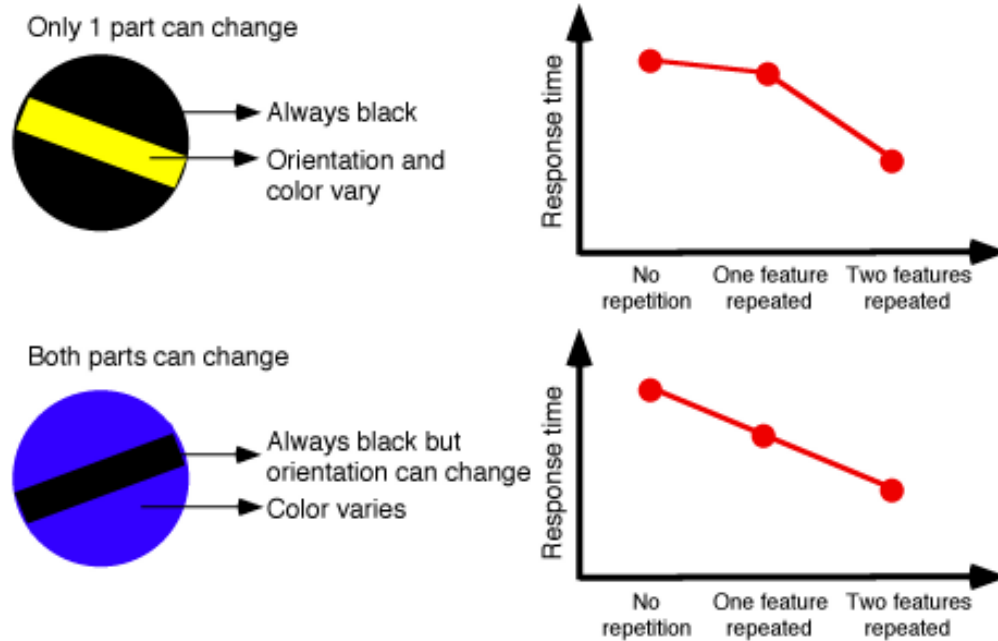


Figure 2.2. Object-based versus feature-based priming patterns dependent on stimulus type. In the upper panel, only one part of the object changes (the orientation or color of the central bar). In the lower panel either the background of the circle changes color or the central black bar changes orientation. Stimuli like the one in the upper panel tend to lead to object-based priming patterns, where priming is only seen if both features are repeated, while repetition of only one feature is sufficient to cause priming for the stimuli in the lower panel, as seen by the response times as a function of repetition of number of features, seen on right, based on Kristjansson et al., 2008).

2.1 The neural substrates of priming in visual search

A number of neurophysiological and neuropsychological studies have followed up on the original behavioral findings on priming in visual search. These studies have revealed that priming in visual search is related to modulations of activity as a function of repetition at various sites in the nervous system, providing more evidence against accounts that focus on any single level in the perceptual hierarchy.

Bichot and Schall (1999, 2002) found that single neurons in the frontal eye fields of macaque monkeys performing visual search tasks discriminated target properties faster and more accurately when the same features distinguished the target as on the last trial, and showed enhanced representations of distractors that had previously been the target. These results are consistent with results from neuroimaging. Priming in visual search, has also been investigated in human fMRI studies. Kristjánsson and colleagues (2007) used a pop-out search paradigm similar to the one used by Maljkovic and Nakayama (1994, see also Bravo & Nakayama, 1992) and found a modulation of activity in frontal and parietal areas when priming occurred. Such areas have been shown to be involved in visual attention (Corbetta & Shulman, 2002; Ruff, Kristjánsson, & Driver, 2007) (Figure 2.3). This result clearly suggests that priming reflects changes to activity in the attentional system. This is consistent with the notion that priming affects attention deployments towards the target (Kristjánsson, 2006b; Kristjánsson & Nakayama, 2003; Maljkovic & Nakayama, 1994). Moreover, Kristjánsson and colleagues (2007) found also a strong modulation of activity in early visual cortex correlated with priming (Figure 2.3). Finally strong activity was found in anterior fusiform cortex, but only when the target identity (position and color) was kept constant indicating that this region is sensitive to priming when the whole object is repeated, that is, when the same stimuli were seen in the same location as on the previous trial. Moreover, differences in activity were dependent on whether color or position was repeated (see also Geng et al., 2006). In particular, modulation of activity was correlated with color priming in area V4, the area that is mainly involved in color vision (see Chapter 1 – Section 3). In addition, Geng et al. (2006) found that the size of the repetition priming effect was modulated by the need for attentional selection on the previous trial, a result which strongly supports the notion that priming affects attention shifts. Taken together these fMRI findings argue strongly against any proposals that priming reflects the involvement of a

single part of perceptual processing, and strongly support the hypothesis that priming involves facilitation of attention shifts towards the primed element.

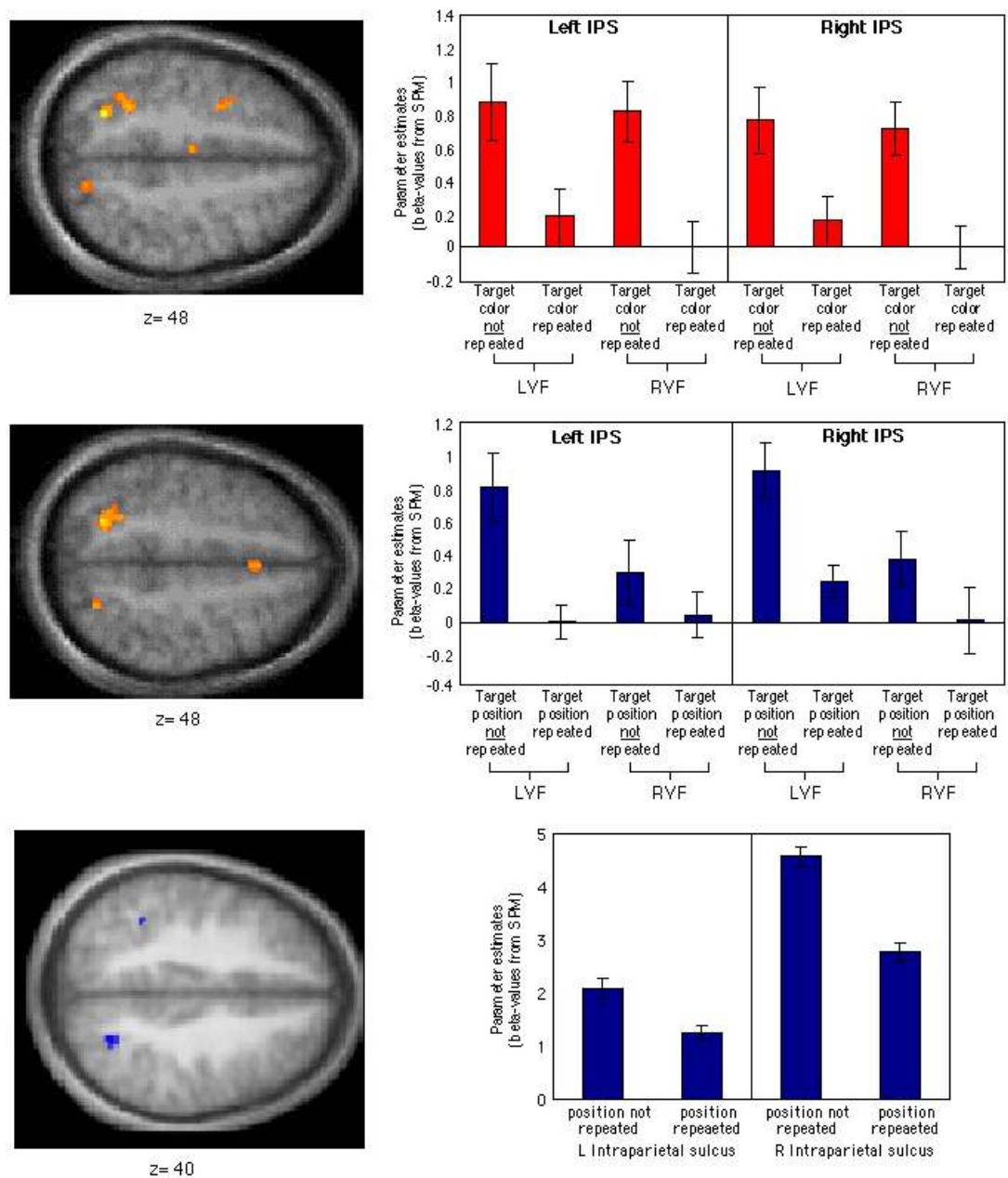


Figure 2.3. Repetition suppression of BOLD signal as a function of repetition of color of the target in pop-out visual search (Panel A) and position of the target (panels B & C). The left panel shows regions in IPS showing significant repetition suppression while on the left are shown parameter estimates as a function of whether the color or position are repeated or changed (Panels A & B replotted from Kristjansson et al., 2007, and panel C replotted from Geng et al., 2006).

Studies of patients suffering from hemispatial neglect are in alignment with these neuropsychological findings. Kristjánsson et al. (2005) studied priming in visual search in neglect patients using again a task similar to that used by Maljkovic and Nakayama (1994; 1996). When the patients did not notice a target presented in their neglected hemifield, priming from the target's color was unaffected, while priming from a repeated position only occurred when the patients were consciously aware of the target. These findings support the aforementioned TMS (Campana, Cowey, & Walsh, 2006; Campana et al., 2007) and fMRI studies (Kristjánsson et al., 2007; Geng et al., 2007), and suggest that priming for color and spatial position are, at least partly, mediated by distinct brain areas.

3. Visual motion priming

Different experimental paradigms have been used to investigate visual motion priming. In a typical visual search task observers have to respond to a particular feature of a target stimulus embodied amongst a number of distractors. Similarly, visual motion priming has been initially investigated testing how a directional stimulus (e.g., a rightward or a leftward drifting grating) influences or biases the perceived motion direction of a subsequent presented ambiguous stimulus. Generally, as well as for priming of other stimulus' features, the results suggest that motion priming might reflect modulations of neural activity at multiple levels of visual processing (e.g., at low-level and high-level of motion processing).

Pinkus and Pantle (1997) were the first to show that when an ambiguous step such as a vertical sine-wave luminance grating shifting 180 deg is followed closely upon an unambiguous step, the ambiguous motion appears to be in the same direction as the unambiguous step. In particular, they used a three-frame motion sequence in which a rightward or leftward phase shift (motion

step) was followed by a 180 deg step. The results showed that motion priming (i) lasted for hundreds of ms (about 770 ms); (ii) reached a plateau when the magnitude of the priming step (i.e., the first step: from frame 1 to frame 2) was 90 deg; and (iii) was not largely affected by spatial frequency, at least in the range of the spatial frequencies tested: 0.7 - 2.8 c/deg. The authors interpreted these results within the framework of the motion energy model of Adelson and Bergen (1985) (Figure 2.4) (see Chapter 1 - Section 2 for more details).

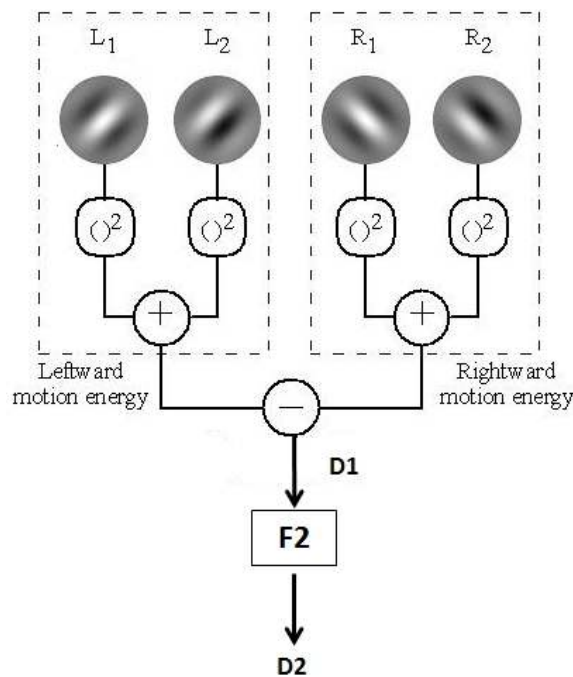


Figure 2.4. Energy model modified by Pinkus and Pantle (1997) to account for the data obtained on visual motion priming. The model consists of a motion energy stage followed by a low-pass filter (F2) which extends the first-stage local opponent motion energy D1 in time (see text for more details) (Adapted from Pinkus & Pantle, 1997).

The result that a motion bias persists for hundreds of milliseconds after a single motion step is easily explained within the energy model framework. Any directional imbalance (D1) in the outputs of first-stage detectors (i.e., an imbalance between leftward and rightward motion energy) which is produced by a motion step (priming stimulus) would be delayed for hundreds of

milliseconds by the second-stage filter (F2), a low-pass filtering, and then integrated with a balanced output produced by a counterphase stimulus (i.e., the ambiguous motion step). The integrated opponent energy (D2) would cause the ambiguous step to be seen in the same direction as the priming step. Moreover, the finding that the visual motion priming is present over two octaves of spatial frequency (from 0.7 to 2.8 c/deg) suggests that the motion signals, in more than one spatially tuned channel are delayed or extended by the second linear stage (F2).

van Santen and Sperling (1985) analyzed the response of elaborated Reichardt detectors to a two-frame grating sequence. In particular, they showed that the directional output of the detectors is positively related to the sine of the phase shift between the grating frames. Pinkus and Pantle (1997) investigated the relationship between visual motion priming and the magnitude of the phase shift of the priming step. If visual motion priming reflects the strength of a temporally delayed directional signal (D2) originated by motion energy units, then it would be expected that visual motion priming would be maximum for a priming step of 90 deg and would decrease for smaller or larger phase shifts. This is because the directional output of the detectors is related to the sine of the phase shift such that a sin of 90 deg would produce the maximum response of the motion detectors ($\sin(90^\circ) = 1$). The results showed that the larger effect was obtained for the 90 deg priming step. The phase effects imply that there are no static nonlinearities prior to the motion detector stage (i.e., prior to the leftward motion detector and the rightward motion detector; Figure 2.4). Thus, Pinkus and Pantle (1997) argued that in order to obtain a reliable output imbalance (D1) from first-stage detectors and the second-stage filter (D2) which is a sine function of phase shift magnitude, inputs to the detectors must be spatial sine-waves with a phase shift of 90 deg.

These results suggest that some aspects of the kind of visual motion priming considered in the experiment of Pinkus and Pantle (1997) can be accounted for by low-level motion energy units. However, the authors noted that interpretations of motion priming should be considered. They

claimed that two-step motion priming may be an example of a more general class of priming phenomena. For example, as pointed out in the previous section, attending a stimulus on one trial can speed the response to it on a succeeding trial (e.g., Stadler & Hogan, 1996). Other measures of performance, detection and discrimination, have also been shown to be enhanced in priming paradigms (e.g. Nakayama & Mackeben, 1989; Posner *et al.*, 1980). Moreover, state-dependent modulations of the activity of single neurons in the monkey cortex provide potential physiological analogs of some forms of visual priming. One of the most relevant experiments is that of Treue and Maunsell (1995). They recorded the activity of a monkey MST cell while two spots moved in opposite directions through its receptive field. When one of the two spots was the object of attention and moved in the preferred direction of the cell, about 90% of the studied MST neurons responded about twice as strongly as they did when an unattended spot moved in the preferred direction. An unambiguous priming step, for example a 90 deg rightward step, might influence the response of a rightward motion detector through an attentional mechanism so that its response magnitude would be higher than that of a leftward motion detector to the 180 deg step. The problem with this interpretation is that little is known about what stimulus variables drive the attention or how they produce state-dependent modulations or sensitization of single-cell activity (Maunsell, 1995). Thus, it is difficult to develop a complete model which can make specific predictions about the effects of stimulus variables like contrast, frame duration and phase-shift magnitude on visual motion priming.

3.1 The neural substrates of visual motion priming

Results from event-related potentials (ERPs), TMS and fMRI studies suggest that visual motion priming relies on cortical areas involved in motion perception. Jiang, Luo, & Parasuraman, (2002) examined the ERPs associated with unambiguous and ambiguous motion perception. The authors used sine-wave gratings with one-step single motion sequences (i.e., only one shift in

phase, either of 90 deg [rightward motion], -90 deg [leftward motion] or 180 deg [ambiguous motion]). Observers had to judge if the gratings drift leftward or rightward. Comparing ambiguous and unambiguous motion, unambiguous left- or rightward motion was associated with an enhancement in amplitude of the P3 component, which is an ERP component with a latency of approximately 300 ms, after the onset of apparent motion. The authors proposed that such enhancement corresponded to the location of area MT. In a second experiment they explored the temporal dynamics of neural activity underlying visual motion priming. ERPs were recorded to two successive motion jumps in which an unambiguous motion step served as a prime for a subsequent ambiguous target motion in a procedure that was very similar to that used by Pinkus and Pantle (1997). The prime-target time interval was varied between 200, 400, and 1000 ms. In a control condition, the two motion steps were both unambiguous but in opposite directions (motion reversal). Observers had to judge if the two successive motion jumps were perceived to be in the same direction or in opposite direction. A comparison between the motion reversal condition and the motion priming condition revealed that motion priming was associated with an enhancement of components P1 and P3 following target stimulus onset. What is more, ERP enhancement was greatest at a short prime-target interval of 200 ms, which was where the behavioral data also showed the strongest priming. Furthermore, both ERP enhancement and behavioral priming were eliminated at the longer prime-target interval duration (i.e., 1000 ms). Jiang et al. (2002) also conducted a Functional magnetic resonance imaging (fMRI) study. They found a significant activation in ventral-occipital area (V1), activation corresponding with MT, superior temporal cortex and intraparietal cortices (Figure 2.5). These areas may have contributed to the source of the ERP responses associated with apparent motion (motion jumps). Taken together the data of Jiang et al. (2002) support the view that visual motion priming involves modulation of neural responses both in early and in later stages of visual motion

processing.

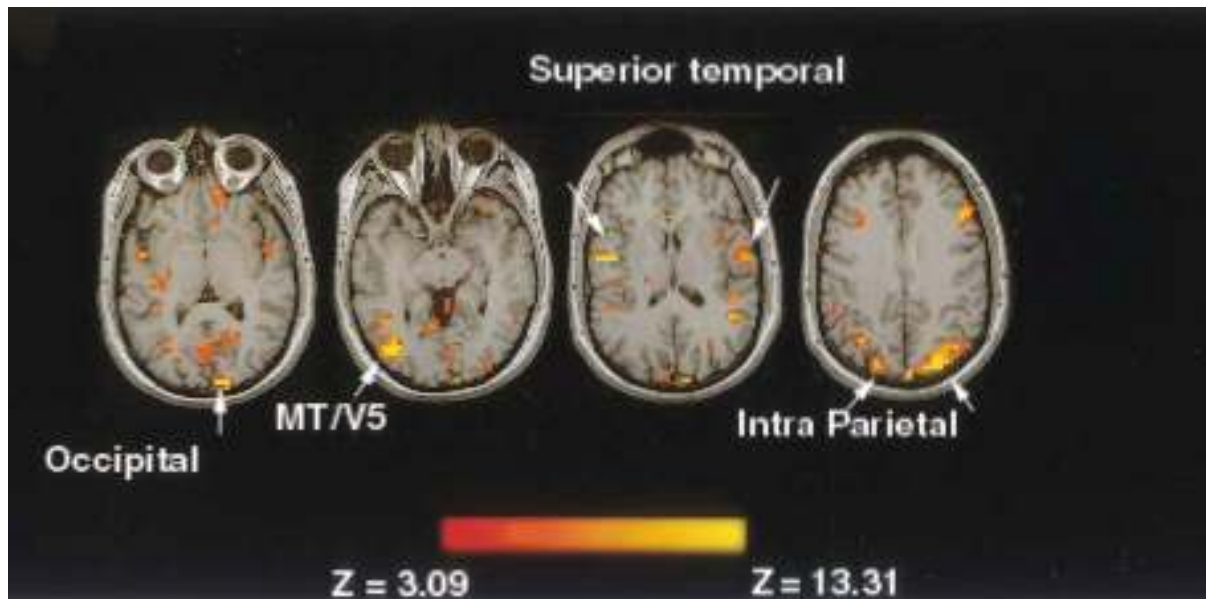


Figure 2.5. Activation of cortical regions involved in the perception of apparent motion (one subject). fMRI revealed the specific cortical regions activated by perceptual judgment of the motion direction compared with perception of the stationary sine-wave gratings (ventral occipital area [V1], area MT, superior temporal, and intraparietal cortices) (Adapted from Jiang et al., 2002).

Campana and colleagues (2006) used TMS to investigate the neural substrates involved in priming for motion direction and spatial position. They presented six sinusoidal gratings arranged in 2 columns (Figure 2.6). The gratings were shown for 300 ms with a speed of 14 deg/s. The three sinusoidal gratings on the left were horizontally aligned and always moved in a bottom-up fashion. The three gratings on the right were vertically aligned and could move left-to-right or vice versa. Two of these gratings were always moving in one direction, whereas the third grating was always moving in the opposite direction and was the target. The target could only appear at the top or at the bottom of the column. Subjects had to fixate the center of the

screen, ignore the gratings on the left as these gratings were introduced to engage the right hemisphere in the processing of motion direction irrelevant to the task. Subjects had to respond to gratings on the right, either to the spatial position or to the direction of motion of the odd grating (in different experimental sessions). After each response a 1000 ms inter-trial blank screen interval was presented, and in the TMS condition, repetitive TMS was delivered during the second 500 ms half of the intertrial interval. The only instruction given to subjects was to judge the spatial position (experiment 1) or the motion direction (experiment 2) of the target. Thus, the authors run a purely perceptual task, not a memory task. Indeed, as pointed out previously, it was expected that priming would occur for the feature (or position) not directly linked to the motor response (Maljkovic & Nakayama, 1994, 1996).

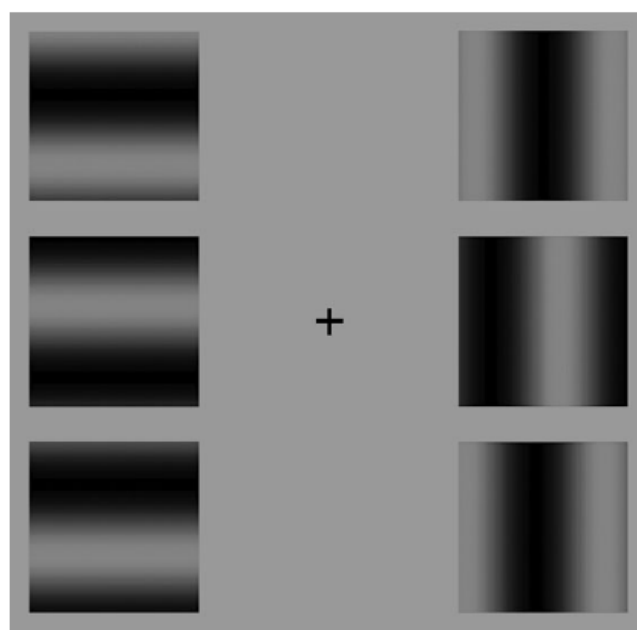


Figure 2.6. An example of the stimulus used in the experiment of Campana et al. (2006).

The results showed that whereas TMS over area MT abolished priming of motion direction (Figure 2.7) this was not the case for priming of spatial position. In a complementary study (Campana et al., 2007) in which a similar experimental procedure was used but rTMS was applied to the right frontal eye field (rFEF) and to the left frontal eye field (lFEF), the data

showed that TMS over the lFEF strongly reduced priming of spatial position but not of motion direction (Figure 2.7). Moreover, whereas area MT in humans has been shown to be not involved in color priming (Campana et al., 2002), the ablation of areas V4 and TEO in monkeys has been found to eliminate color priming despite normal color discrimination (Walsh et al., 2000). These studies suggest that the areas involved in the processing of a given perceptual attribute (e.g., color, motion direction, spatial position etc.) also generate priming for that attribute. Indeed, area MT is known to be strongly involved in processing motion stimuli, whereas areas V4 and TEO have a primary role in color processing (Chapter 1 – Section 3) whilst the frontal eye fields are involved in visuo-spatial attention, even in absence of saccadic programming (Muggleton et al., 2003).

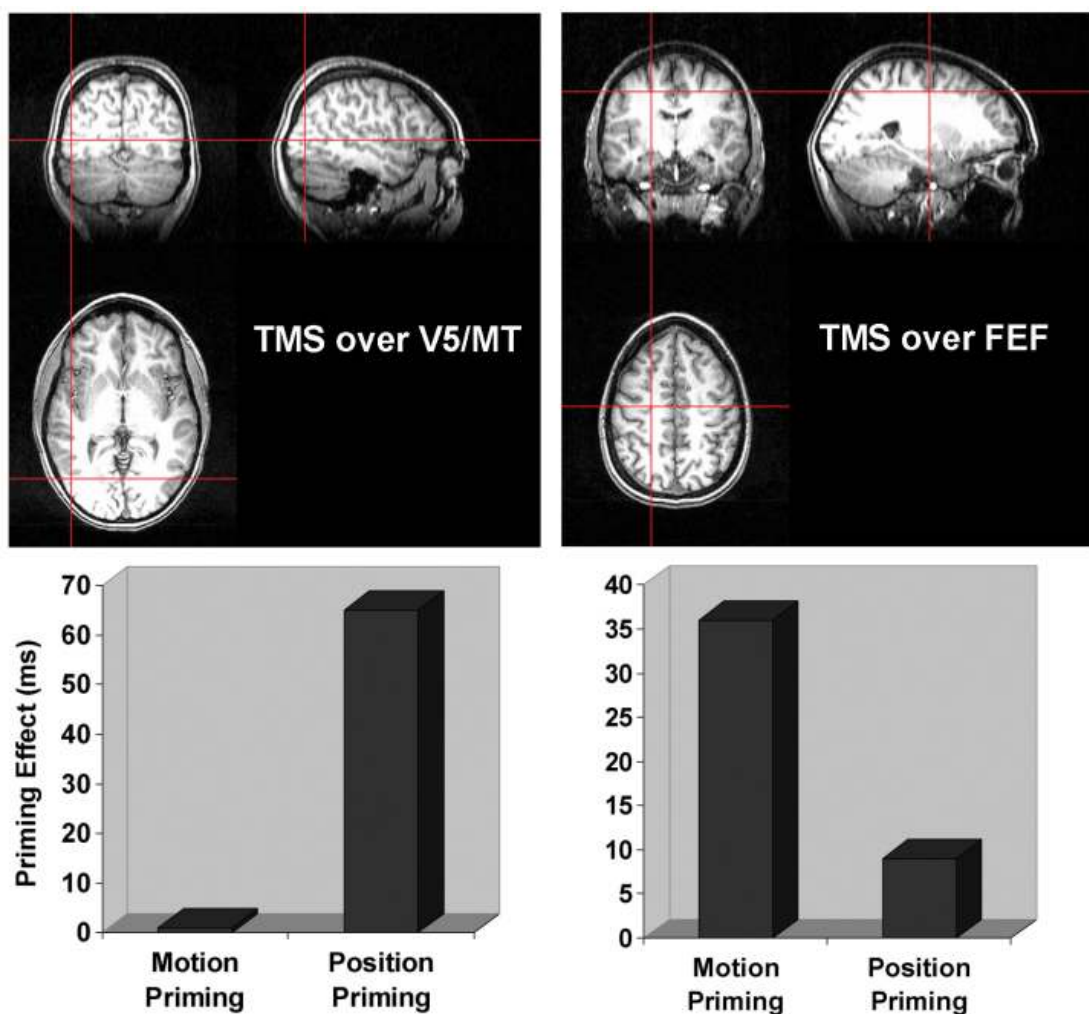


Figure 2.7. Double dissociation of the effects of TMS over two different cortical sites on visual priming. TMS over area MT (left panels) abolishes priming of motion direction but not priming of spatial position (left column). Conversely, TMS over left FEF (right panels) strongly reduces priming of spatial position, but has virtually no effect on priming of motion direction (Adapted from Campana et al., 2006, 2007).

4. A hybrid model of priming

The experimental results discussed in this chapter show that a single mechanism or brain module is not sufficient to account for priming. The results cannot be accounted for by assuming that priming in vision is always based on single features, or always on episodic representations of what has gone before involving features assembled into objects. Instead, a hybrid model of priming seems to be more appropriate and fit the data outlined above. In particular, the implicit memory producing visual priming is assumed to operate locally on features or object representations, or both, and it seems to be held in multiple sites along the visual pathways. Moreover, it can exist in multiple types of representations, the simplest ones involving separate features of a visual stimulus (e.g., color, motion direction, spatial frequency etc.) and relying on low-level functionally specialized visual areas, to areas holding compound and complex representations involving objects or parts of objects, based in higher-level visual areas. This view is supported by evidence from neurophysiology (Bichot & Schall, 1999, 2002), lesion studies (Walsh et al., 2000), TMS studies (Campana et al., 2002, 2006, 2007) and fMRI studies (Jiang et al., 2002; Geng et al., 2007; Kristjánsson et al., 2007). The findings indicate that multiple levels of the perceptual processing can show modulations of activity correlated with priming, depending on the task or the particular feature involved. According to a hybrid model of priming, the specific level of representation triggering the priming effect depends on the specific stimulus,

task and context. Indeed, as found by Kristjánsson et al. (2008), small changes in the stimulus or task demands can shift the level of representation at which priming occurs, such as changing feature-based priming into object-based priming. Thus, feature priming appears to be based on the activity of low-level visual areas functionally specialized for the processing of that specific feature, while object-based priming reflects activity changes at higher levels of the hierarchy, where the neurons respond to the whole object. For example, priming for motion direction seems to depend on the activity of areas involved in motion perception such as V1, V2/V3 and MT (Jiang et al., 2002). Position priming is mainly based on the activity of areas specialized in spatial cognition in parietal areas and frontal eye fields (Campana et al., 2007), whilst the fronto-parietal attentional network plays a crucial role in the development of priming effects and in the attention-grabbing effect of the primed element.

However, some critical questions concerning the dynamics between the various brain areas involved in priming effects remain unanswered. For example, what are the specific factors that determine at which level of processing the priming effects occur? And what is the role of attention in the different kinds of priming explored in this chapter? One possibility is that the attentional system simply focuses attention on a given feature or object, and then priming occurs locally at the level in which the feature or the object is encoded, while another possibility is that the attentional system plays a more central role in priming. The answers to these and other related questions will best be addressed using a multidisciplinary approach, integrating results from experiments using behavioral, neurophysiological (e.g., fMRI, TMS and single-cell recordings) and neuropsychological studies.

Chapter 3

The Motion Aftereffect

1. Introduction

After prolonged exposure (adaptation) to a visual scene moving in a certain direction, observation of a stationary scene evokes an experience of motion in the opposite direction. This perceptual effect, called the motion aftereffect (MAE) (Anstis, Verstraten, & Mather, 1998; Mather, Verstraten, & Anstis, 1998), is easy to generate and very robust. Research on the MAE has had a crucial role in the development of theories relating motion perception to neural activity. Sutherland (1961) was the first to suggest a simple neural explanation of the MAE, inspired by Hubel and Wiesel's (1959) discovery of direction selective cortical cells in the cat:

‘...the direction in which something is seen to move might depend on the ratios of firing in cells sensitive to movement in different directions, and after prolonged movement in one direction a stationary image would produce less firing in the cells which had just been stimulated than normally, hence movement in the opposite direction would be seen to occur’ (p.227 in Hubel & Wiesel, 1959). In 1963, Barlow and Hill reported adaptation induced changes in responsiveness in single cells in the rabbit retina. Moreover, the results of Barlow and Hill (1963) are in agreement with the Sutherland's (1961) ratio model, in that, to perceive movement in one particular direction, the firing rate of motion detectors tuned to that direction must exceed, by a certain minimum ratio, the firing rate of motion detectors tuned to the opposite direction. Thus, after adaptation to one particular motion direction, the corresponding motion detectors will fire less, allowing those tuned to the opposite direction to exceed the critical ratio and to produce

erroneous motion signals in the opposite direction when a stationary stimulus is subsequently presented.

Later discoveries of adaptation effects in cat and primate cortex encouraged the general view that the origin of the MAE was probably adaptation in motion-selective cells in primary visual cortex. The essential principle of the MAE is still universally accepted, but discoveries made possible with the introduction of new experimental techniques indicate that major changes to theoretical explanations of the MAE are required. These discoveries include work in human psychophysics (Alais, Verstraten, & Burr, 2005; Ashida & Osaka, 1994; Bex, Verstraten, & Mareschal, 1996; Bex, Metha, & Makous, 1999; Cavanagh & Favreau, 1980; Culham et al., 2000; Morgan, Chubb, & Solomon, 2006; Moulden, 1980; Nishida & Ashida, 2000; Nishida, Ashida, & Sato, 1994; Nishida & Sato, 1995; Ledgeway, 1994; Smith, Scott-Samuel, & Singh, 2000; van de Grind, Verstraten, & van der Smagt, 2003; van de Grind, van der Smagt, & Verstraten, 2004; Verstraten et al., 1996; Verstraten et al., 1996; Verstraten et al., 1999; Verstraten et al., 1998), primate physiology (Kohn & Movshon, 2003; Kohn & Movshon, 2004; Petersen et al., 1985; van Wezel & Britten, 2002), human neuroimaging (Ashida et al., 2007; Culham et al., 1998; Culham et al., 1999; Hautzel et al., 2001; He et al., 1998; Huk et al., 2001; Nishida et al., 2003; Seiffert et al., 2003; Taylor et al., 2000; Tootell, Reppas, Dale, Look, Sereno, Malach, Brady, & Rosen, 1995), human electrophysiology, Visual Evoked Potentials, (VEPs), magnetoencephalography (MEG) (Bach & Hoffmann, 1996; Bach & Ullrich, 1994; Kobayashi et al., 2002; Newsome & Paré, 1988; Stewart et al., 1999; Tikhonov et al., 2007) and transcranial stimulation (Antal et al., 2004; Théoret et al., 2002). Results indicate that the MAE is the combination of neural adaptation at several visual cortical sites.

2. Psychophysical evidence: How many after-effects?

The classical MAE seen in natural viewing conditions involves an observer viewing movement for a while, such as a waterfall or the view from a moving vehicle, then being presented with a static test pattern that although stationary appears to move. We shall refer to this effect as the static MAE or SMAE. In the late twentieth century, laboratory researchers began using dynamic test patterns such as dynamic visual noise or counter-phase flicker to study the aftereffects of motion adaptation. A dynamic visual noise (DVN) pattern contains a dense field of randomly positioned dots which are replaced by a completely new set of random dots at pre-defined time intervals, typically up to 100 times every second. DVN has the appearance of an un-tuned television display. Counter-phase flicker is created by reversing the contrast of a luminance sine-wave grating repetitively such that black bars become white and white bars become black at a pre-defined frequency. Exactly the same effect can be created by spatially superimposing two identical gratings drifting in opposite directions. The properties of MAEs obtained using these dynamic test patterns, which are known as dynamic motion aftereffects (DMAE), are markedly different from those obtained using stationary patterns and have led to the conclusion that the two aftereffects are mediated by different populations of cells. In particular, the use of dynamic and static test patterns has allowed exploration of whether the MAE depends on a single source of adaptation, or if it reflects adaptation at several sites along the motion processing pathway. Using transparent motion stimuli to investigate this question, 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 are used after the adaptation period. In these experiments subjects were adapted to transparent motion stimuli, consisting of two superimposed random-dot patterns moving in orthogonal directions at different speeds, including a low speed component of 2 deg/s^{-1} , and a faster component of 8 deg/s^{-1} .

Despite the fact that these kinds of patterns do not produce a perceptual coherence during adaptation, in fact the components are perceived separately, the MAE is usually perceived in the direction opposite to the vector sum of the two components (Verstraten, Fredericksen, & van der Grind, 1994). The results showed that the MAE using a static test pattern (static visual noise), was more opposite to the direction of the slower speed component, whereas dynamic test patterns (DVN refreshed at 90 Hz) produced a MAE mostly opposite the direction of the fastest component. Thus, the same adaptation conditions produced different MAE directions depending on the kind of test pattern used. Verstraten, van der Smagt, & van de Grind (1998) suggested the presence of at least two distinct motion detectors: detectors that encode high velocities and support short temporal delays (transient channel); and detectors for slower velocities that support longer temporal delays (sustained channel). The authors proposed that these different channels tuned for different velocities could be implemented in different neural substrates, contributing differently to the MAE.

Further evidence support for the presence of independent speed-tuned channels has been provided by van der Smagt, Verstraten and van de Grind (1999). Using transparent patterns found that when the components moved at different speeds (e.g., 4 and 12 deg/s), and the random dot test pattern refresh frequency was varied from 0 Hz (static) to 90 Hz (dynamic), the MAE direction was closer to the direction opposite the fast adaptation component for test frequencies above 20 Hz. Although it approached the direction opposite the slow adaptation component for lower test frequencies. Since these results again suggest the presence of independent channels tuned for slow and fast speed, the authors also used a test pattern containing both static and dynamic components. If there are independent speed-tuned channels, separate MAEs for each of the two components would be expected. In such a mixed test condition, both MAEs were present, and both components of the combined test pattern elicited a MAE. The directions of these MAEs were similar to those elicited by the static or dynamic test

pattern alone. The combined test pattern was perceived as a transparent, bi-directional MAE, with the static component slowly moving opposite the low speed adaptation component and the dynamic component moving rapidly opposite the high-speed-adaptation vector. The combined test pattern tapped both kinds of channels simultaneously, resulting in the perceptual manifestation of both MAEs. This perceptual duality provides strong evidence about separate slow and fast channels.

In order to selectively tap either the fast or the slow channel, Alais, Verstraten and Burr (2005) measured the MAE using particular kinds of static and dynamic test patterns. In their experiment dynamic test patterns consisted of a stack of 40 random binary luminance arrays passed through a Fourier transformation, that is, the dynamic test patterns were filtered in the temporal frequency dimension by a band-pass filter centered on different frequencies (ranging from 0.8 to 12.8 Hz). The temporal modulation was subsequently obtained by cycling through the stack of the 40 random luminance arrays. The filtering for the static test pattern was centered on a frequency of 0 Hz. In the first experiment the authors assessed the MAE duration from adapting subjects to a random-dot pattern that moved coherently either at fast or slow speed. The results for the fastest adaptation speed showed that MAE duration increased with the temporal frequency of the test pattern, producing no MAE at the lowest temporal frequencies. Alternatively for the slowest adaptation speed, MAE duration was highest at low temporal frequencies, decreasing at high test temporal frequencies. These results suggest that different adaptation speeds activate distinct speed-tuned temporal channels. Thus, the findings of Alais et al. (2005) confirm the previous results that high speed components seem to adapt exclusively a fast channel, and low speed components adapt uniquely a slow channel (Figure 3.1).

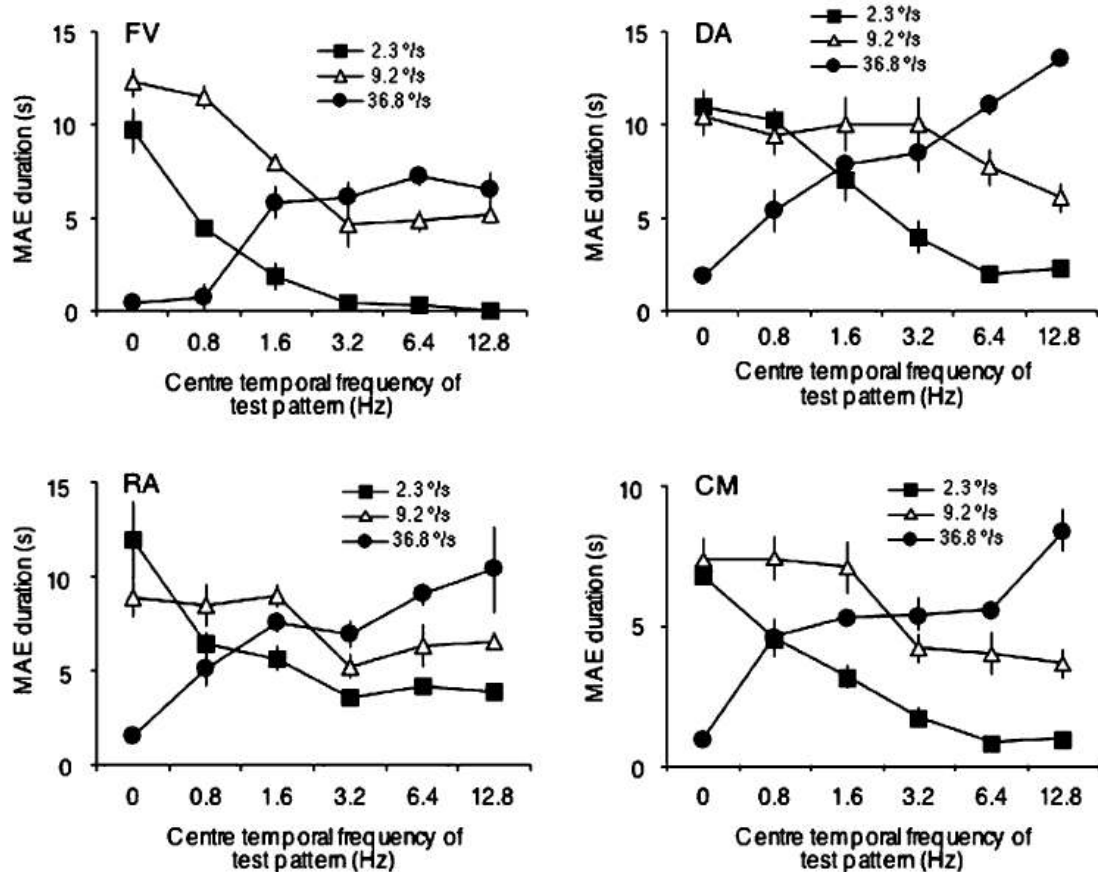


Figure 3.1. MAE duration as a function of the test temporal frequency and the speed of the adapting stimulus (different plot symbols). Results are shown for four subjects. For the slowest adapting speed ($2.3^{\circ} \text{ sec}^{-1}$, squares) MAE duration is maximal for stationary tests and absent at the highest test temporal frequency; for the fastest adapting speed ($36.8^{\circ} \text{ sec}^{-1}$, circles) the MAE is absent for stationary tests and maximal at the highest test temporal frequency (Adapted from Alais et al., 2005).

Since 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. Nishida and colleagues measured the degree of interocular transfer (IOT), that is, the strength of MAEs is measured by presenting adaptation and test stimuli either to the same eye or to different

eyes. For SMAE and DMAE the authors found that SMAE produce only partial IOT, reflecting adaptation at low-level where there are few binocular neurons (Nishida & Ashida, 2000; Nishida, Ashida, & Sato, 1994). Conversely, DMAEs reflect adaptation at both low and high-levels, showing perfect IOT when the MAE duration is measured in the central visual field and the subjects pay attention to the adapting stimulus and showing partial IOT when measured with the nulling method (a technique in which the MAE seen in counter-phase flicker is cancelled out by increasing the contrast of the component drifting opposite to the MAE direction [Nishida & Ashida, 2000]), when the adaptation stimulus was presented in the peripheral visual field and when subjects were distracted by an interfering task (Nishida & Ashida, 2000; Nishida, Ashida, & Sato, 1994). A more recent study of von Grünau (2002) provided further evidence that transparent motion stimuli can adapt both low and high-level mechanisms, and that static and dynamic test patterns can tap separately each of these levels. In order to investigate the locus at which transparent stimuli produce MAEs, the author measured the IOT of the SMAE and the DMAE. In particular, the adapting stimuli used by von Grünau (2002) consisted of: coherent plaids made of two superimposed gratings having a large angle between them (i.e., 90 deg); transparent plaids, consisting of two superimposed gratings having a small angle between them (i.e., 30 deg); and a horizontal grating. Test stimuli were horizontal static and counter-phase gratings with the same periodicity as the adapting stimuli. The results showed a stronger static MAE when adapting and test stimuli were similar in orientation, confirming that the static MAE depends on the orientation of both adapting and test patterns. Such a difference was not due to the different amount of transparency of the adaptation plaids because in a separate experiment in which the same transparency difference was used and the orientation difference was kept constant, the static MAE was the same for both coherent and transparent plaids. On the other hand, the magnitude of the dynamic MAE was independent of the orientation difference between the components of the adapting pattern and the test pattern. In addition, no significant differences

were found between coherent and transparent adapting plaids. This result suggests that the dynamic MAE reflects adaptation at motion integration level. Another difference between static and dynamic MAEs was the amount of IOT. For the static MAE little IOT was found, while dynamic MAE showed a larger and almost complete IOT, replicating the findings of Nishida & Ashida (2000). It is well known that low-level mechanisms show partial IOT, whereas higher-level mechanisms show larger transfer, probably due to the presence of a large number of binocular neurons in higher level areas. The findings of von Grünau (2002) support the hypothesis that the static MAE reflects adaptation at low-levels of the motion processing pathway, while dynamic plaid MAE reflects adaptation also or mainly at higher levels, where the components have already been integrated into a global pattern.

Further evidence of the multiplicity of the MAE mechanisms arises from studies that employed second-order motion stimuli. First-order motion involves patterns defined by variations in the luminance of single image points, such as drifting luminance gratings or dot patterns (the studies reviewed above employed such kinds of patterns). Second-order patterns contain features defined by variations in the luminance of pairs of image points, such as variation in texture contrast, size, orientation or binocular disparity. In moving second-order patterns the texture elements defining the pattern are usually replaced by new texture in each animation frame, so the pattern does not contain point-by-point correspondences over time (see Chapter 1 for more details). Adaptation to second-order motion does not produce a static MAE. This could be due to the presence of distinct low-level motion detectors for different kinds of second-order motion (Ledgeway & Smith, 1994a,b; Derrington, Badcock, & Henning, 1993; McCarthy, 1993; Pantle & Turano, 1992): stationary second-order patterns may mask weak motion signals that rise from adapted and unadapted detectors (Ledgeway & Smith, 1994a,b). Moreover, there could be some luminance artifacts that introduce noise during the adapting period, weakening further the motion signals (Ledgeway & Smith, 1994a,b). On the other hand, it has been shown that adaptation to

second-order patterns produces a remarkable MAE if a dynamic second-order test pattern is then displayed (Ledgeway & Smith, 1994a,b; Nishida, Ashida, & Sato, 1994; Nishida & Sato, 1995). These studies suggest that dynamic test stimuli are rather insensitive to the kind of motion presented during the adapting period. Moreover, first-order and second-order adapting patterns differ in terms of their inter-ocular transfer (IOT). For example, Nishida and colleagues (Nishida et al., 1994; Nishida & Sato, 1995) used DVN at a frequency of 2 Hz and a pattern that contained features which could be tracked by attention. Their DMAE from adaptation to second-order motion decreased progressively at higher temporal frequencies.

At least three populations of cells are required to explain the diverse empirical properties of the aftereffects reviewed so far. One low-level population mediates the classical SMAEs from first-order adaptation seen using static test patterns, and perhaps DMAEs seen in very low temporal frequency dynamic test patterns. A second low-level population mediates DMAEs from adaptation to rapid first-order motion seen using high temporal frequency test patterns. A third, 'higher level' population mediates DMAEs from second-order motion seen using low temporal frequency test patterns. A corollary of this conclusion is that DMAEs do not tap a single population of cells, but different populations depending on the properties of the adapting and test stimuli. Maruya and colleagues (2008) provided further evidence that the SMAE taps low-level stages and DMAE taps both low and high-level stages of motion analysis, using binocular suppression, where visual awareness of the adapting stimulus is suppressed, resulting in adaptation to invisible motion. Observers view moving stimuli with one eye, while the other eye receives flickering gratings varying by contrast, size or position (Tsuchiya & Koch, 2005). Maruya et al.'s (2008) observers were adapted and tested using invisible motion to the same eye, or adapted using one eye and tested using the other eye (IOT), using both static and flickering test patterns. Results showed that binocular suppression reduces both the SMAE and the DMAE in the same manner when the same eye is tested, indicating that low-level motion detectors adapt

to some extent even when the moving stimulus does not reach awareness. However, in the IOT condition that prevented low-level adaptation, no DMAE at all was obtained following exposure to suppressed adapting motion. These results indicate that invisible motion cannot produce adaptation at a high level of motion analysis, and that DMAEs reflect adaptation both at low and high-level stages of motion processing. Recent psychophysical results have implicated two further sites of adaptation in motion aftereffects. Several studies have found evidence for adaptation at a relatively late stage in the motion pathway, in which global movements such as rotation and expansion are computed. Aftereffects have been reported using adapting and test patterns of varying complexity (Bex et al., 1999; Cavanagh & Favreau, 1980; Smith et al., 2000). Bex et al. (1999), for example, found that adaptation to radial and rotational patterns produced stronger MAEs than adaptation to translating patterns. Several papers report so-called ‘phantom’ MAEs, which appear when the test stimulus is projected onto a region of the retina that was not exposed to the adapting stimulus, and that did not seem to contain motion during adaptation (e.g. Price, et al., 2004; Meng, et al., 2006; Snowden & Milne, 1997). Meng et al. (2006), for instance, found phantom MAEs only when the adapting pattern contained radial expansion rather than translation. The presumed cortical location of phantom aftereffects is middle temporal area (MT) or medial superior temporal area (MST), where receptive fields are very large and sensitive to large-scale rotary or radial motion. Culham et al. (2000) argued that apparent motion mediated by attentional tracking can also generate an aftereffect. During adaptation subjects viewed an ambiguous counter-phase grating, and were instructed to ‘...use attention to mentally track the bars of a radial grating in one of the two ambiguous directions...’. Tests on a static pattern showed no aftereffect, but tests on a 2 Hz counter-phase grating did reveal an aftereffect. Culham et al. (2000) argued that their DMAE from attentive tracking arose in relatively late cortical areas, perhaps MST. Their adapting stimulus offered equal and opposite signals for motion sensors, so it is possible that attention served to modulate these signals rather than generate its

own motion signal. The fact that their effects were confined to DMAEs might indicate the site at which the attentional modulation occurred. So far, the psychophysics indicates that up to five populations of cells all potentially contribute to motion aftereffects. Are these populations functionally distinct? Do they occupy different cortical locations? Perhaps recent electrophysiological and brain imaging can clarify these fundamental questions.

3. Physiological evidence: how many sites?

3.1 Single-unit recordings

Important recent studies by Kohn and Movshon (2003, 2004) measured adaptation-induced changes in the response of direction-selective cells in macaque MT. One of their aims was to determine whether adaptation effects occur at the level of MT, or are effects inherited from V1 feed forward. In the latter case, the spatial extent of adaptation in MT should be limited by the smaller size of receptive fields in V1. Kohn and Movshon (2003) did indeed find spatially specific adaptation within MT receptive fields consistent with adaptation ascending from V1 (Figure 3.2). Other results reported by Kohn and Movshon (2003) indicate a particular role for MT responses in DMAEs. They found that adaptation to the null direction of an individual MT cell enhanced its response to a balanced counter-phase flickering grating, a neural correlate of the DMAE. Adaptation weakened the opponent input to the MT cell, enabling an enhanced response to motion balanced stimuli. Kohn and Movshon (2003) do not rule out the possibility that adaptation can also occur in MT neurons themselves.

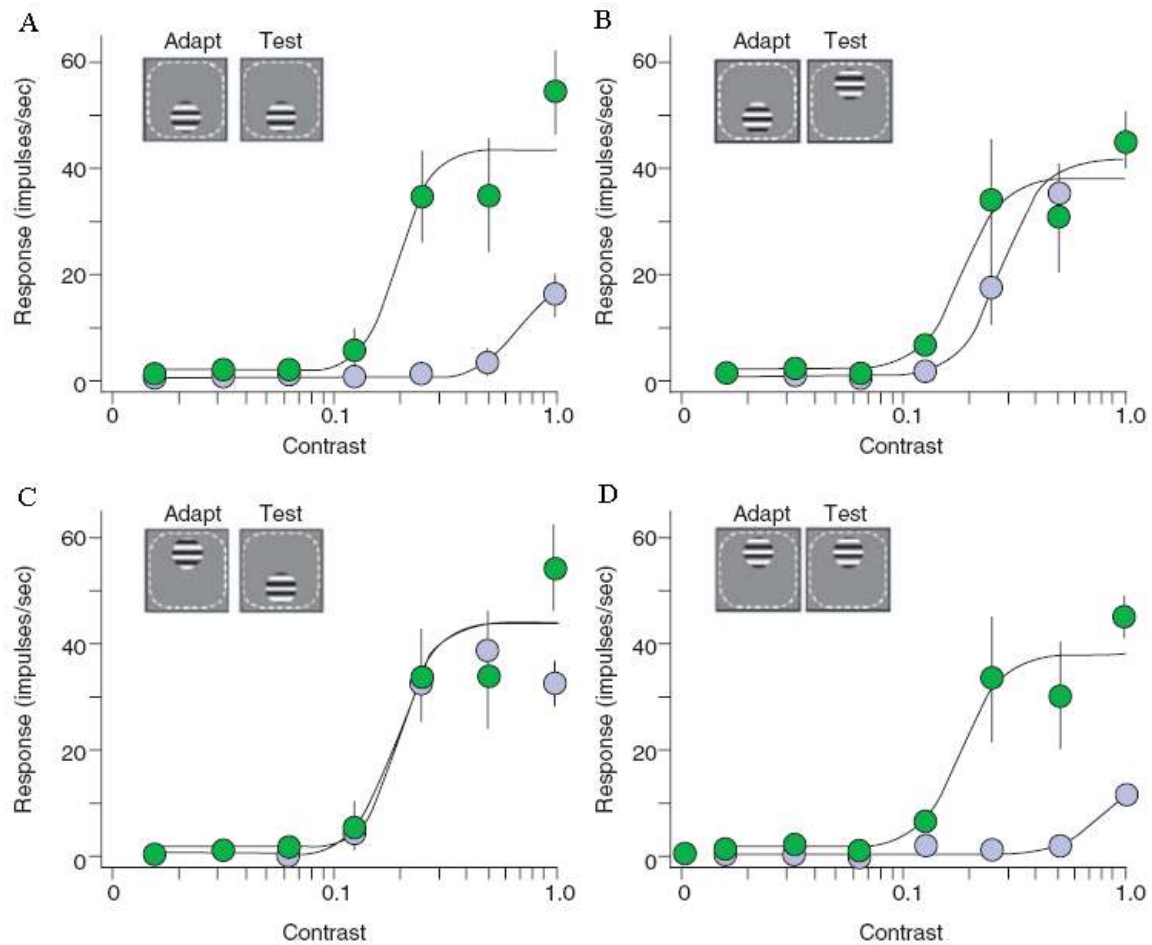


Figure 3.2. Contrast response functions of an MT neuron measured before adaptation (green circles) and after adaptation (blue circles). The inset in each graph shows the spatial arrangement of adapting and test stimuli in the receptive field of the cell (broken lines). When adapting and test locations overlapped, (A) and (D), the response of the cell was strongly reduced; when the adapting and test locations differed, (B) and (C), response was largely unaffected by adaptation (Adapted from Kohn & Movshon, 2003).

3.2 Human brain imaging

Results from recent functional magnetic resonance imaging (fMRI) studies of human motion processing support a functional distinction between at least two populations of motion sensors responsive to first- and second-order motion, but these populations do not seem to occupy

anatomically segregated locations. Ashida et al. (2007) employed a fMRI adaptation paradigm. Where repeated presentation of similar stimuli reduced the blood oxygen level dependent (BOLD) response, their interpretation was that the change in response (fMRI adaptation) reflected changes in the responsiveness of cortical cells activated all stimuli. When there was little or no reduction in BOLD response they inferred that different cells were activated by the different stimuli. Using this technique they found evidence for separate populations of cells sensitive to first-order and second-order motion in several visual areas including V3A, MT and MST. Nishida et al. (2003) and Seiffert et al. (2003) had previously found fMRI responses to both first-order and second-order motion in several visual areas including V1, V2, V3, VP, V3A, V4v and MT. These data are important because they are inconsistent with earlier brain imaging studies of the MAE that strongly implicated area MT (Tootell et al., 1995). Indeed other recent imaging studies have disputed the role of MT in MAEs (Culham et al., 1999; He et al., 1998), and indicate that several brain areas are activated during the perception of MAEs. In Taylor et al.'s (2000) study, subjects were adapted for 21 s to drifting bars or to reversing bars, the control condition. Immediately after adaptation stationary bars were presented for 21 s, and subjects were instructed to press a button once the subjective experience of a SAME ceased. During perception of the SMAE, significant activation was indeed found in MT, but also in a network of posterior and anterior cortical sites (Figure 3.3).

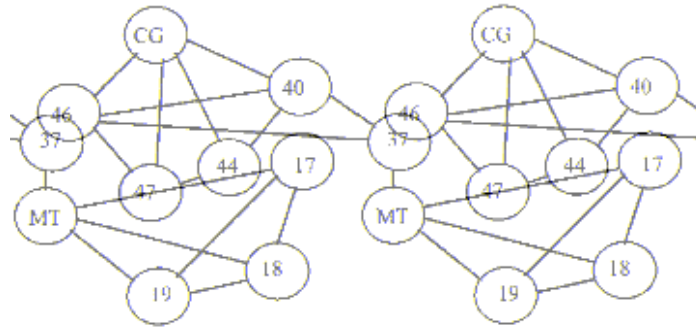


Figure 3.3. The posterior and anterior neural networks active during the perception of MAE; the connections between sites are derived from the correlation coefficients of the activation time courses. The lines join cortical sites that have cross correlations of at least $r=0.5$. Numbers refer to Brodmann areas (Adapted from Taylor et al., 2000).

In particular there was consistent activation in the anterior cingulate gyrus (CG), BA47 and BA40. Taylor and colleagues (2000) argued that these brain regions could be candidates for mediating awareness of the MAE. Correlation analysis showed that two different neural networks are involved in the MAE, a posterior network mainly involved in motion analysis, and an anterior network involved in the experience of the MAE. The posterior network includes V1, V2, V3 and MT; the anterior network includes BA37, BA40, BA44, BA46, BA47 and CG. As shown in Figure 3.3, the most posterior region of the anterior network is the BA37. There is evidence that this area belongs to the anterior network and is anatomically and functionally distinct from area MT. Therefore, BA37 may be considered a bridge between the anterior and the posterior network. The joint activity of the two networks may constitute the neural basis of MAE perception. The same conclusion transpires from Hautzel et al. (2001), who measured regional cerebral blood flow (rCBF) with positron emission tomography (PET) during the perception of MAE. In particular, their stimuli consisted of 10 black and 10 white bars oriented horizontally on

a black monitor screen. Subjects were instructed to fixate a central fixation cross and were asked to press a button whenever they experienced the illusion.

They found increased rCBF in areas V2, V3a and MT. In addition, when subjects perceived the MAE, an increase in rCBF was also seen in the lateral parietal cortex (BA40) predominantly on the right side, in the right dorsolateral prefrontal cortex (DLPFC), in the anterior cingulate and in the left cerebellum. These results are in broad agreement with those of Taylor et al. (2000), and provide evidence of activation in multiple cortical areas during perception of the MAE. The increased rCBF in BA40 and DLPFC may represent activation of cognitive functions during perception of the MAE, such as alertness, attention and working memory. The participation of attentional networks raises the question of whether activity detected in visual areas such as MT actually reflects attention to the MAE. Huk and colleagues (2001) tried to disentangle this question. In previous experiments there was no attentional control and when subjects perceived MAE, they could attend to the stimulus stronger than in a control condition in which MAE is not perceived. In addition, subjects were free to allocate and shift attention differentially between MAE and control conditions and the attention could have enhanced the MT response. In the first experiment Huk et al. (2001) replicated previous findings using a paradigm similar to that of He et al. (1998). Stimuli were two gratings, one placed to the left, and the other to the right of a central fixation point. fMRI results are in line with the previous work: there was a larger increase in MT response in the MAE condition (when adaptation stimulus was unidirectional motion) than in the control condition (when adaptation stimulus reversed its motion direction at 2 Hz). However, the authors argued that if increased attention during the MAE conditions caused the MT response increase, then forcing subjects to pay equal attention to MAE and control conditions should decrease or eliminate the MT response difference. To equate the attention during the test periods of both MAE and control conditions, subjects had to perform a sequence of 2-alternative forced-choice speed discriminations during a 5 second test period between the

two gratings. During both MAE and control conditions the grating with an added threshold-level physical motion appeared to drift slightly faster. The results showed no differences between MAE and control condition (Figure 3.4). Therefore by requiring subjects to direct attention to performance on a speed discrimination task removes all differences in MT responses.

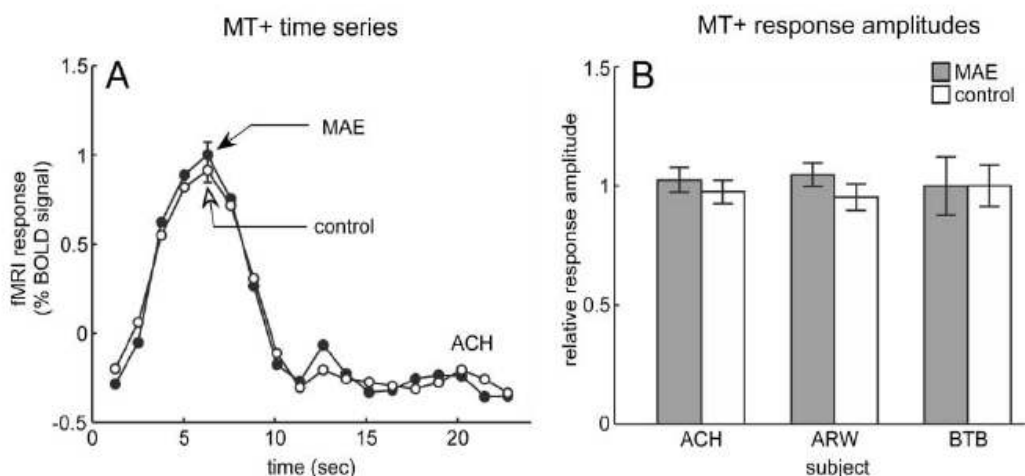


Figure 3.4. MT responses during directed attention show no difference between MAE and control condition. A. Percent of BOLD signal in function of the time course of one subject. B. Response amplitudes for all subjects. Dark bars, MAE conditions; light bars, control conditions (Adapted from Huk et al., 2001).

After eliminating this attentional confound, Huk and colleagues (2001) performed another experiment to test direction-selective adaptation. Subjects were adapted to a given motion direction, and then viewed test stimuli moving in either the adapted direction or the direction opposite to the adapted direction. Direction-selective adaptation was observed in MT, V1 and V2. These results indicate first that motion adaptation causes an imbalance in direction-selective neurons by decreasing the responses of neurons selectively tuned for the adaptation motion direction, second, that previous neuroimaging experiments confounded the decrease in responses

due to adaptation with a response increase caused by a stronger attention to the MAE condition. Thus, there are no grounds for claiming that MT has any unique status in terms of MAE locus.

3.3 Human transcranial stimulation studies

Stewart and colleagues (1999) were the first to succeed in reducing the duration of SMAE (but not of the colour aftereffect) with magnetic stimulation over MT, indicating a role for MT in the SMAE. Théoret et al. (2002) applied rTMS over MT during a storage period in between MAE adaptation and testing. Stimulation shortened the duration of the subsequent MAE, compared to the No-TMS condition. There was little effect of stimulation to V1 on storage. In a second experiment rTMS was applied to MT during perception of the MAE, and was found to reduce MAE duration, but stimulation to DLPFC and to posterior parietal cortex had no effect on aftereffect duration. It should be noted, however, that Théoret et al. (2002) used complex radial/rotational stimuli. Therefore, it is not surprising that they found a specific involvement of the MT complex. Antal et al. (2004) used a relatively new technique, namely transcranial direct current stimulation (tDCS), to explore the role of MT in MAEs. They found that stimulation of MT significantly decreased MAE duration. However, the authors argued that the negative results over area V1 and the adjacent posterior occipital areas do not necessarily imply that area V1 is not involved in the MAE. Since their adaptation stimulus was placed outside the fovea, the neural representation of the adaptation stimulus was expected to be not in the occipital pole but more anterior along the calcarine sulcus in the ventral surface of the occipital lobe. Therefore, the lack of the tDCS effects on the MAE strength as a result of occipital pole stimulation might be due to the fact that tDCS was unable to reach the neural representations of the adapting and test stimuli in our experimental conditions (Antal et al., 2004). Overall, TMS and tDCS studies clearly implicate MT in the MAE, but the role of other areas cannot be excluded.

3.4 VEPs and MEG

Which components of the VEP reflect activity related specifically to the MAE? Human electrophysiological studies have shown that the amplitude of a negativity peak at ~200 ms (N2) is affected by motion adaptation (Bach & Ullrich, 1994), but it is not clear whether this effect is direction selective. More recently, Kobayashi et al. (2002) found a significant bilateral increase of a positive component at ~160 ms (P160) in the occipitotemporal region after motion adaptation. They also observed a laterally biased effect in the right posterior temporal region, perhaps related to the engagement of attentional circuits. Neural gamma-band activity (GBA, high-frequency neural activity in the range 40–100 Hz) seems to be associated with synchronization among different brain regions, which is thought to be important for visual feature binding and motion perception (Rose & Buchel, 1994). Tikhonov et al. (2007) investigated GBA associated with the MAE using MEG (a non-invasive technique used to measure magnetic fields generated by the electrical activity in neurons). Adaptation and test patterns were presented either in the right or left visual hemifield. Results showed GBA reflecting the MAE in channels over two locations (indicating the presence of two dipole sources), providing evidence that MAE depends on the synchronization of different brain regions. The first location was in parieto-occipital cortex (in the region of area MT). The second location was more posterior, but it was not possible to precisely locate the origin of this source. Two possibilities discussed were striate cortex and the cerebellum.

4. Conclusions

4.1 A Global framework of the motion aftereffect

Figure 3.5 is a simple functional diagram that attempts to summarize the main stages of visual motion processing from the perspective of the motion aftereffect research reviewed here. Motion sensors in the earliest cortical areas (V1, V2 and V3) feed into a computation underlying the perception of ‘static’ and also into a local motion integration stage. First-order motion sensors tuned to slow velocities contribute to ‘static’ computations, whereas first-order sensors tuned to higher velocities and second-order sensors both feed into motion integration. Thus, adaptation in sensors contributing to the static computation leads to the SMAE, adaptation in sensors contributing to motion integration leads to a DMAE, probably in area MT. Adaptation of cells involved in computation of optic flow in area MST mediates phantom MAEs. Attention mediated motion aftereffects and subjective awareness of motion aftereffects involve more anterior cortical areas such as parietal and cingulate cortex. The varieties of motion aftereffect reviewed here tend to be regarded as a cognate group of effects but this framework highlights the fact that, in functional terms, they are distinct and separate. The SMAE, for example, involves an entirely different population of neurons and separate computations from those involved in phantom MAEs, in the same way that the tilt aftereffect involves different processes from those underlying the size aftereffect.

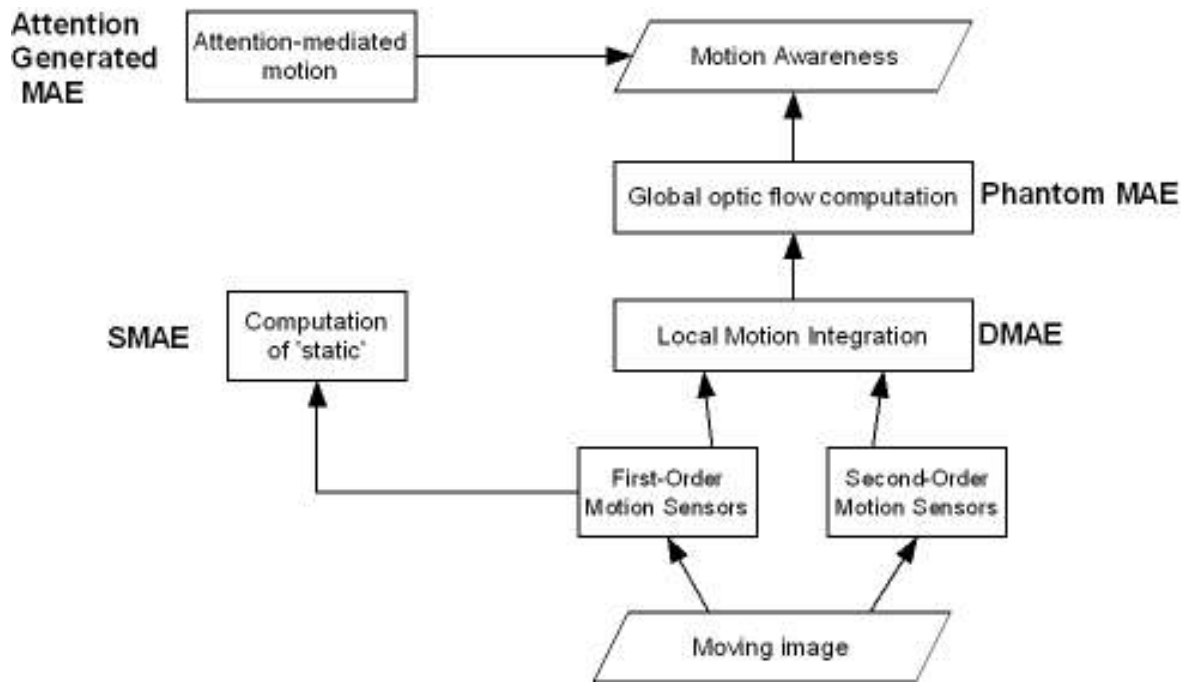


Figure 3.5. Functional diagram relating the main stages of motion processing in the human brain to MAE adaptation sites. SMAEs are mediated by motion sensors that contribute to computation of ‘static’, whereas DMAEs are mediated by motion sensors that contribute to motion integration computations. Phantom MAEs involve sensors contributing to the computation of optic flow.

4.2 Where do SMAEs and DMAEs arise?

One can infer from Kohn and Movshon’s (2003) single-unit recording study that the SMAE reflects adaptation-induced changes in the response of first-stage cells in V1, whereas the DMAE reflects changes in the response of second-stage MT neurons that receive opponent inputs from V1 cells. The psychophysical study of Morgan et al. (2006) supports this inference. They argue that SMAEs represent a shift in the population response of cells tuned to relatively slow velocities (we see ‘static’ when the outputs of low velocity units are balanced), whereas DMAEs arise from adaptation-induced disinhibition in higher level cells tuned to higher velocities (Verstraten et al., 1999). Why do some adapting stimuli, such as second-order patterns, only

produce aftereffects on dynamic tests? Perhaps the cells activated by such stimuli are not themselves involved in the computation of ‘static’, so an adaptation-induced imbalance does not lead to a SMAE, but their responses nevertheless feed forward to influence later motion computations and cause DMAEs.

4.3 What is the mechanism and function of adaptation?

Adaptation can be viewed as a form of automatic gain control, in which a unit attenuates its own response to continuous intense stimulation. Van de Grind et al. (2003, 2004) developed a detailed computational model of MAE adaptation that uses divisive feed-forward inhibition as the gain control mechanism. During adaptation, a leaky integrator in the gain control circuit of active cells charges up, and during testing the charge leaks out to cause an imbalance in output between adapted and unadapted units. The results of psychophysical experiments conducted by van de Grind and colleagues were consistent with their model. Other psychophysical (Morgan et al., 2006) and electrophysiological (Kohn & Movshon, 2003) results are also consistent with this kind of gain control mechanism. What function does gain control serve, and why should it be present at several different sites in the processing hierarchy? One idea is that gain control improves the efficiency of encoding by striving to maximize the information about the stimulus conveyed in neural spike trains (Brenner et al., 2000). Visual motion analysis involves the transmission of information between multiple processing stages. Gain control at each stage of transmission should serve to optimize the efficiency of coding in the system as a whole. According to this view, there should be as many sites of adaptation for MAEs as there are processing stages in the motion analyzing system.

Chapter 4

Motion-induced position shift

1. Introduction

Apparent motion influences the perceived position of an object. A vast number of studies have shown that when observing a moving object, its position appears shifted in the direction of motion (Chung, Patel, Bedell, & Yilmaz, 2007; De Valois & De Valois, 1991; Durant & Johnston, 2004; Edwards & Badcock, 2003; Fang & He, 2004; Fu, Shen, Gao, & Dan, 2004; Harp, 2007; McGraw, Levi, & Whitaker, 1999; Mussap & Prins, 2002; Nishida & Johnston, 1999; Ramachandran & Anstis, 1990; Snowden, 1998; Whitaker, McGraw, & Pearson, 1999; Whitney, 2002; Whitney & Cavanagh, 2000; Whitney & Cavanagh, 2003; Zanker, Quenzer, & Fahle, 2001). For instance, when a flashed object and a moving object appear in the same location, they are perceived to be offset from one another such that the flashed stimulus is lagged with respect to the moving object. This is known as the flash-lag effect, for a review see Nijhawan (1994). A possible explanation of this effect was provided by Krekelberg et al. (2000). They hypothesized that the offset between two objects perceived at a particular instant is given by the average of the difference of the two position signals over a *time window*. In the *time window* the flashed object is hidden whilst the moving object is visible across all positions. In the absence of an updated position signal an integration mechanism will resort using the last visible and available position of the flashed object.

The flash-lag effect plus several other phenomena in which motion influences the perceived position of a stationary object (Snowden, 1998; Nishida & Johnston, 1999; Whitney, 2002;

Bressler & Whitney, 2006) suggest the presence of interactions between visual areas that encode and possibly integrate motion and position.

2. Spatial and temporal properties of a Motion-induced position shift

A number of studies assessed the spatiotemporal tuning of the illusory motion-induced position shift (MIPS), testing the influence of moving patterns (e.g., dynamic random dots or drifting gratings) on the perceived position of stationary objects (Arnold & Johnston, 2005; Bressler & Whitney, 2006; De Valois & De Valois, 1991; Durant & Johnston, 2004; Fu et al., 2004; McGraw, Whitaker, Skillen, & Chung, 2002; Mussap & Prins, 2002; Shim & Cavanagh, 2004; Sundberg, Fallah, & Reynolds, 2006; Watanabe, 2005; Whitaker, McGraw, & Pearson, 1999; Whitney, 2005; Yokoi & Watanabe, 2005). DeValois and DeValois (1991), using first-order Gabor patches with sine-wave carriers drifting in opposite directions showed that the perceived position of the stationary Gaussian window was shifted in the direction of the sinewave carrier's motion. In particular, the bias was greater at temporal frequencies ranging from 4 to 8 Hz and for low spatial frequencies (1 c/deg). However, the authors found that the directional bias was not directly proportional to the pattern velocity. Moreover, they found that the positional shift increased rapidly with retinal eccentricity (about 15 arcmin at 8 deg eccentricity).

However, recent findings do not support the results of De Valois and De Valois (1991) that MIPS is not proportional to velocity. Bressler and Whitney (2006), indeed, showed that the magnitude of the illusory MIPS for drifting first-order Gabor patches increases with increasing velocity, even if the peak effect at higher velocities occurred only for the lower spatial frequency employed (0.18 c/deg). Adapting to first-order drifting Gabor patterns, McGraw et al. (2002) showed that MIPS increased with an increasing carrier drift velocity, until reaching a plateau at

approximately 1 deg/s. Moreover, they found that varying the spatial frequency between adaptation and test patterns (up to two octaves) the magnitude of the positional shift was unchanged, showing that first-order MIPS shows little if any spatial frequency tuning. Despite the results of DeValois and DeValois (1991), McGraw et al. (2002) reported that the magnitude of the illusory MIPS does not depend on the spatial frequency, implying that the MIPS might depend on the velocity of the carrier. Chung et al. (2007) used Gabor patches presented at different durations, velocities and levels of eccentricity. They found that the MIPS increased monotonically as the velocity of the drifting carriers increased. Moreover, confirming the findings of De Valois and De Valois (1991), the magnitude of the positional shift was approximately three times higher for the more eccentric stimuli. However, the rate of change of the MIPS with velocity was not the same across stimulus duration. In particular, for stimulus durations of about 100 and 450 ms, the perceived position shift reached a plateau at a velocity of approximately 1 deg/s. In contrast, for brief stimulus duration (e.g., 50 ms), the magnitude of the MIPS increased continuously across the velocities tested. Thus, producing evidence that velocity influences temporal properties of the illusion. Consequently, Arnold and Johnston (2005) found that MIPS increases monotonically as a function of the stimulus duration at lower velocities. In addition, as the velocity of the carrier grating increases, the magnitude of the MIPS grows most quickly for stimuli of short duration. In particular, Chung et al. (2007) found that at 16 deg/s the MIPS reaches a steady-state value when the stimulus duration is approximately 100 ms. These findings suggest the presence of specific velocity tuned channels that play a relevant role in mediating the first-order motion-induced position shift (Burr, 1979; Burr & Ross, 1982, 2002; Burr, Ross, & Morrone, 1986; Fahle & Poggio, 1981; Geisler, 1999; Morgan, 1976, 1980; Nishida, 2004).

In addition to velocity tuning, McGraw et al. (2002) showed, using a motion-adaptation paradigm, that MIPS is relatively insensitive to changes in contrast of either adaptation or test

patterns. Indeed, despite noticeable variations in the contrast of the adapting pattern with respect to that of the test and vice versa, the magnitude of the MIPS showed no significant change. Similarly, changing the orientation of the adapting stimulus relative to that of the test pattern (i.e., when the orientation of the adapting stimuli was parallel respect to that of the test or orthogonal) does not influence the magnitude of the MIPS. McGraw and colleagues (2002) also found that the positional shift transferred almost perfectly when the adapting stimulus is presented to one eye and the test stimulus to the other, suggesting that motion and position are combined after binocular integration of the inputs from each eye. Moreover, it seems that the positional shifts resulting from motion adaptation show different characteristics from those of the traditional MAE. For example, static MAE is tuned for a many visual features such as orientation, spatial temporal frequencies, contrast and so on. Nevertheless, the magnitude of the MIPS remains relatively unchanged despite the introduction of marked differences between adapting and test stimuli for each of these dimensions. One possibility is that motion-induced positional shifts are mediated by a different type of motion aftereffect (McGraw et al., 2002).

Bressler and Whitney (2006) have shown that drifting second-order Gabor stimuli shift the perceived position as well, even though with a different temporal tuning respect to first-order stimuli. In particular, they found that second-order motion shifts the perceived position over a narrow range of temporal frequencies, peaking at about 4 Hz. In addition, their data suggest that the effect does not vary as a function of spatial frequency, or at least the tuning is very broad. However, in contrast to the previous studies, they found that first-order motion influenced the spatial position over a narrow range of spatial frequency, preferring low spatial frequencies. However, it should be noted that Bressler and Whitney (2006) presented their stimuli at a very large eccentricity of 10.1 deg. It has been shown that at high eccentricities first- and second-order motion show a different spatiotemporal tuning than when they are presented in fovea or at lower eccentricities, thus it is possible that the differences found between the different studies are

due to the different eccentricities used (Pantle, 1992; Smith, Hess, & Baker, 1994; Solomon & Sperling, 1995; Wang, Hess, & Baker, 1997).

In addition, because of the narrow temporal frequency tuning of the second-order MIPS, it exists only for low velocities. These data suggest that the temporal frequency dependence of the second-order MIPS is band-pass, whereas first-order MIPS shows a more high-pass temporal frequency dependence.

The time dependence of the MIPS has been pointed out by Arnold and Johnston (2005). They showed that motion distorts the form of the object changing the apparent contrast of the edges of a Gabor pattern (Whitney et al., 2003; Arnold & Johnston, 2005; Whitney & Bressler, 2007); the changes in form and position increase linearly with stimulus duration.

Generally, these findings suggest that motion mechanisms can encode and integrate form, motion and position. Moreover, the presence of different spatiotemporal tunings found for first-order and second-order motion further suggest the presence of separate and independent motion-detecting mechanisms that encode and assign the spatial position of a moving object.

So far, the most important finding relative to the MIPS have been reviewed. The following sections will take into account some possible explanations and the neural substrates underlying this motion illusion.

3. Contribution of high and low-level motion processes to the perceived position

The different spatiotemporal tunings for first- and second-order MIPS outlined in the previous section suggest the involvement of different levels of motion processing in which position, form and motion are integrated. For example, Bressler and Whitney (2006) argued that the narrow temporal frequency tuning for second-order MIPS is compatible with the range of temporal

frequencies over which the attention is deployed. Seiffert and Cavanagh (1998, 1999), found that second-order pattern are tracked by a position-sensitive mechanism sensitive to low contrast and low speeds. This suggests that the positional shift induced by second-order motion could be due to a slow attentional mechanism.

A number of studies using high-level motion (i.e., when the percept of motion is driven by top-down processes and there is no physical motion) have shown the involvement of attentional processes in the MIPS. Shim and Cavanagh (2004) measured the motion-induced position shift with a bistable quartet and found a shift in position for flashed stimuli in the direction of the perceived motion of the bistable stimuli. Such a result indicates that high-level motion processes that resolve ambiguity can produce a position shift in stationary objects (Shim & Cavanagh, 2004).

Moreover, another recent study has shown that high-level mechanisms can modulate the magnitude of the motion-induced position shift. Watanabe (2005) found that suppressing a moving stimulus with binocular rivalry and thereby abolishing the awareness of the motion of the stimulus, eliminates or at least strongly reduces the shift in position.

Although top-down processes influence the perceived position of a moving object (Shim & Cavanagh, 2004; Whitney 2006), and second-order motion may be processed by such mechanisms, recent studies have shown that the awareness of first-order motion is not necessary to shift the perceived position. Whitney (2005) found a reliable shift in position after a period of adaptation to a crowded display (He et al., 1996). A crowded display consists of an array of drifting Gabors for which the motion directions are randomly chosen trial by trial, except for two Gabor patches placed in a certain location into the array and always drifting in opposite direction. In such display subjects are unaware of the two opposite drifting Gabor patches. The positional shift observed by Whitney (2005) with this paradigm was relatively stable across different spatial frequencies, replicating the previous findings of McGraw (2002). This

demonstrates that passive luminance-based motion detectors can code position without the involvement of top-down processes. These findings show that both top-down and bottom-up processes can influence the perceived position of a first-order moving object.

However, it is still unclear if second-order MIPS is mediated exclusively by top-down processes, such as attentive tracking (Shim & Cavanagh, 2004), or can be obtained without awareness of motion. Harp and colleagues (2007) tried to assess this issue using a crowded display (He et al., 1996) of drifting contrast-defined, second-order Gabor patches. The subjects were adapted to two opposite drifting second-order Gabors placed in different regions inside an array of second-order Gabors for which the directions were randomly chosen trial by trial. As well as in the study of Whitney (2005) the subjects were unable to discriminate the motion direction of the Gabors presented within any of the adapted regions. The results showed a reliable position shift of the test patterns for the crowded conditions. Moreover, Harp et al. (2007), in a secondary experiment, found that the net global motion, normally present in a crowded display, can produce a local shift in position even at an unadapted location. These results suggest that: (i) even in the absence of awareness, local adaptation to second-order motion can shift the perceived position of an object. That is, the assignment of the position can occur passively without top-down attention or awareness also for second-order patterns. (ii) The perceived position of second-order patterns might depend on a mechanism that pools second-order motion over a relatively large region and this spatial summation does not depend on awareness of motion direction. This could be due to passive (i.e., not relying on feature- or position-tracking mechanisms) second-order motion processes, probably based on global second-order motion detectors that operate over relatively large distances (Harp et al., 2007).

Generally, the different spatiotemporal tunings found for first- and second-order moving patterns suggest the presence of multiple motion detectors that encode and assign the spatial position of a moving object. Moreover, the findings that both low and high-levels can influence and modulate

the perceived position of a moving stimulus, suggest that the assignment of the location might depend on multiple motion pathways, and may occur at multiple stages. Bressler and Whitney (2006) argued that position coding might be subserved by different mechanisms or levels along the visual hierarchy, since the position information is represented at multiple levels of the visual system. Indeed, as reported previously, many visual areas maintain a retinotopic organization, such redundancy could be relevant for a more efficient coding of visual information (e.g., visual binding). Moreover, redundant position coding suggests the presence of independent perceptual access to position information at multiple stages, and this could explain why many different types of visual motion can influence the perceived position, but each with specific spatiotemporal tunings (Bressler & Whitney, 2006).

4. Neural substrates of the Motion-induced position shift

A number of electrophysiological and neuroimaging studies attempted to shed light on the neural basis of the illusory MIPS. Berry et al. (1999) recorded many rabbit's OFF ganglion retinal cells in order to assess whether processing in the retina contributes to the flash-lag effect. In particular, they found that when a black bar is flashed over the receptive field centre of OFF-type ganglion cells, they remain silent for 40 ms then a hump of activity appears that peaks at about 60 ms, vanishing at about 100 ms, corresponding to the bar (Figure 4.1A). Conversely, the hump of activity of a continuously moving bar appeared ahead respect to the centre of the bar, peaking near the bar's leading edge. The results showed that the peaks of activity of the flashed and the moving bars were clearly offset, with the response of the moving bar about 100 μm ahead in the direction of motion (Figure 4.1B). The authors argued that this apparent anticipation of the moving bar is due to the presence of cells ahead of the bar that start to fire early, when the bar

begins to enter into the centre of their receptive field. Moreover, they found that the position of the peak activity is strictly dependent on the contrast of the stimulus where at low contrast the peak in firing occurred behind the bar's leading edge, and at very high contrast the peak of the profile was ahead of the leading edge.

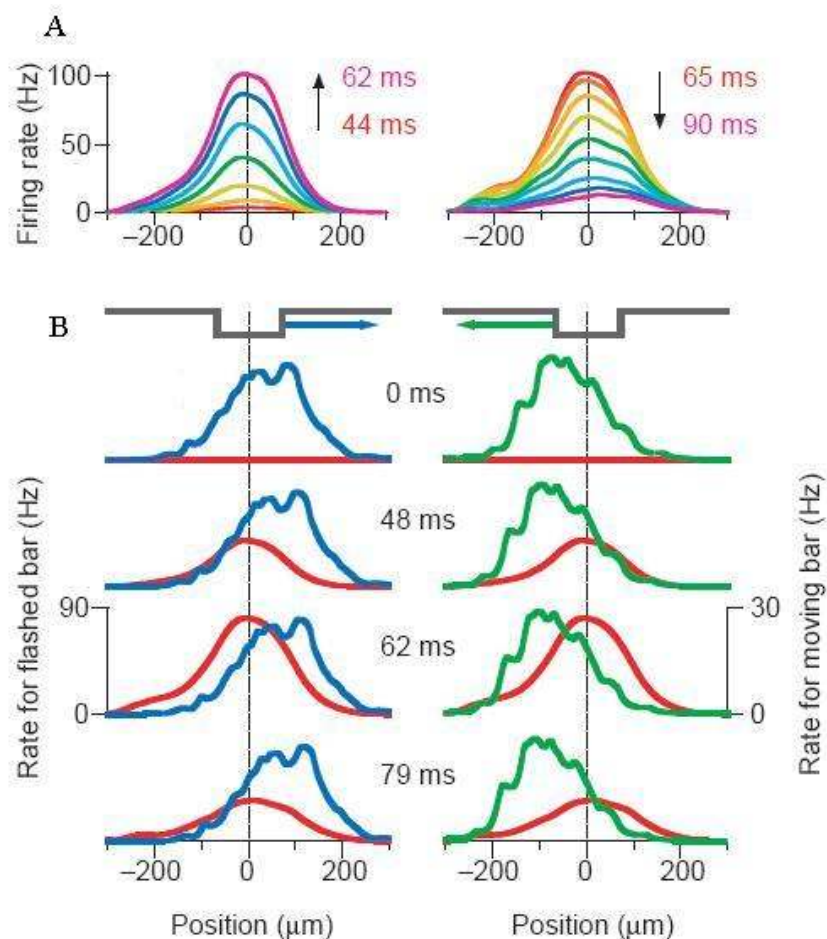


Figure 4.1. Responses to flashed and moving bars. A. Firing rate of OFF ganglion cells in response to a flashed dark bar (see the stimulus profile in the upper part of B) at a series of times after the flash. B. Profile cell's response at four time points following a flashed bar (red lines, from A), and the same bar travelling at 0.44 mms^{-1} rightward (blue) and leftward (green). At 0 ms, the moving bars were aligned with the position of the flash. At 62 ms the flash response was maximum, the peaks of activity of the flashed and the moving bars are offset. Curves in A and B derived from 15 cells (Adapted from Berry et al., 1999).

Thus, when the bar's leading edge enters into the centre of the receptive field of a ganglion cell placed ahead of the bar and the contrast of the bar is high, the cell is strongly excited, but then its response gain is reduced and the cell's activity declines even before the edge is crossed through the receptive field. Such modulation mechanism is called "contrast-gain control" (Shapley & Victor, 1978; Sakai, Wang, & Naka 1995; Benardete, Kaplan, & Knight, 1992). In alignment with this explanation the authors found that if the velocity of the moving bar was high enough to avoid the set of the contrast-gain control, the peak activity lagged behind the leading edge. Anticipation of a moving object can be explained by the coexistence of at least three retinal factors: (i) the presence of spatially extended receptive fields, (ii) a biphasic temporal response, (iii) a contrast-gain control mechanism. Such retinal mechanisms contribute strongly to human motion perception and seem to provide the early neural basis of the positional shift (Berry et al., 1999).

However, Whitney et al. (2003) showed that the position of a moving object in the visual cortex is not simply shifted toward its motion direction, other mechanisms look like they are involved, and are different to those described by Berry et al. (1999) at the retinal level. By conducting an fMRI experiment they tried to assess whether positional shift is reflected by neural activity in the human visual cortex. In particular, they used Gabor patterns containing motion toward or away from the fovea (Figure 4.2C, D). The results show distinct regions of activation for inward and outward motion. When the activation of outward motion was subtracted from inward motion (Figure 4.2C) there was significant extrastriate activation, whereas subtracting the two conditions in the reverse order (Figure 4.2D) produced activation near the occipital pole. Patterns that contained inward motion and perceived to be closer to the fixation point (i.e., closer to the fovea) originated an activity which peak was more eccentric in the visual cortex (orange activity in Figure 4.2B). The pattern of activation obtained by Whitney et al. (2003) (Figure 4.2B) is counterintuitive as many studies have shown that a more eccentric stimulus gives rise to activity

in further anterior regions in the cortex (Daniel & Whitteridge, 1961; Sereno et al., 1995; Tootell, et al., 1982; Tootell, et al., 1998). Indeed, a control experiment in which flickering Gabor patches were presented at two different eccentricities showed that when the patterns were located closer to the fovea, the peak activation was closer to the occipital pole, alternately, when flickering patterns were placed at greater eccentricities, the peak activation was located in a more eccentric position (Figure 4.2E). These findings show a “reversed retinotopy” where motion biases the perceived position of the drifting Gabor patches in a particular location of the visual field, but these locations are represented in different regions of the visual cortex.

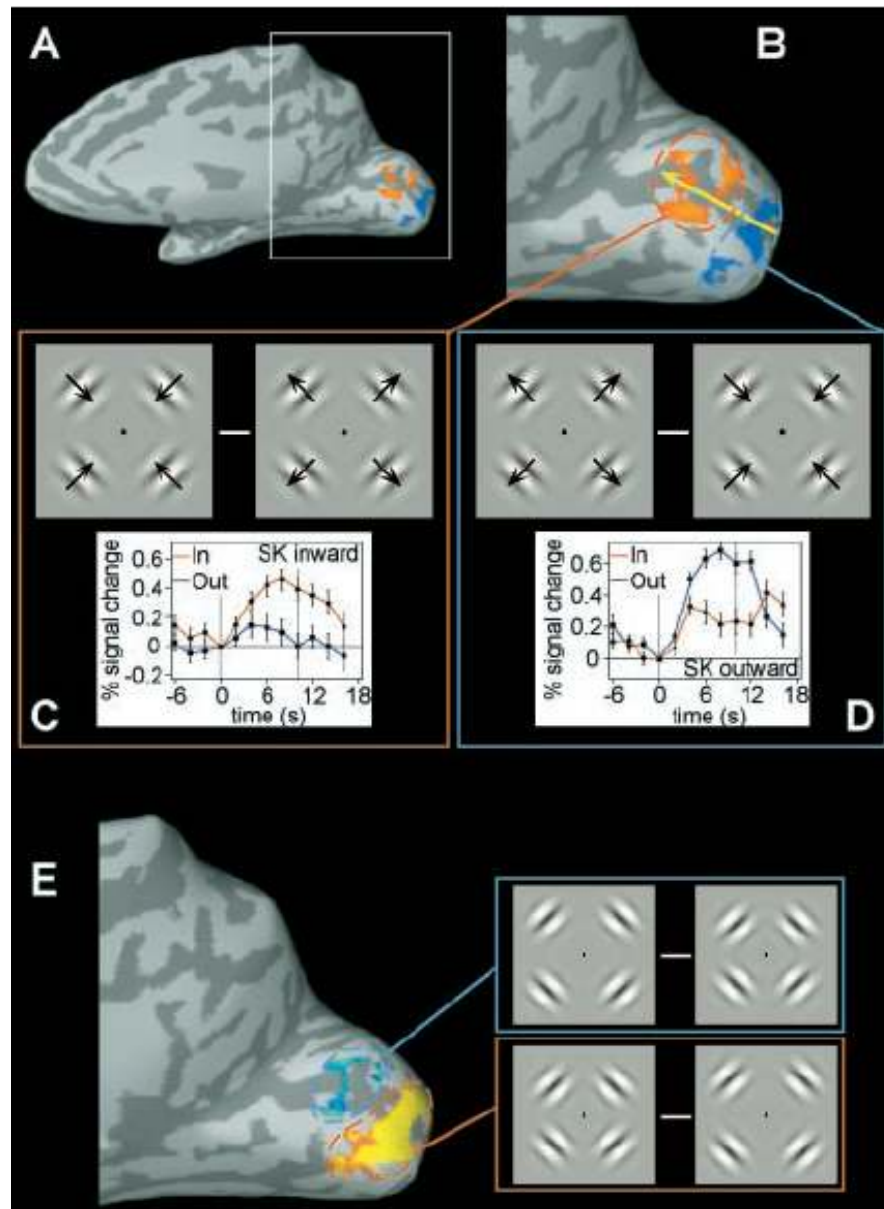


Figure 4.2. A. The cortical surface of the right hemisphere, showing the occipital region. B. An expanded view of the same surface. The yellow arrow indicates an increase of the eccentricity in the visual field. C. When the two experimental conditions were subtracted (inward motion minus outward motion) there was a significant resulting activation (orange line). The chart in the lower panel of (C) shows the event-related average for inward and outward motion for the voxels that were significantly activated [orange activity in (B)] by this subtraction. D. When the two conditions were subtracted in reverse order (outward minus inward), there was another significant activation (blue line). The chart in the lower panel of (D) shows the event-related averages for the voxels that were significantly activated by this subtraction [blue activity in (B)] (see text for more details). E. The results of a control experiment using flickering patterns. When

flickering patterns were closer to the fovea, activation was more posterior, whereas flickering patterns presented more eccentrically produced a more anterior activation (Adapted from Whitney et al., 2003).

Moreover, they found that the peak of activation occurred in correspondence with the trailing edge of the patterns (i.e., at the origin of the motion). Many studies have shown that when an object moves, it produces a motion smear (Burr, 1980; Geisler, 1999) which is removed by a deblurring mechanism to render clear the percept. It is likely that the activity measured by Whitney and colleagues (2003) is related to deblurring processes that operates more strongly on the trailing edges of the moving objects. According to this explanation the authors found that the trailing edge was less visible in terms of contrast with respect to the leading edge of the patterns due to a compression of the apparent size of the Gabor patches. The results showed that the trailing edge of the pattern was perceptually shifted (or compressed) in the direction of motion more than the leading edge. To some extent, these results explain why the perceived positions of the patterns appeared to be shifted in the direction of motion. Since the contrast of the trailing edge is perceptually reduced, the midpoint of the whole pattern appears displaced toward the leading edge.

Fu et al. (2004) further investigated the mechanisms and the neural substrates underlying the MIPS. In particular they examined two types of MIPS; type I, when a motion signal within a stationary envelope (i.e., Gabor patch) induces a bias in the perceived envelope position toward the motion direction, and type II; the positional mislocalization obtained adapting, for example, to a drifting Gabor. In this latter case adaptation causes not only an illusory movement of the object in the opposite direction (MAE – see Chapter 3), but also a positional shift of the object.

The authors recorded the activity of complex cells from cat striate cortex. In particular, they examined the effect of motion signal on cortical RFs using stationary strips containing drifting gratings (Figure 4.3A). For each drift direction, the RF was measured by the neuronal response as a function of the strip position. As shown in Figure 4.3B, Fu et al. (2004) found an effect of motion signal on the measured RF position, with the RF displaced in the direction opposite to grating motion. Moreover, adapting for 1 min to directional motion the authors found a shift of the RFs in the direction of adaptation. What are the mechanisms underlying these effects of motion on RF position? The authors showed that motion signals differently influence the two sides of the RF, for example, rightward motion tend to enhance the response on the left side of the RF resulting in a leftward displacement of the RF and vice-versa for leftward motion. This suggests the presence of an asymmetry in the spatial distribution of the direction-selective inputs to the cortical neuron, with, for example, a leftward bias of the excitatory inputs preferring rightward motion.

Moreover, the RF shift in the adaptation direction could require short-term modification of the inputs in a spatially asymmetric manner. Adaptation selectively reduces the excitability of the presynaptic neurons preferring the same direction. This reduction in excitability has been shown for direction-selective neurons in V1 (Marlin et al., 1988), so the RF of a certain neuron should shift in the adaptation direction.

The effects of motion on RF position found in the study of Fu et al. (2004) support the asymmetric circuit model. Although, it is not clear which neurons provide the direction selective inputs in such asymmetric circuit. Good candidates could be the direction-selective cells present in V1. It has been shown that a spatial asymmetry in the intra-cortical connections from these cells may arise naturally from spike timing-dependent plasticity (STDP), a phenomenon present at the local excitatory connections in the visual cortex (Sjostrom et al., 2001; Froemke & Dan, 2002).

In STDP, the direction of synaptic modification depends on the relative timing of presynaptic and postsynaptic spikes. Presynaptic spiking occurs within tens of ms before postsynaptic spiking induces synaptic potentiation, whereas spikes in the reverse order result in synaptic depression (Markram et al., 1997; Bi & Poo, 1998). Consider a simple neural circuit in which a target neuron receives excitatory inputs from other neurons preferring rightward or leftward motion. For the neurons preferring rightward motion, a rightward moving object causes the neurons on the left to spike before the target neuron and those on the right to spike with a certain delay. Due to STDP, such a spiking pattern strengthens the rightward inputs from the left and weakens those from the right. The authors suggest that such asymmetric circuit could account for the RF properties that cause type I and type II MIPS.

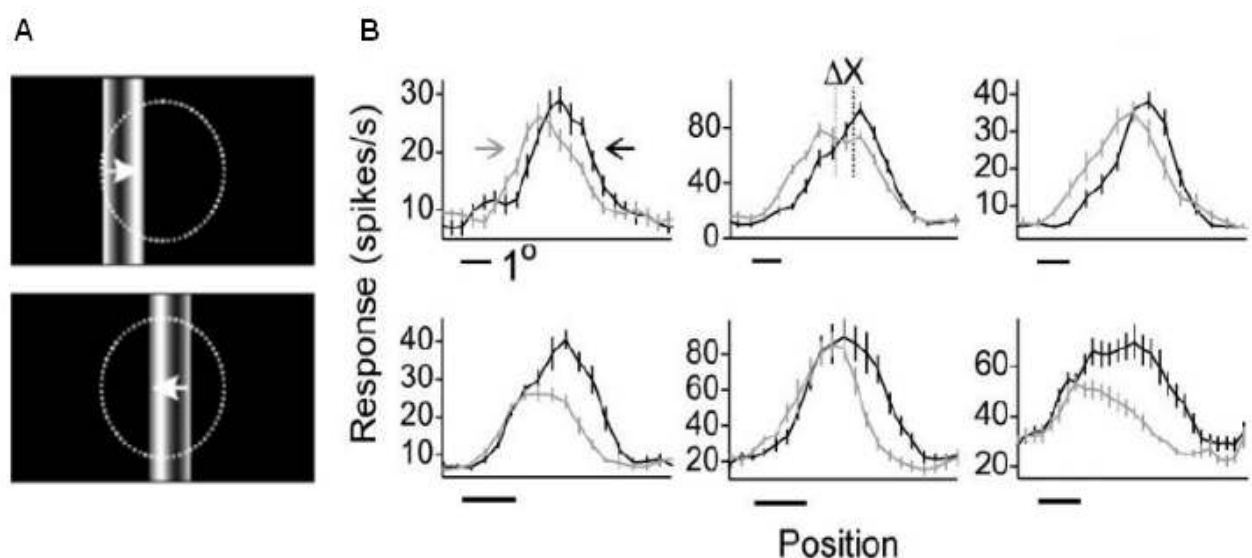


Figure 4.3. A. Test stimuli used for mapping cat RFs. White arrows indicate the grating's motion direction inside the strip. Dotted circles represent the RF. B. Responses of six neurons recorded in cat visual cortex stimulated with either rightward (gray line) or leftward (black line) motion. The cells recorded prefer leftward motion. Error bars indicate SEM. Dotted vertical lines indicate peak position of the Gaussian fit. ΔX represents the distance between the gray and black dotted lines. For all six cells ΔX resulted significantly different from zero (Adapted from Fu et al., 2004).

The research reviewed above, reveals that visual illusions involving the interaction between motion and position can be divided into two categories. The first category in which perceptual mislocalization of an object is caused by translational motion of the whole object (Frohlich, 1929; Nijhawan, 1994; Fu et al., 2001) can be explained by mechanisms such as temporal integration (Lappe & Krekelberg, 1998), or the presence of mechanisms such as biphasic temporal responses and contrast-gain control (Berry et al., 1999; Fu et al., 2001). In the second category, the perceptual shifts do not depend on translational motion of the whole object (Ramachandran & Anstis, 1990; De Valois & De Valois, 1991; Snowden, 1998; Nishida & Johnston, 1999; Whitaker et al., 1999; also see Whitney & Cavanagh, 2000), and cannot be explained by the same mechanisms (Whitney, 2002).

The receptive field properties reported by Fu et al. (2004) are likely to contribute to the MIPS. However, the spatially asymmetric connections may also be present in other cortical areas containing direction-selective neurons (e.g., MT), which has been shown to further contribute to the motion-induced perceptual mislocalization. Indeed McGraw et al. (2004) using a motion adaptation paradigm found that area MT is involved in modulating the positional representation of objects presented after the adaptation period. They disrupted the MT cortical activity in human observers using transcranial magnetic stimulation (TMS) immediately after motion adaptation. When TMS was delivered to MT the perceived misalignment of the test stimulus was greatly reduced, suggesting the involvement of MT in the MIPS.

Taken together these results suggest that motion signals might be relayed through reentrant input from high to low-levels cortical areas, indeed, anatomical pathways connecting motion area MT with lower cortical areas have been described in detail by Shipp and Zeki (1989). Thus, the receptive properties found in the primary visual cortex can account partly for the two categories of illusory motion-induced position shift (Fu et al., 2004). However, other studies are necessary to clarify the relationship between the neuronal responses found in electrophysiological studies,

the blood oxygen level-dependent signal measured in fMRI and the pattern of results found in transcranial magnetic stimulation studies.

5. A comprehensive model of Motion-induced position shift

A property of the MIPS obtained with drifting patterns enveloped by a stationary window, is that it occurs only when the stationary window has sufficiently blurry edges, and is almost absent when the edges of the window are sharp (Whitney et al., 2003). Arnold and Johnston (2005) found that the central part of a drifting Gabor is not shifted, despite a substantial illusory MIPS of the Gabor as a whole. A receptive field shift, as proposed by Fu et al. (2004), should cause a perceived shift in the entire spatial extent of the drifting stimulus. However, recent work has pointed out the possibility that the illusory shift of a stationary object, such as the envelope of a drifting Gabor, may result from an interaction between motion processing in areas MT and the representation of the spatial location of the stimulus in early cortical areas such as V1 and V2 (McGraw et al., 2002; Nishida & Johnston, 1999; Snowden, 1998; Watanabe, 2005). However, the nature of these interactions has not described adequately yet.

Recently, Whitney et al. (2003), Arnold and Johnston (2005) and Tsui et al. (2007) showed that, during motion, the perceived contrast of a Gabor patch increases at its leading edge (where the motion ends) and decreases at its trailing edge (where the motion starts). These studies, however, did not propose a specific mechanism to account for the observed modulations of perceived contrast at the leading and trailing edges of the stimulus. For this reason Chung and colleagues (2007) reported a formal model to show how the MIPS and its phenomenal properties can be explained on the basis of the motion-dependent modulation of perceived stimulus form. [Figure 4.4](#) shows how the perceived position of a stationary Gaussian window is shifted due to drifting

motion of its sinewave carrier. Chung et al. (2007) argued that when the carrier drifts, the envelope attenuates, across space, the amplitude of the *temporal luminance modulation* in the sinewave carrier. However, in their model the temporal frequency of the drifting carrier remains constant across all spatial locations within the envelope (Chung et al., 2007).

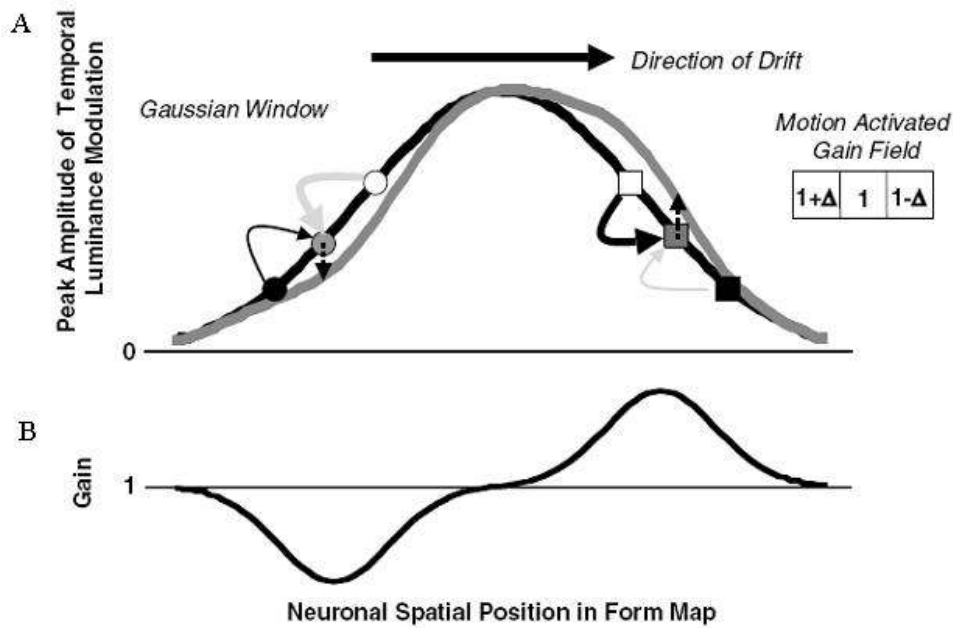


Figure 4.4. A motion-activated gain field involved in generating the MIPS. A. The figure shows the role of a motion activated gain field (e.g. inset at top right) on the peak amplitude of temporal luminance modulation at various spatial position in the form map (see text for more details) produced by a drifting sinusoidal carrier (thick black curve) windowed by a stationary Gaussian. The long arrow at the top represents the drift direction. The small curved arrows represent the gain control that a single neuron receives from its neighbors. The thickness of the arrow represents the magnitude of the gain control. Black arrows represent gain-increase (amplification) signals while gray arrows represent gain-decrease (attenuation) signals. Two example locations are illustrated: one within the leading (filled gray square) and another within the trailing (filled gray circle) half of the drifting Gabor stimulus. The thick gray curve illustrates the distortion of the luminance modulation following the activity of the gain fields and consequently the shift in centroid of the activity pattern, which leads to a shift in the perceived position of the drifting Gabor stimulus in the direction of motion. B. Profile of the gain control of the neurons in the form map. Gains are lower than unity within the trailing half of the drifting

stimulus. The gain is minimum near the spatial regions where the slope of the Gaussian window of the drifting Gabor is steepest. Conversely, the gains are close to unity near the spatial regions where the slope of the Gaussian window of the drifting Gabor is close to zero (Adapted from Chung et al., 2007).

The authors assume that the luminance profile of a Gabor stimulus is encoded in a *form map* by an array of retinotopically arranged neurons and that the gains of these neurons are modulated by signals from neighboring neurons dependently on the motion direction of the pattern. Moreover, they assume the existence of a *motion map* (not reported in Figure 4.4) in which motion signals are retinotopically arranged. Such motion signals activate the direction-dependent interactions between units in the form map (Chung et al., 2007). Moreover, Chung et al. (2007) defined the spatial distribution of gain-control signals, generated in correspondence of each neuron in the form map by its neighbors as the *motion-activated gain field* of that neuron; a gain-field interaction has the function to modulate the neuron's activity of a certain neuron.

More specifically, a rightward drifting stimulus produces a motion-activated gain field, in such case, a neuron in the form map receives a signal to increase or decrease its gain from neighboring neurons that are retinotopically to the left or right. The gain-increase signal is a signal that prepares the neurons in the form map to respond to an incoming moving stimulus, in order to increase the speed of the response. On the other hand, the gain-decrease signal has the function of quickly removing persisting signals in the form map in order to avoid residual signals from an object that has moved to another location on the retina (Bex, Edgar, & Smith, 1995; Chen, Bedell, & Ogmen, 1995; Purushothaman, et al., 1998). Chung et al (2007) argued that when gain-increase and gain-decrease signals are combined, a motion-activated gain field can improve both the spatial and temporal resolution of the visual system in representing the form of a moving stimulus. On the other hand, when a drifting carrier is enveloped by a stationary

window, both types of interactions are activated simultaneously at a single retinotopic location (Figure 4.4A). Such simultaneous activation can distort the perception of the form of the windowed pattern.

Thus, in which way can the motion-activated gain fields explain the MIPS and its properties for windowed drifting stimuli? For a Gabor pattern, the neural responses in the form map differ for the leading and trailing edges. Figure 4.4A shows this difference for two neurons in the form map indicated by the gray circle and square. Since the amplitude of temporal luminance modulation is lower near the edges than near the center of the Gaussian window, a neuron that samples the trailing edge of the stimulus (the gray circle) will receive stronger gain-decrease (the thick gray arrow) than gain-increase (thin black arrow) signals from its neighboring neurons. Thus, the net temporal luminance modulation of this neuron will be reduced (shown by the downward dotted arrow). On the other hand, a neuron that samples the leading edge of the drifting stimulus (gray square), the gain-increase signals (thick black arrow) will be stronger than the gain-decrease signals (thin gray arrow) and its temporal luminance modulation will therefore increase (shown by the upward dotted arrow). These asymmetrical gain-field interactions at the leading and trailing edges shift the centroid of the neural activity in the form map, and consequently the perceived position of the drifting Gabor is shifted toward its motion direction (Chung et al., 2007).

Chung and colleagues (2007) proposed that these asymmetric gain-field interactions are local, dynamic and dependent on the properties of the stimulus, as opposed to the static asymmetric synaptic interactions proposed by Fu et al. (2004). Moreover, such a model accounts for many properties of the illusory MIPS. For instance, since the motion-activated gain field interactions rely on the amplitude and not on the temporal frequency of luminance modulation, the MIPS is expected to be independent of the drifting carrier's characteristics. Indeed, previous findings found that MIPS does not show spatial frequency tuning (McGraw et al., 2002; Chung et al.,

2007). Additionally, it has been shown that MIPS increases as a function of the eccentricity (De Valois & De Valois, 1991) probably due to an increase in size of the gain-fields. This possibility is supported by the fact that at high levels of eccentricity both the retinal and the cortical sampling becomes more coarse. In addition, Lisberger and Movshon (1999) found a change in the responses of MT neurons (from sustained to transient) varying the speed of the pattern. These dynamics are very similar to the temporal dynamics of the MIPS and are compatible with the dynamics of the motion signals that control the gain field. In addition, recent findings of Tsui et al. (2007) further support the hypothesis of the motion-activated gain fields. They demonstrate that the perceived size of a drifting Gabor increased as a function of speed. In particular, they found that the leading edge appeared elongated relative to the trailing edge, due to an increased contrast at the leading side of the pattern, producing also a shift of the pattern's centroid toward the motion direction.

Thus, Tsui and colleagues (2007) provided psychophysical evidence that a drifting grating enveloped by a stationary Gaussian exhibits a contrast imbalance at the leading and trailing edges respectively causing a shift of the centre toward the motion direction of the sine-wave carrier. These results are fully compatible with the framework of the gain field model outlined by Chung et al. (2007).

Chapter 5

Priming of first- and second-order motion: Mechanisms and neural substrates

1. Introduction

A number of studies support the notion that different mechanisms exist for the detection (and probably for the storage) of first- and second-order motion. In this experiment we aimed to explore the implicit short-term memory mechanisms for these two motion cues using a repetition priming paradigm (see Chapter 2). Repetition of features, positions or even context across trials (i.e., priming) in visual search tasks has been shown to facilitate performance, independently of response repetition or task switching (Kristjánsson, Wang, & Nakayama, 2002; Maljkovic & Nakayama, 1994, 1996; Wang, Kristjánsson, & Nakayama, 2005). Visual priming has been explained in terms of increased saliency of primed features, or facilitated deployment of attention to those features (Kristjánsson, 2006; Kristjánsson & Nakayama, 2003; Maljkovic & Nakayama, 1994, 1996). According to the perceptual representation system hypothesis (PRS: Tulving & Schacter, 1990), and the sensory memory hypothesis (Magnussen & Greenlee, 1999) (see Chapter 2), the visual priming of simple stimulus attributes relies on the same low-level areas that are responsible for the analysis and representation of such attributes. In agreement with these accounts, Campana, Cowey, and Walsh (2002, 2006) found that interfering with the normal activity of MT by transcranial magnetic stimulation (TMS) abolishes priming for motion

direction with first-order motion cues, but had no effect on priming for spatial position, which is strictly dependent on the functional integrity of left FEF (Campana, Cowey, Casco, Oudsen, & Walsh, 2007). Although MT has a retinotopical organization, no interaction between priming for motion direction and spatial position has been found (Bar & Biederman, 1999; Campana et al., 2006). However, the use of TMS in previous experiments might have masked the existence of such an interaction. In this study, we investigated whether the lack of interaction between priming for motion direction and spatial position was real, or whether it was an artifact of either TMS, or the small sample size used previously. Next we wanted to investigate whether priming for motion direction also exists with second-order motion and whether, in this case too, an interaction between priming for motion direction and spatial position can be found. Such an interaction, if present with both first- and second-order motion, would suggest a neural locus of representation of priming for the two types of motion where retinotopicity is still preserved (Bar & Biederman, 1999). Since priming for first-order motion direction has already been shown to depend upon the functional integrity of visual area MT (Campana et al., 2002, 2006), and since this cortical region seems to be implicated in the processing of second-order motion (Vaina & Cowey, 1996), a similar interaction between priming for motion direction and spatial position in the two kinds of motion would suggest an analogous locus of representation of priming, situated within the MT complex but before MST, where receptive fields are large enough to encompass most of the visual field (Raiguel et al., 1997). However, shared areas of representation do not necessarily imply shared neurons. Indeed, we know that in area MT only a minority of neurons exhibit selectivity for direction of second-order motion, and these cells are typically more sensitive to contrast modulation. The majority of neurons in area MT are sensitive only to first-order motion (O'Keefe & Movshon, 1998). If the memory trace for these two types of motion relies upon exactly the same neurons, we should find that second-order motion primes first-order motion and vice versa. On the other hand, the absence of priming would indicate that different

neurons within the same area are responsible for the two types of motion priming. Moreover, if this cross-order motion priming is represented by the same neurons in area MT, we should find the same direction by spatial position interaction as in first- and second-order motion separately. If priming for motion direction is not sensitive to spatial position in cross-order priming, we should conclude that the locus of representation where first- and second-order motion converge is situated in MST or beyond (Raiguel et al., 1997); for this reason, we also explored the presence of cross-order priming and its interaction with spatial position.

2. Materials and methods

2.1. Subjects

Twenty-four subjects (12 for the first two experiments and 12 for the third one) aged between 21 and 35 participated in the experiments. Subjects were instructed to fixate on a central point and were given training to familiarize them with the stimuli and task. The eye movements of four subjects were monitored with an eye tracker. The monitored subjects did not show any problem with fixating on the centre of the screen, showing a shift larger than 1 deg away from fixation point in less than 1% of the trials, and the pattern of their results did not differ from that of the other subjects. All subjects had normal or corrected-to-normal visual acuity. The experiments were undertaken with the understanding and written consent of each subject, according to the Declaration of Helsinki.

2.2. Stimuli and procedure

Stimuli were presented on a 17-in. “NEC V72” flat-screen monitor with a refresh rate of 85 Hz. Stimuli were generated in real time by E-Prime software running on a “ASEM” Pentium III computer. Subjects were seated 57 cm from the screen. Three vertical sinusoidal moving gratings were presented, arranged in a column at the centre of the screen (see Figure 1). Each grating had a spatial frequency of 0.5 cycles per degree of visual angle and occupied a square area of 2.3×2.3 deg of visual angle. The upper edge of the top grating and the lower edge of the bottom grating were each 3.95 deg from the fixation point, while the centre of the middle grating overlapped the fixation point. Moving gratings were shown for 500 ms at a speed of 4.6 deg/s. The three gratings could move left to right or vice versa. Two of these gratings always moved in the same direction, whereas the third grating always moved in the opposite direction. The odd grating could only be the top one or the bottom one and the odd direction could be left to right or vice versa. Subjects were instructed to fixate on the centre of the screen and respond according to the position of the odd grating. Each trial began with a black cross appearing at the fixation point for 1000 ms, followed by the three moving gratings, then a blank screen was shown for 1000 ms, after which the next trial began. Subjects had to respond to the spatial position of the odd grating using one of two keys on a standard computer keyboard. The target was present on each trial and could appear with same or different position with respect to the previous trial, and with the same or different motion direction with respect to the previous trial.

The spatial position and motion direction of the target were randomized across trials but constrained to present the same number of leftward as rightward motions, the same number of top as bottom positions, and the same number of repeated positions or motion directions as non-repeated ones. No more than three consecutive instances of the same position or motion direction were allowed. Each session consisted of 240 trials. Accuracy and reaction times were measured. In the first experiment we used first-order motion gratings (Figure 1A) containing a sinusoidal

modulation of luminance of microtextural squares (4×4 pixels, corresponding to 0.11 deg of visual angle) with a spatial frequency of 0.5 cycles per degree of visual angle, ranging from 91.95 cd/m² to 31.83 cd/m². Contrast between adjacent microtextural squares ranged between 0.1 and 0.2 (Michelson contrast). In order to make the difficulty of first- and second-order motion tasks equivalent, first-order motion cues had 60% of microtextural squares of random luminance (ranging between 91.95 cd/m² and 31.83 cd/m²). The amount of noise (percentage of microtextural squares of random luminance) used in first-order motion cues has been chosen on the basis of pilot experiments. By using a constant-stimuli psychophysical procedure, varying the percentage of noisy (i.e., random luminance) microtextural squares, we were able to calculate the psychometric function. Then we used the value corresponding to 85% accuracy: i.e., the accuracy obtained with second-order motion cues without any added noise. In the second experiment, we used second-order motion gratings (Figure 1B) containing a sinusoidal modulation of contrast (mean luminance held constant) of microtextural squares (4×4 pixels) with a spatial frequency of 0.5 cycles per degree of visual angle, ranging between 0.72 and 0.1 (Michelson contrast). Luminance of microtextural squares ranged between 91.95 cd/m² and 14.95 cd/m². Although luminance artifacts are possible when using second-order motion cues, these were minimized by the use of relatively low contrast and resolution (microtextural squares instead of single pixels, to avoid non-linearity of adjacent pixels), thus their effect should be negated by the use of global motion. Indeed, first-order energy is unsystematic with respect to correlated second-order motion because the position of the light and dark squares within a texture is randomized from frame to frame (Cowey et al., 2006). Background luminance was set at 53.5 cd/m² in all experiments. The spatial phase of the luminance (contrast) waveform was randomized in each trial for each single grating. In the third experiment, we used both first- and second-order motion cues, the same ones used in the previous experiments, alternating the two types of motion on a trial-by-trial basis.

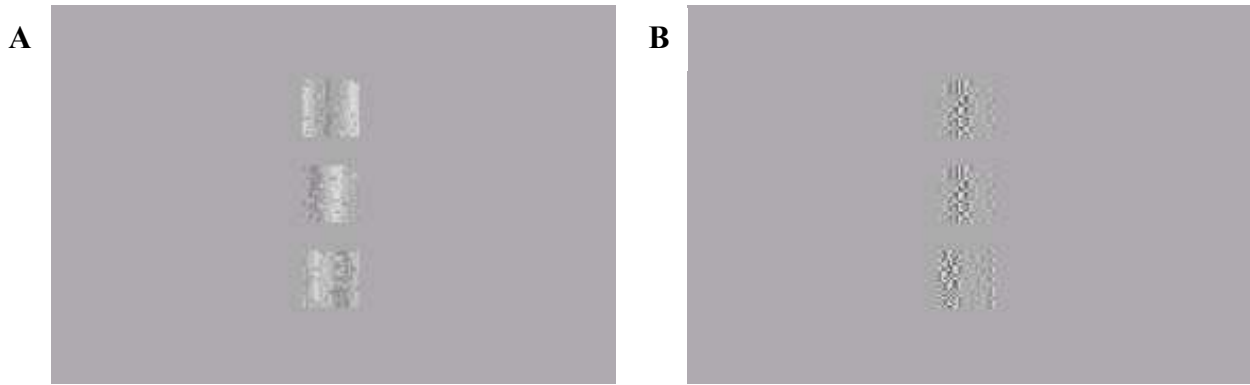


Figure 1. Examples of the stimuli used: A. First-order (luminance-modulated) motion gratings with added noise; B. Second-order (contrast-modulated) motion gratings.

2.3. Statistics

The results of the first and second experiments were analyzed using two univariate two-way repeated-measures analysis of variance (ANOVA), with previous direction (same versus different) and previous position (same versus different) as factors. The results of the third experiment were analyzed using a univariate three-way repeated-measures analysis of variance, with previous order (first versus second), previous position (same versus different) and previous direction (same versus different). For each experiment the sphericity assumption was assessed with Mauchly's test but never yielded significant effects. Bonferroni-corrected t-tests were used for planned post hoc comparisons.

3. Results

3.1. Experiment 1 (priming with first-order motion)

There was no significant difference found between accuracy conditions and mean accuracy was 87% or higher across all conditions. Reaction time results showed that when subjects were judging the spatial position of the target (Figure 2) they were faster when the direction of motion was the same as on the previous trial (direction: $F_{(1,11)} = 9.60, p < 0.01$). The effect of target position was not significant (position: $F_{(1,11)} = 0.88, p > 0.05$). A significant interaction between previous direction and previous position was also found (direction by position: $F_{(1,11)} = 9.2, p < 0.05$). Indeed, priming for motion direction was significant ($p < 0.02$) and considerable (50 ms) when target position was repeated, but small (14 ms) and non-significant ($p > 0.05$) when target position was changed. These results confirm the robustness of priming for motion direction. Moreover, they show that first-order motion priming is dependent on spatial position, suggesting a locus of representation where the retinotopical organization is still preserved (Bar & Biederman, 1999).

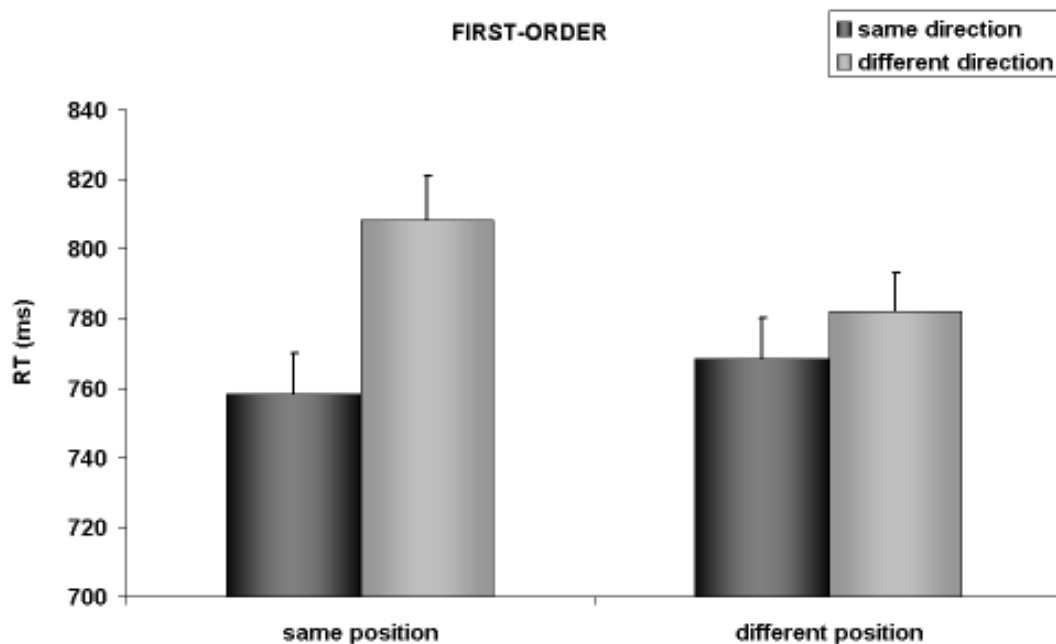


Figure 2. Results of Experiment 1 (first-order motion). Mean reaction times for same and different motion direction as a function of previous spatial position of the target are shown. Error bars $\pm$ SEM.

3.2. Experiment 2 (priming with second-order motion)

Mean accuracy for second-order motion was 81% and was slightly lower than that for first-order motion (87%). This difference is likely due to the greater difficulty of discriminating motion direction with second-order motion patterns. Note that this is despite noise having been added to first-order patterns in an attempt to equate stimulus difficulty. Accuracy results showed a significant interaction only between previous position and previous direction (position by direction: $F_{(1,11)} = 11.9$, $p < 0.01$). Despite this, no significant differences were found for post hoc tests. Reaction time results (Figure 3) showed that subjects were faster when the direction of motion was the same as on the previous trial (direction: $F_{(1,11)} = 20.68$, $p < 0.05$). Target position was not significant (position: $F_{(1,11)} = 3.10$, $p > 0.05$). As in the first experiment, which involved first-order motion, we found significant interaction between previous motion direction and previous position (direction by position $F_{(1,11)} = 8.92$, $p < 0.05$). Likewise, priming for motion direction was significant ($p < 0.002$) and substantial (52 ms) when target position was repeated, but small (12 ms) and not significant ($p > 0.05$) when target position was changed. The significant interaction between direction and position suggests that priming for motion direction is not confined to first-order motion, but occurs with second-order motion as well. Moreover, priming for motion direction is position sensitive with both first- and second-order motion, suggesting for both processes a locus of representation situated within the MT complex but earlier than MST, where retinotopicity is still maintained (Raiguel et al., 1997).

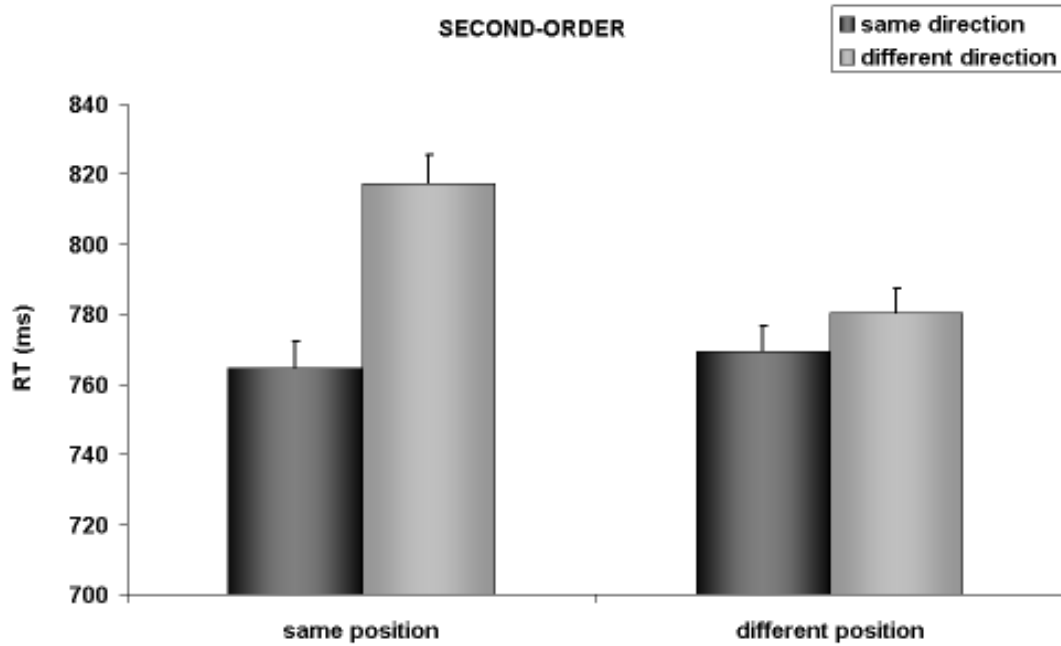


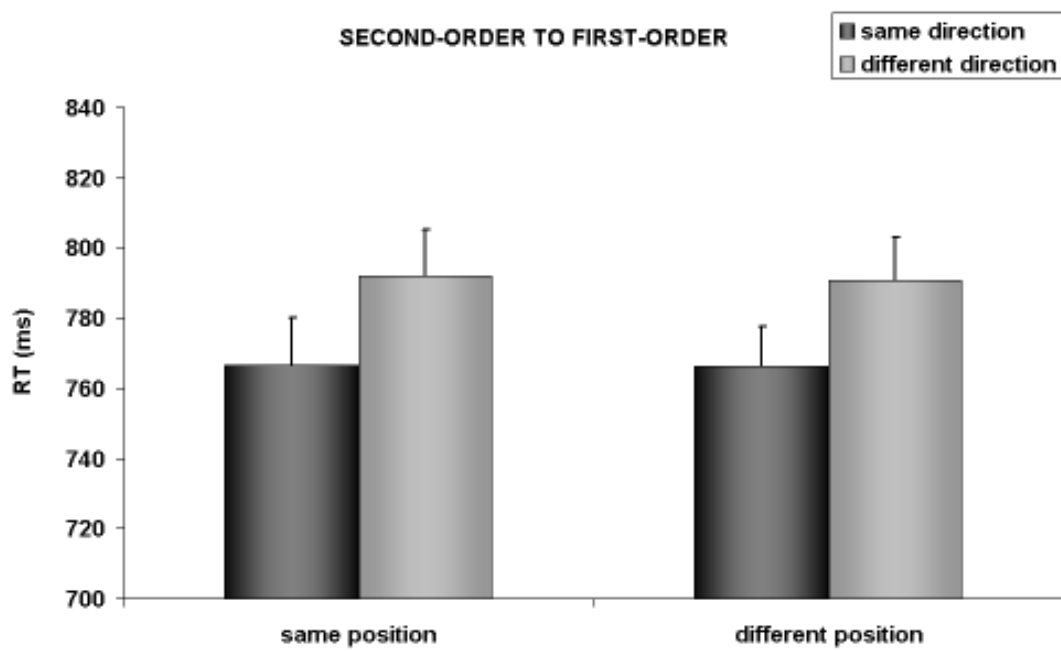
Figure 3. Results of Experiment 2 (second-order motion). Mean reaction times for same and different motion direction as a function of previous spatial position of the target are shown. Error bars $\pm$ SEM.

3.3. Experiment 3 (cross-order priming)

Mean accuracy (80%) did not show any significant effect, indicating a similar level of motion direction discriminability with the two types of cues. Motion order had no effect on reaction time results ($F_{(1,11)} = 1.6, p > 0.05$), confirming that in this experiment the two motion types were perceived as equally salient. The only significant main effect was previous motion direction ($F_{(1,11)} = 7.66, p < 0.05$), no other main effects or interactions were significant (Figure 4). In particular, the interaction between previous motion direction and previous position, which was significant in the first two experiments, was not at all significant here ($F_{(1,11)} = 0.54, p > 0.05$). In order to make sure that this lack of effect was genuine and applied to both first- and second-order motion, we looked for the interaction between previous motion direction and previous position for the two orders of motion separately. Here too we found previous motion direction statistically

significant for both first ($F_{(1,11)} = 6.68, p < 0.05$) and second-order motion ($F_{(1,11)} = 6.7, p < 0.05$), but found no evidence for interaction ($F_{(1,11)} < 1, p > 0.05$ in both cases). Indeed, the size of the effect of cross-order priming was very similar when target position was repeated (24 ms), and when target position was changed (21 ms). Moreover, it should be noticed that these cross-order effects are about the half to that obtained with first- and second-order motion presented separately when both motion direction and spatial position were repeated.

A



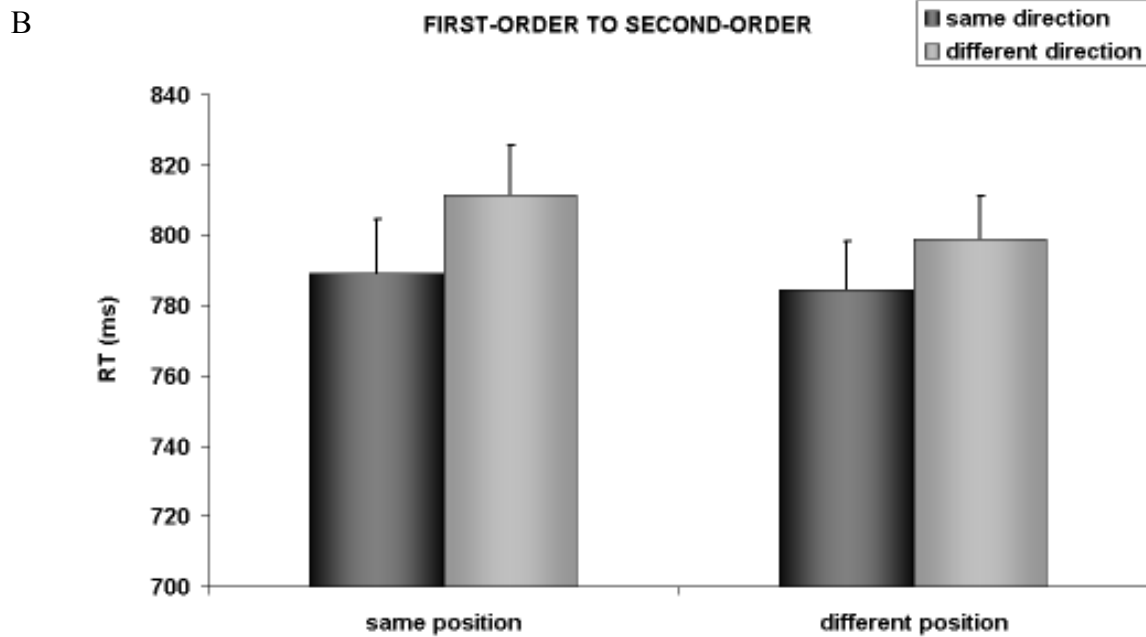


Figure 4. Results of Experiment 3 (cross-order priming): A. Mean reaction times for first-order motion when preceded by second-order motion cues; B. Reaction times for second-order motion when preceded by first-order motion cues. In both cases same and different motion direction is plotted as a function of previous spatial position. Error bars $\pm$ SEM.

4. Discussion

The results demonstrate not only the presence of priming for first- and second-order motion, but also cross-order priming; i.e., first-order motion can prime second-order motion and vice versa, resulting in faster reaction times when motion direction is repeated, no matter the order of motion used. Indeed, in both cases we have priming for motion direction as well as interaction between motion direction and spatial position. This result points to a locus of representation of the memory trace where the retinotopical organization is still well preserved (Bar & Biederman, 1999). Previous results (Campana et al., 2002, 2006) point to visual area MT as the neural substrate necessary for first-order motion priming to occur. Indeed, this area is retinotopically

organized and includes neurons that encode second-order (contrast-defined) moving stimuli (Cowey et al., 2006; Vaina et al., 1999, 1998). The similarity of results of motion priming with first- and second-order motion and the interaction with spatial position in both types of motion suggest for both processes a locus of representation within the MT complex, but earlier than MST, where retinotopicity is still maintained (Raiguel et al., 1997). Previous results of Campana and colleagues (2006) failed to show a significant interaction between priming for motion direction and spatial position. However, it should be noted that in the NOTMS condition in that study, the effect of motion priming was 56 ms when target spatial position was repeated, and 34 ms when target spatial position was changed with respect to the previous trial. A smaller sample size and the inclusion of the TMS condition in the data analysis might have masked this interaction. Cross-order motion priming gives a slightly different picture in that priming does occur from first- to second-order motion and vice versa, but this time without any interaction with spatial position. This suggests that the neural substrate for priming of motion direction may change depending on task demands and stimulus characteristics, whereas with first- and second-order motion presented separately, priming can be based on the activity of retinotopically organized areas such as MT, when the two kinds of motion are interleaved across trials, the neural locus mediating priming may shift to higher visual areas, where retinotopicity is lost or at least is very coarse. Although priming with first- and second-order motion is likely to occur within the same cortical area (MT), the neurons responsible for priming within that area might be different for the two kinds of motion (Ashida et al., 2007). Indeed, the locus of representation where the same neurons hold the memory trace of priming for both first- and second-order motion is position insensitive, meaning it is at a level of processing at or higher than MST, where receptive fields are large enough to encompass most of the visual field (Raiguel et al., 1997).

Chapter 6

Distinct position assignment mechanisms revealed by cross-order motion

1. Introduction

The motion priming results show that, whereas in the within-order conditions motion priming is dependent on the repetition of the same target's position, in the cross-order condition, priming is not sensitive to spatial position. In agreement with recent fMRI findings (Ashida et al., 2007) we hypothesized that first- and second-order motion cues remain distinct and separate up to the level in which global motion is extracted (i.e., MT), thus the two types of motion could be integrated at a level of motion processing where the retinotopic organization is lost or at least it is very coarse. In addition, these findings suggest that both first- and second-order mechanisms are able to encode the spatial position of a moving pattern.

As outlined in Chapter 4, previous studies have shown positional shifts with both first- and second-order motion. In particular, Bressler and Whitney (2006) showed that second-order motion influences perceived position, but with a different spatiotemporal tuning from that of first-order motion. On the other hand, second-order motion shifts perceived position over a relatively narrow range of temporal frequencies, peaking at about 4 Hz, and this effect is roughly invariant with spatial frequency. These results suggest that two separate and independent mechanisms are involved in the detection of first- and second-order motion, with different spatiotemporal tuning. However, it is not clear whether two independent mechanisms also encode position or if a single, common mechanism is responsible for assigning the location of both first- and second-order moving stimuli. Since there is evidence that first- and second-order

moving patterns are initially detected by separate and independent mechanisms, each type of motion could independently influence position. Alternatively, it is possible that the mechanism involved in position assignment could be the same for first- and second-order motion; for instance, at a stage where motion information is integrated and neurons respond both to first- and second-order motion patterns, such as area MT. In this latter case the differential spatiotemporal tuning found for first- and second-order motion-induced position shift could reflect the differences between the two lower level detector systems. In this experiment we assessed whether first- and second-order motion encode and assign the position of a moving pattern by means of a single and common mechanism, or whether there are two distinct mechanisms for position assignment. To this purpose we measured the shift in the perceived position induced by drifting first- and second-order Gabors (De Valois & De Valois, 1991; Durant & Johnston, 2004; Edwards & Badcock, 2003; Fang & He, 2004). We first measured separately the motion-induced position shift for first- and second-order moving patterns. We subsequently conducted an experiment in which first- and second-order drifting Gabors were presented within the same trial, to see if cross-order motion shifts perceived position as well. The rationale was that if there is a common position assignment mechanism for both first- and second-order motion, one would expect a cross-order motion-induced position shift that reflects a contribution from both first- and second-order motion systems. So, we should observe an effect that is intermediate between the first-order and the second-order motion-induced position shifts. On the other hand, no effect for cross-order stimuli would indicate the presence of separate and independent position assignment mechanisms.

2. Methods

2.1 Subjects

The two authors and six subjects who were unaware of the purpose of the study participated in each experiment. Subjects sat in a dark room and were immobilized with a chin rest placed at 57 cm from the screen. Viewing was binocular. They were instructed to fixate a point at the centre of the screen and were given training at the beginning of each experiment to familiarize them with the stimuli and task. All subjects had normal or corrected-to-normal visual acuity.

2.2 Apparatus

Stimuli were displayed on a Sony Trinitron G400 monitor with a refresh rate of 100 Hz and generated by a CRS VSG2/5 graphics system. The screen resolution was set at 1024 x 768 pixels. The mean luminance was 60.67 cd/m². Luminance was measured using a Minolta LS-100 photometer. A gamma-corrected lookup table (LUT) was used to ensure stimulus linearity.

2.3 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 3.3 degrees at half maximum amplitude. Formally the first-order Gabors used can be defined as

$$L_{(x,y,t)} = L_{mean} \left\{ [1 + m \sin(2\pi f_x x + 2\pi f_t t + \phi)] + C_n R_{(x,y,t)} \right\} e^{-\frac{(x^2+y^2)}{\sigma^2}} \quad (\text{Eq.1})$$

where $L_{(x,y,t)}$ represents the luminance at each point of the stimulus at the instant t , L_{mean} is the mean luminance of the resultant pattern, m is the modulation depth (Michelson contrast) of the sine wave carrier (range 0-1 Michelson contrast), f_x is the spatial frequency (1 c/deg), f_t is the temporal frequency (4 Hz), ϕ is the phase shift of the sinusoidal carrier, C_n is the contrast (0.5 Michelson contrast) of the dynamic noise carrier $R_{(x,y,t)}$. The noise carriers were generated by assigning each screen pixel (2.14 arcmin) the value of 0 (black dot) or 1 (white dot) with an equal probability, so in each noise carrier 50% of pixels were black and 50% were white and there was no luminance variation within each noise pixel. The noise carriers were updated every frame, resulting in dynamic noise. The Gaussian envelope is expressed by the exponential of the Eq.1; x and y represent the respective horizontal and vertical distances from the Gaussian peak, σ is the spatial constant of the Gaussian (1.1 degrees). The Gaussian envelope was always static, whereas the sine wave drifted at a constant velocity of 4 deg/s either leftwards or rightwards. 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

$$L_{(x,y,t)} = L_{\text{mean}} \left\{ 1 + [1 + E + m \sin(2\pi f_x x + 2\pi f_t t + \phi)] + C_n R_{(x,y,t)} \right\} e^{-\frac{(x^2 + y^2)}{\sigma^2}} \quad (\text{Eq.2})$$

where $L_{(x,y,t)}$, L_{mean} , m , f_x , f_t , ϕ , C_n , $R_{(x,y,t)}$ and σ are the same parameters as in Eq. 1. E is the subject's equiluminance value (established using the technique described in the next section). Equiluminant stimuli were used in order to ensure that contrast-defined motion did not contain any residual luminance (first-order) artefact.

2.4 Procedures

The experiment involved four different stages: (i) determining the contrast threshold for both first- and second-order drifting Gabors; (ii) estimating the subjective equiluminance point in second-order Gabors; (iii) measuring the perceived positions for first- and second-order drifting Gabors separately and in a cross-order stimulus; and finally (iv) measuring perceived positions of cross-order Gabors after having equated the saliency of second-order Gabors with respect to first-order Gabors. The procedure used in each phase is described below.

2.4.1 Contrast threshold

For first-order contrast thresholds, two Gabors were displayed at 9.7 degrees above and below the fixation point respectively. The two Gabors could drift either in the same or different directions and motion direction was balanced and randomized across trials. Using the method constant stimuli (MCS), subjects performed a discrimination task, pressing a response button to report whether the Gabors drifted in the same or different directions. Gabors had a spatial frequency of 1 c/deg and drifted at 4 Hz. Each subject performed 240 trials; 40 trials for each of the 6 contrast levels used (0.01, 0.015, 0.02, 0.025, 0.03 Michelson contrast). The procedure used to estimate the contrast modulation threshold for second-order stimuli was identical to that used for first-order stimuli, except for the 6 contrast modulation levels (0.20, 0.30, 0.40, 0.50, 0.60, 0.70 Michelson contrast). Contrast threshold (corresponding to 75% accuracy) was estimated by fitting a logistic function to the data. The contrast value used in subsequent experiments was obtained by multiplying the threshold value by three, in order to ensure that all subjects could reliably perceive the motion direction of both first- and second-order patterns.

2.4.2 Minimum motion technique

A modified minimum motion technique (Anstis & Cavanagh, 1983; Nishida, Edwards, & Sato, 1997; Seiffert & Cavanagh, 1998) was used to find the subjective equiluminance value for second-order patterns. Subjects fixated a point at the centre of the screen. First- and second-order Gabors were presented 9.7 degrees above the fixation point and interleaved in a four-frame sequence such that each Gabor's sine wave was shifted by 90 degrees, with first-order Gabors presented in odd frames and second-order Gabors presented in even frames. A first-order luminance modulation was added to second-order Gabors, and was varied from trial to trial according to a simple Up-Down staircase (Levitt, 1971). The rationale was as follows. Since successive frames are in quadrature phase, when second-order frames contain a residual luminance artefact subjects should perceive unidirectional motion in the four-frame sequence, either in one direction or the opposite depending on the contrast polarity of the artefact; when the luminance modulation added to second-order frames nulls or cancels out the artefact subjects should perceive no consistent apparent motion.

At the beginning of the procedure a very low contrast luminance modulation (0.01 Michelson contrast) was added to second-order frames in order to produce a unidirectional motion percept, and the initial staircase step size was chosen to be half this value. After the first, third, seventh, fifteenth and thirty-first reversal of apparent direction the step size was halved and after each halving of the step size the subsequent run was started with a value of the luminance artifact that was the average of the peaks and valleys for the preceding step size. On each trial (480 ms), subjects were asked to indicate perceived motion direction, either leftward or rightward, using a button press. Testing was terminated after a total of 40 runs and the average of peaks and valleys of all the runs was taken as an estimate the point of subjective equality (PSE; Finney, 1971; McKee, Klein, & Teller, 1985); this corresponds to the amplitude of the nulling luminance modulation added to second-order Gabors that produced a percept of ambiguous motion.

We assume that thresholds for second-order motion measured in phase (i) were not significantly affected by luminance artifacts because the nulling contrasts indicated in phase (ii) were so low that they would be vanishingly small at detection threshold.

2.4.3 Position shift

We used the contrast values and equiluminance points estimated in previous phases to measure the perceived position of first-, second-, and cross-order motion. As before, Gabors had a spatial frequency of 1 c/deg and drifted at 4 Hz. These values were chosen on the basis of data in Bressler and Whitney, 2006, to produce at least a moderate position shift for both first- and second-order Gabors. The spatial frequency we employed was higher than that used by Bressler and Whitney (2006). In pilot observations using the same spatial frequency as Bressler and Whitney (2006), namely 0.18c/deg, we found that it was extremely difficult to discriminate the motion direction of second-order patches located 9.7 deg into the periphery and Bressler and Whitney, 2006, reported relatively little difference between results at 0.18c/deg and at 1 c/deg. Subjects fixated a point at the centre of the screen and judged the relative position of two vertically oriented Gabors placed at 9.7 degrees above and 9.7 degrees below the fixation point. The sine wave carriers of the top and the bottom Gabor always drifted in opposite directions. On each trial, the two Gabors were presented horizontally offset in opposite directions by one of six values (-0.71, -0.43, -0.14, 0.14, 0.43, 0.71 degrees of visual angle; positive values indicate rightward offset, negative values indicate leftward offset). Each trial was presented for 500 ms, after which the subject indicated with a button press whether the top Gabor appeared more to the left or more to the right of the bottom one. Each subject performed 240 trials in each the three stimulus conditions. MCS was used for all three conditions. A logistic function was fitted to the data in order to estimate the 50% corresponding to the physical misalignment between the

Gabors required for apparent alignment (the point of subjective equality, PSE; Finney, 1971; McKee et al., 1985).

2.4.4 Position shift with matched salience

A possible complication in the third phase of the study was that, while first- and second- order patterns were equated in terms of motion discriminability, both three-times discrimination threshold, they were not equated in terms of subjective pattern salience (the first-order pattern appeared much more salient), and this may have influenced position judgments. Therefore, the position shift measurements and associated threshold measurements in previous phases were repeated (using a different set of eight subjects) so that we could employ a cross-order stimulus in which first- and second-order Gabors were equated for perceptual salience. In phase (iv) we reduced the contrast of first-order Gabors in the cross-order stimulus to psychophysically equate their salience with second-order Gabors. We used another variant of the minimum motion technique (Anstis & Cavanagh, 1983) to estimate the required level of contrast. Subjects fixated a point at the centre of the screen. First- and second-order Gabors were presented at 9.7 degrees above the fixation point and interleaved in a six-frame sequence where first-order Gabors were presented in odd frames and second-order Gabors presented in even frames. Each first-order Gabor's sine wave carrier was shifted by 90 degrees (i.e. quadrature phase) on each appearance, and each second-order Gabor's sine carrier was shifted a corresponding distance in the opposite direction on each appearance. We then manipulated the contrast of the luminance-defined carrier in the first-order Gabor while keeping constant the contrast of the second-order Gabor. Initially the contrasts of the first- and second-order Gabors were set equal to those used in the previous phase for each subject. 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 carrier was very low or zero, the perceived motion direction of the six-frame sequence followed the second-order carrier.

We measured the contrast of the first-order carrier required to null the unidirectional motion of the second-order carrier, assuming that this contrast equated the salience of first-order carriers with second-order carriers. We then measured the motion-induced position shift while first- and second-order Gabors were displayed within the same trial. In this last experiment we used the same parameters as in the previous experiments. Each subject performed 240 trials (40 repetitions for each of the 6 horizontal offsets). MCS was used, followed by computation of the best-fitting logistic function.

3. Results

Results show that both first- and second-order motion shift the perceived position of the static envelopes in the direction of the moving carriers. For instance, if the envelopes of the two Gabors are physically aligned (Figure 6.1A, B, left), they appear shifted towards the direction of the carriers (Figure 6.1A, B, right).

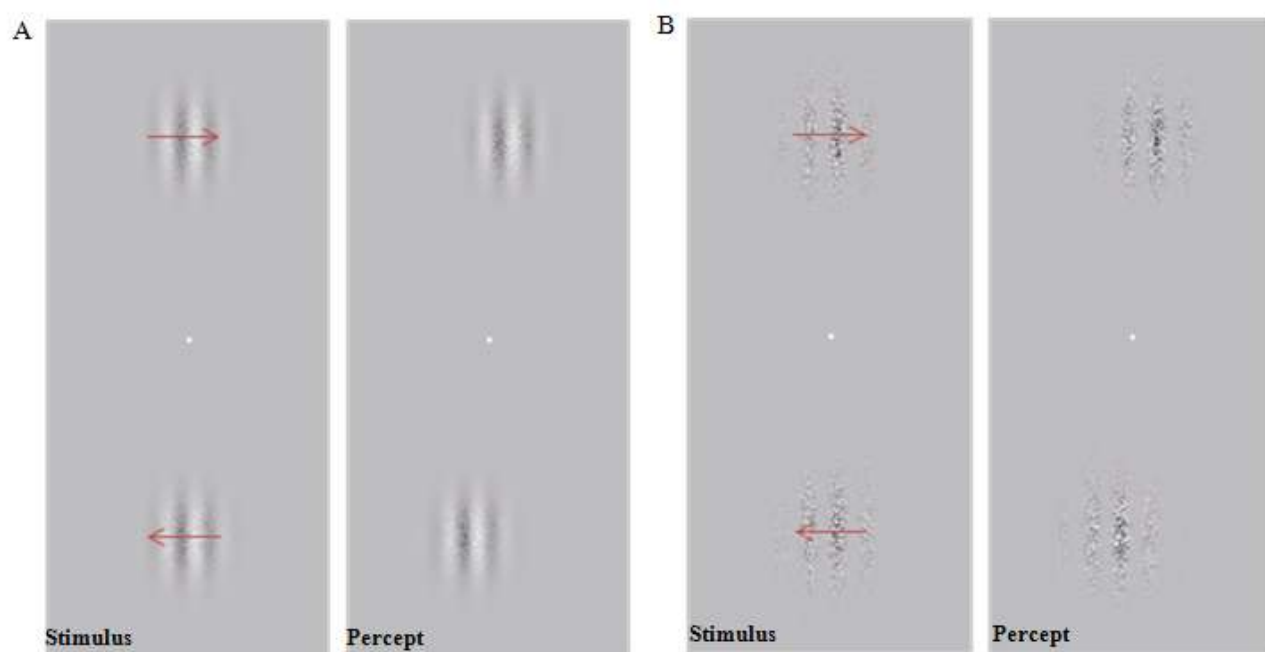


Figure 6.1. A. Stimulus and percept for first-order drifting Gabors (luminance-defined motion). B. Stimulus and percept for second-order drifting Gabors (contrast-defined motion). The figures show an example in which two first- and second-order Gabors are physically aligned (we did not include such a condition in our experiments; see Methods) but when the luminance-defined carriers (A) and the contrast-defined carriers (B) drift in opposite directions the Gabors appear misaligned. For illustrative purposes the Gabors reported here have sinusoidal carriers with exaggerated contrast.

Figure 6.2 shows the psychometric functions for subject GM, illustrating the magnitude of the motion-induced position shift for first-order drifting Gabors (Figure 6.2A), for second-order drifting Gabors (Figure 2B) and for cross-order motion (Figure 6.2C). The effect is marked for first-order Gabors (0.5 degrees), small both for second-order drifting Gabors (0.06 degrees) and virtually absent for cross-order motion (0.03 degrees). Although some psychometric functions such as that shown (Figure 6.2A) did not drop to zero (or alternatively reach 100%), they always spanned values that were significantly different from the mid-point, and all curve fits passed χ^2 goodness-of-fit test.

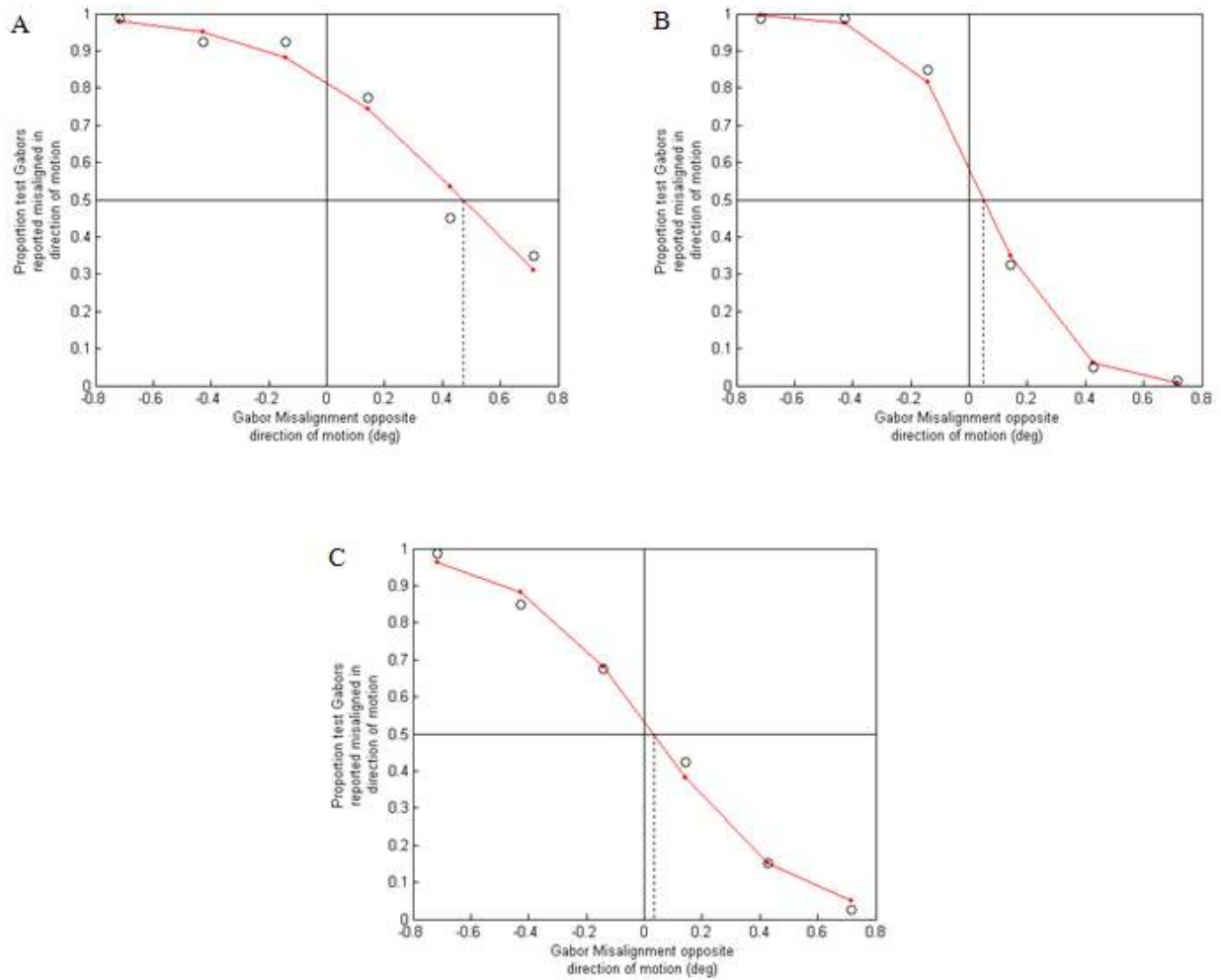


Figure 6.2. Psychometric functions for subject GM using (A) first-order drifting Gabors, (B) second-order drifting Gabors and (C) cross-order motion. The abscissa shows the physical alignment between the Gabors in degrees of visual angle (positive values indicate that the Gabors were physically displaced opposite the direction of the carrier motion). The ordinate shows the proportion of responses in which subjects judged the Gabors to be shifted in the direction of the carrier motion. The point of subjective equality (PSE) is the physical misalignment between the Gabors that created an apparent alignment; this estimates the magnitude of the illusory position shift. The PSE of GM for first-order drifting Gabors was 0.5 degrees, 0.06 degrees for second-order drifting Gabors and 0.03 degrees for cross-order motion.

This pattern of results is consistent across all subjects. One subject was excluded from further analysis because their data never fell below 50%, indicating an extreme apparent misalignment between the Gabors (over two standard deviations larger than the remaining seven subjects).

Figure 6.3 summarises the mean position shift across all remaining seven subjects (± 1 SE). The mean position shift found for first order stimuli was 0.42 degrees, whereas second-order motion shifted perceived position by 0.09 degrees. There is a significant difference between first- and second-order results ($t_{(6)} = 4.60, p = 0.004$). Though the position shift found with second-order motion was very small, it was still significantly higher than that found for cross-order motion ($t_{(6)} = 2.69, p < 0.05$), for which we found a position shift of 0.039 degrees. We also found a significant difference between the first-order and cross-order motion-induced position shift ($t_{(6)} = 4.43, p = 0.004$). Though the position shift found for cross-order patterns was significantly lower than that obtained for second-order patterns, it was still significantly different from zero ($t_{(6)} = 4.87, p = 0.003$). This result could be due to the different salience between first-order and second-order patterns, that is, the higher salience of first-order patches may have influenced the performance of the subjects. In the phase four of the experiment we addressed this issue.

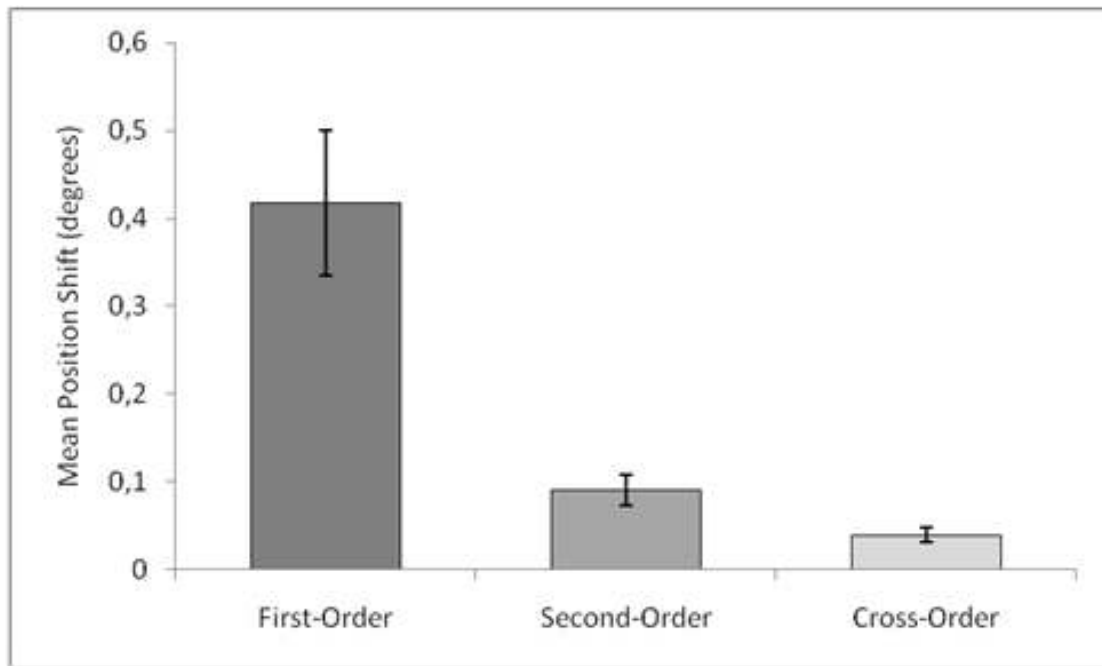


Figure 6.3. Perceived misalignment for first-order, second-order and cross-order motion. The size of the offset for first order stimuli is about 0.42 degrees, whereas for second-order motion is 0.09 degrees. The positional offset obtained for second-order stimuli, though very small, is higher than that obtained for cross order motion (0.039 degrees), for which we observed a lack of the effect. Error bars $\pm$ SEM.

In addition, in phase three we also found a significant difference between the slopes of the psychometric functions for the three stimulus conditions (Figure 6.4). The slopes were calculated as the reciprocal of the standard deviation of the psychometric function. A paired-samples *t* test conducted on the slopes revealed a significant difference between first-order and second-order patterns ($t_{(6)} = 4.98, p = 0.003$), for which the mean slopes were 0.006 and 0.009 degrees respectively, and between second-order and cross-order motion patterns (0.007 degrees) ($t_{(6)} = 4.64, p = 0.004$), but no significant differences between first-order and cross-order patterns ($t_{(6)} = 1.84, p > 0.05$). The difference in position sensitivity between first- and second-order stimuli could be due to the lower contrast employed for first-order than for second-order stimuli. Indeed

the contrast thresholds estimated in phase one of the experiment were always much lower for first-order motion than for second-order motion. However, despite the difference in sensitivity, the shift in position obtained for first-order cues was significantly higher than that obtained for second-order cues.

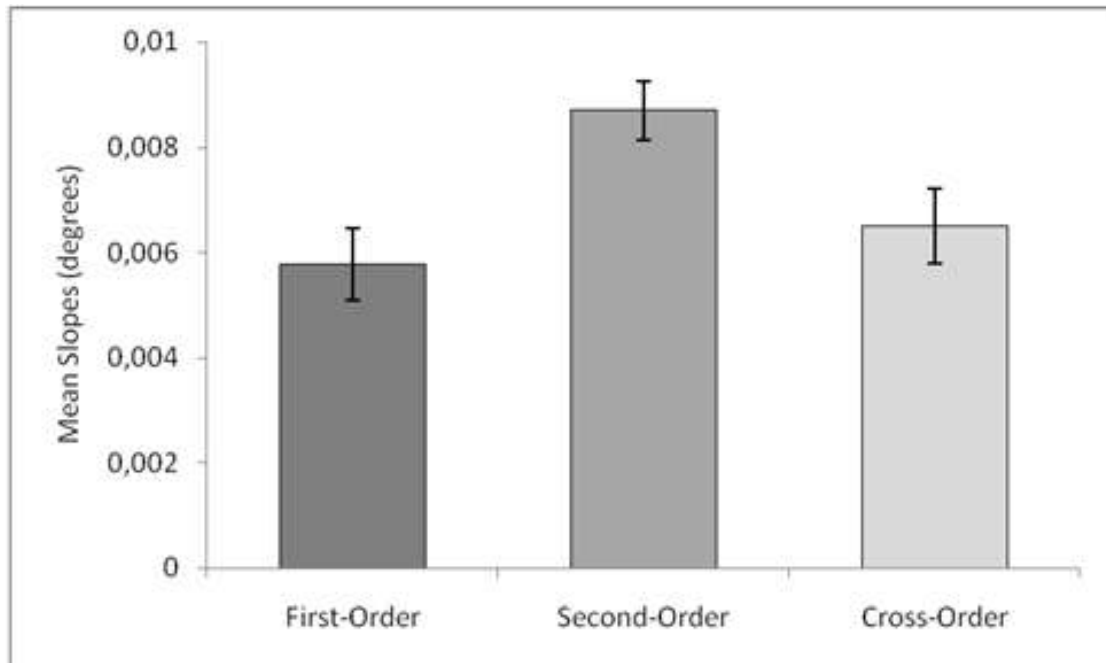


Figure 6.4. Mean slopes for first-order, second-order and cross-order motion relative to the position shift experiments. The slopes were calculated as the reciprocal of the standard deviation of each psychometric function. The mean slope for first-order motion was 0.006 degrees, 0.009 degrees for second order motion and 0.007 degrees for cross-order motion. A paired-samples t test showed significant differences between first- and second-order motion, between second- and cross-order motion, but not between first- and cross-order motion patterns (see text for more details). Error bars $\pm$ SEM.

Figures 6.5 and 6.6 show mean position shifts and psychometric function slopes in phase four of the study, in which cross-order stimuli were matched for perceptual salience. The pattern of

results is very similar to that shown in Figures 6.3 and 6.4. However, interestingly when stimuli were matched for salience the position shift obtained for cross-order patterns is not significantly different from zero ($t_{(6)} = 0.50, p > 0.05$). In the previous phase of the experiment, in which first- and second-order stimuli were not matched for salience, the position shift obtained for cross-order stimuli, though smaller than that obtained for second-order motion was significantly different from zero. The match in salience between first- and second-order patterns may have cancelled any possible influence of the first-order pattern.

Furthermore, in both phases of the experiment, the shifts in position for first- and second-order patterns were significantly different from zero, $t_{(6)} = 5.06, p = 0.002$; $t_{(6)} = 5.18, p = 0.002$, respectively for first- and second-order patterns in the phase three, and $t_{(6)} = 5.79, p = 0.001$; $t_{(6)} = 4.49, p = 0.004$, respectively for first- and second-order patterns in the phase four of the experiment.

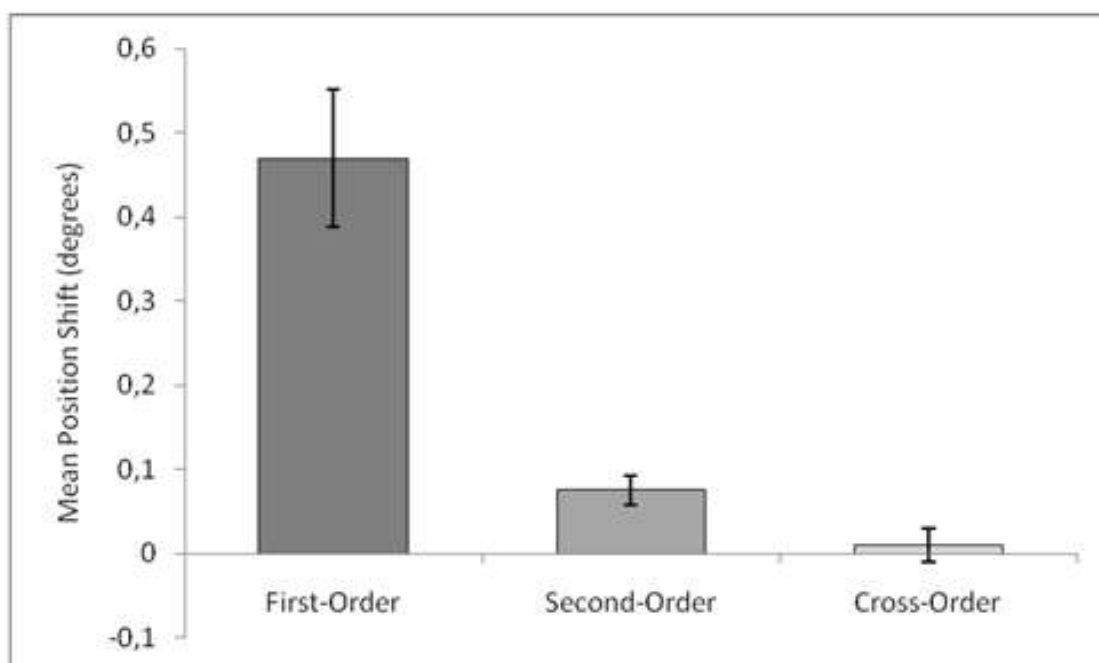


Figure 6.5. Perceived misalignment for first-, second- and cross-order motion in phase four of the study, in which cross-order stimuli were matched for salience. The size of the offset for first order stimuli is 0.47 degrees, and is significantly higher than that obtained for second-order

Gabors (0.075 degrees) ($t_{(6)} = 5.79, p = 0.001$). The positional offset obtained for second-order stimuli is still higher than that obtained for cross order motion (0.01 degrees) ($t_{(6)} = 4.67, p = 0.003$). A paired-samples t test showed no significant difference between the position shifts for cross-order stimuli calculated in phase three (i.e. without the match in salience) and in phase four of the study (i.e. with the match in salience) ($t_{(6)} = 1.14, p > 0.05$). Error bars $\pm$ SEM.

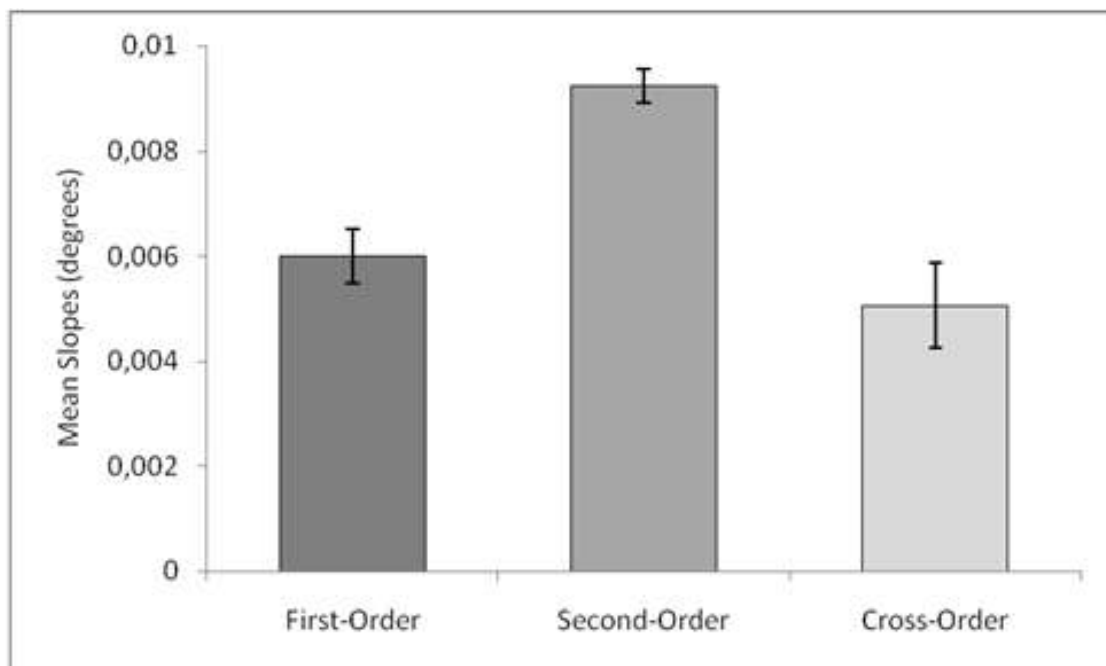


Figure 6.6. Mean slopes for first-order, second-order and cross-order motion in four phase of the study. The slopes were calculated as the reciprocal of the standard deviation of each psychometric function. The mean slope for first-order motion was 0.006 degrees, 0.009 degrees for second order motion and 0.005 degrees for cross-order motion. A paired-samples t test showed significant differences between first- and second-order motion ($t_{(6)} = 7.92, p < 0.001$), between second- and cross-order motion ($t_{(6)} = 7.28, p < 0.001$), and no between first- and cross-order motion ($t_{(6)} = 1.26, p > 0.05$). In addition, were found no significant differences between the slopes for cross-order stimuli calculated in phase three and four of the study ($t_{(6)} = 1.38, p > 0.05$). Error bars $\pm$ SEM.

4. Discussion

The magnitude of the motion-induced position shifts obtained for first-order motion are broadly consistent with the findings of previous studies (Bressler & Whitney, 2006; Whitaker, McGraw, & Levi, 1997), but we obtained a relatively small second-order position-shift (0.09 degrees in phase three and 0.075 degrees in phase four of the study) compared to those reported previously. For instance, Bressler and Whitney (2006), in a similar condition in which they used a spatial frequency of 0.71 c/deg and a temporal frequency of 4 Hz, obtained a mean second-order position of about 0.36 degrees, three or four times larger than our effect. A contributory factor in the present experiment may be the slightly higher spatial frequency of the carrier employed, which is less than optimal for second-order patterns. However, we also conducted pilot observations employing optimal spatial and temporal frequencies for second-order patterns based on Bressler and Whitney (2006) (i.e. 0.18 c/deg and 4 Hz respectively), but still, we did not obtain any appreciable position shift. In fact, displaying second-order patches at 9.7 degrees above and below the fixation point made the task very hard to discriminate the relative motion direction of the second-order Gabors at those spatio-temporal frequencies. It is possible that the greater second-order effect reported by Bressler and Whitney (2006), and their success at a lower spatial frequency reflects incomplete removal of luminance artifacts in their stimulus. While Bressler and Whitney (2006) employed a minimum motion technique similar to that used in our experiments, their minimum motion stimulus was not a Gabor patch but a grating windowed by a circular aperture 11.2 degrees in diameter, with fixation 4.49 degrees above the edge of the aperture. Our minimum motion stimulus was a Gabor patch matching that used in our position shift experiments, viewed at the same peripheral location. Perhaps equiluminance settings inside the edge of the grating aperture, 4.5 degrees from fixation of Bressler and Whitney's (2006) windowed stimulus were not appropriate for their Gabor patches which were centered at up to 10

degrees into the periphery (actually, 8.15 degrees above and 10.1 degrees below fixation in Bressler and Whitney's experiment). Thus residual luminance artifacts may have contributed to performance for second-order Gabors. They reported a strong position shift with luminance-defined Gabors even at low contrast, so it is possible that the luminance artifact could contribute to position shifts.

It is possible that our results are due to the unbalanced spatial-frequency tuning for first- and second-order motion. That is, in order to properly test for possible interactions between these two motion cues, detectors sensitive to first- and second-order motion stimuli should be stimulated with their optimal spatial frequencies. However, O'Keefe and Movshon (1998) showed that MT neurons responsive to both first- and second-order motion tend to prefer roughly similar directions and spatial frequencies for first- and second-order motion stimuli, and tend to prefer slightly lower temporal frequencies for second-order motion. On the basis of these findings, if first- and second-order motion position shifts are detected by a common mechanism employing detectors that respond to both first- and second-order motion, we should expect to obtain a reliable cross-order effect using the same spatial frequencies and roughly the same temporal frequencies for first- and second-order stimuli. The most interesting feature of our data is the absence of apparent position shift with cross-order stimuli when first- and second-order stimuli have been carefully matched for salience. This result clearly indicates that first- and second-order motion are processed by different mechanisms (Cavanagh & Mather, 1989; Derrington & Badcock, 1985; Edwards & Badcock, 1995; Ledgeway & Smith, 1994a,b; Mather, 1991; McCarthy, 1993; Nishida & Sato, 1995; Seiffert & Cavanagh, 1998), as indeed does the differential spatio-temporal tuning of first- and second-order motion-induced position shifts reported in previous studies. But it also implies separate and distinct position encoding mechanisms. The simplest account of position coding by a single mechanism shared between first and second-order patterns would predict a cross-order position shift that is the average of the

position shifts obtained using first- and second-order patterns presented separately. Yet there is hardly any apparent position shift at all with cross-order stimuli, even though the first-order patterns generated a large position shift. The effect cannot be due to unequal salience between the first- and second order patches, since they were matched for salience in the data of Figure 6.5. Nevertheless, if judgments were dominated by the first-order patch in cross-order stimuli, one would expect a cross-order position shift equal to half that obtained using only first-order patches. Moreover, the slope values plotted in Figures 6.4 and 6 indicate that subjects did not find the judgement any more difficult for cross-order stimuli than for first-order stimuli which produce much larger position shifts. We conclude that the effect is due to a real difficulty faced by the visual system when it attempts to compare the position of first- and second-order stimuli, reflecting a segregation of position encoding mechanisms for the two classes of stimulus.

Chapter 7

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

1. Introduction

The findings of the two previous experiments support the notion that first-order and second-order stimuli are encoded by distinct mechanisms and each mechanism is able to encode different characteristics of a moving stimulus such as spatial frequency, temporal frequency and spatial position. A variety of psychophysical studies have highlighted relevant differences between these two motion mechanisms in terms of their spatial and temporal tuning. For example, adaptation studies pointed out that the mechanism responsible for detecting first-order motion is band-pass, whereas the mechanism underlying the detection of second-order motion seems to be low-pass (in the temporal domain). The findings of Bressler and Whitney (2006) on the motion-induced position shift for first- and second-order moving stimuli confirmed that a first-order motion mechanism is temporally band-pass, but also has narrow spatial frequency tuning. Conversely, they found that second-order mechanism is temporally low-pass and more broadly tuned for spatial frequency. As pointed out in Chapter 1, it has been shown that first- and second-order motion differ also in terms of their temporal acuity (Derrington, Badcock & Henning, 1993). Derrington, Badcock and Henning (1993) have shown that to correctly discriminate the motion direction of a second-order drifting stimulus (beat pattern) its duration should be ≥ 200

ms. Indeed, most of the previous studies concerning adaptation and motion priming used long periods of stimulus exposure, therefore it is possible that in most of these studies the involvement of high-level, feature-tracking mechanisms influenced performance.

Generally, MAE is induced by adapting for tens of seconds (see Chapter 3). 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 close temporal succession, the neural response corresponding to the second presentation is considerably reduced (Nelson, 1991; Chance, Nelson, & Abbott, 1998; Finlayson & Cynader, 1995; Stratford, Tarczy-Hornuch, Martin, Bannister, & Jack, 1996). This pattern of activity is present both at low-level (V1) and high levels of motion analysis (e.g., MT) (Lisberger & Movshon, 1999). 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 (e.g., Castro-Alamancos & Connors, 1996; Hempel, Hartman, Wang, Turrigiano, & Nelson, 2000). These two opposite forms of neural plasticity 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, for example. 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 motion very brief exposures to directional stimuli (fast adaptation) 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 adaptation-test blank interval (i.e., 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. Specifically, using brief adaptation durations (e.g., 80 or 160 ms) and ISIs (e.g., 40 or 120 ms)

Kanai and Verstraten (2005) showed that the perceived direction of an ambiguous test pattern was biased toward the direction of the adaptation pattern, originating a rapid form of visual motion priming (rVMP). Alternatively, slightly increasing the adaptation duration (e.g., 320 or 640 ms), and using the same ISI resulted in a perceived bias in the opposite direction of the adaptation pattern (rapid motion aftereffect - rMAE). According to the findings of Kanai and Verstraten (2005) 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 again toward the motion direction of the adaptation pattern. Kanai and Verstraten called such form of facilitation Perceptual Sensitization (PS), that is, a kind of priming for motion direction similar to that described in Experiment 1 (Chapter 5). This effect arises gradually over time and reflects potentiation (i.e., facilitation) at higher-levels (e.g., MT) along the motion processing hierarchy.

In this experiment we assessed if 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 could be useful to selectively tap the response of low-level first- and second-order motion detectors, as well as the motion detectors present at higher levels of motion processing. In particular, we aimed to investigate: (i) if second-order rVMP, rMAE and PS exist and exhibit the same or different temporal course to those observed for first-order motion, and (ii) using a cross-adaptation condition, if first-order and second-order signals are integrated or are kept separate. In this case we expect similar results to that obtained for first- and second-order motion presented separately or at least intermediate time courses for rVMP, rMAE and PS. Since a number of studies have shown a different temporal acuity for first- and second-order motion signals, we expected different time courses for first- and second-order rVMP, rMAE and PS.

Moreover, based on our previous results, we expected no interaction between first- and second-order motion in the cross-adaptation condition.

2. Method

2.1 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 x 1024 pixels. The mean luminance was 15.47 cd/m². Luminance was measured using a Minolta LS-100 photometer. A gamma-corrected lookup table (LUT) was used to ensure stimulus linearity.

2.2 Subjects

Two authors and six subjects who were unaware of the purpose of the study participated in the experiments with first-order and second-order stimuli presented separately. In the cross-order adaptation experiment the two authors and ten naïve subjects participated. Subjects sat in a dark room 57 cm from the screen. Viewing was binocular. They were instructed to fixate a point at the centre of the screen and were given training at the beginning of each experiment to familiarize them with the stimuli and task. All subjects had normal or corrected-to-normal visual acuity.

2.3 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

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

where $G_{(x,y,t)}$ represents the luminance at each point of the stimulus at the instant t , L_{mean} is the mean luminance of the resultant pattern, m is the modulation depth (Michelson contrast) of the sine wave carrier (range 0 - 1 Michelson contrast), f_x is the spatial frequency (1 c/deg), f_t is the temporal frequency, ϕ is the phase shift of the sinusoidal carrier, C_n is the contrast (0.5 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 0 (black dot) and 1 (white dot) with an equal probability. There was no luminance variation within each noise pixel. The noise carriers were updated every frame, resulting in dynamic noise. The Gaussian envelope is expressed by the exponential of the Eq.1; x and y represent the respective horizontal and vertical distances from the Gaussian peak, 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:

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

where $G_{(x,y,t)}$, L_{mean} , m , f_x , f_t , ϕ , C_n , $R_{(x,y,t)}$ and σ are the same parameters as in Eq. 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) artefacts (i.e., each subject's equiluminance value was established using the technique described in the next section).

2.4 Procedures

The experiment involved four different stages: (i) determining the contrast threshold; (ii) estimating the subjective equiluminance point for second-order Gabors; (iii) equating first- and second-order motion cues for salience; (iv) the Experiment in which observers had to judge whether an ambiguous test pattern drifted in the same direction or in the opposite direction respect to the adaptation pattern, for first-order, second-order and cross-order motion (i.e., adapting to first-order and testing with second-order, and vice-versa). The procedure used in each phase is described below.

2.4.1 Contrast threshold

A two-alternative forced-choice (2AFC) procedure was used to estimate the contrast threshold corresponding to 90% correct answers. For first-order contrast thresholds, two drifting Gabors were presented successively at the centre of the screen and could drift either rightward or leftward. 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 of the background (15.47 cd/m²). In addition, a white fixation point (0.16 deg in diameter) was drawn in the center of the gray disk. The Gabors were displayed for 480 ms, and between them there was a blank period (ISI) of 480 ms. The white fixation point was present during the ISI. To obtain directional stimuli the phase of the sine wave was shifted by ± 90 , deg every 80 ms, that is, the Gabors drifted with a constant velocity of 3.12 deg/s. Observers performed a 2AFC task, pressing a response button to report whether the

Gabors drifted in the same or different directions. The contrast of the Gabors, determined by the modulation depth of the sine wave, was varied adaptively (i.e., according to the correctness of the response) using a maximum likelihood procedure (MLP; Green, 1990; 1993; see *Appendix*); the range of the modulation depth varied from 0.01 to 0.1 Michelson contrast. We employed this procedure to track the 90%-correct point on the psychometric function. For each participant we considered the measurement of the threshold at the end of each block (32 trials). The procedure used to estimate the contrast modulation threshold for second-order stimuli was identical to that used for first-order stimuli, except for the range of the modulation depth (from 0.1 to 0.4 Michelson contrast). The range of the modulation depth for first- and second-order was chosen based on pilot observations. The contrast value used in subsequent experiments was obtained by multiplying the threshold value by four, in order to better ensure that all subjects could perceive the motion direction of both first- and second-order patterns.

2.4.2 Minimum motion technique

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 centre of the screen and interleaved in a four-frame sequence such that each Gabor's sine wave was shifted by 90 deg, such that first-order Gabors were presented in odd frames and second-order Gabors were presented in even frames (2.08 deg/s). Subjects fixated a point displayed at the centre of the stimuli and to aid fixation the central part of the stimuli was replaced by a disk (0.7 deg in diameter) with the same luminance of the background with a white fixation point (0.16 deg in diameter) inside.

The percentage of 'black dots' (i.e., the number of dots whose value was 0) in the second-order noise carriers was varied from trial to trial according to a simple Up-Down staircase (Levitt,

1971). The rationale was as follows. Varying the percentage of ‘black dots’ (i.e., the contrast of the noise carrier) we produced a luminance imbalance in second-order frames, originating a net directional motion in the four-frame sequence. We aimed to estimate for each subject the percentage of ‘black dots’ of the second-order noise carriers required to null or cancel out any net directional motion (Nishida, Edwards, & Sato, 1997).

At the beginning of the procedure the percentage of the ‘black dots’ was set at 40% (corresponding to 0.4 Michelson contrast of the noise carrier), and the initial staircase step size was 0.05%. After the first, third, seventh and fifteenth reversal of apparent direction the step size was halved and after each halving of the step size the subsequent run was started with a percentage of ‘black dots’ that was the average of the peaks and valleys for 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 percentage of the ‘black dots’ when the observer perceived the pattern to move rightward and decreasing the their percentage 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 the point of subjective equality (PSE; Finney, 1971; McKee, Klein, & Teller, 1985). Therefore PSE directly this corresponded to the percentage of the ‘black dots’ of the second-order noise carrier that produced a percept of ambiguous motion.

2.4.3 Equating stimuli for salience

A possible complication was that while first- and second- order patterns were equated in terms of motion discriminability, they were not equated in terms of subjective pattern salience because the first-order pattern appeared much more salient. This could give rise some differences in the judgments of the direction of the test pattern between first- and second-order when presented separately, and when tested in the cross-adaptation condition. Therefore, in phase (iii) we

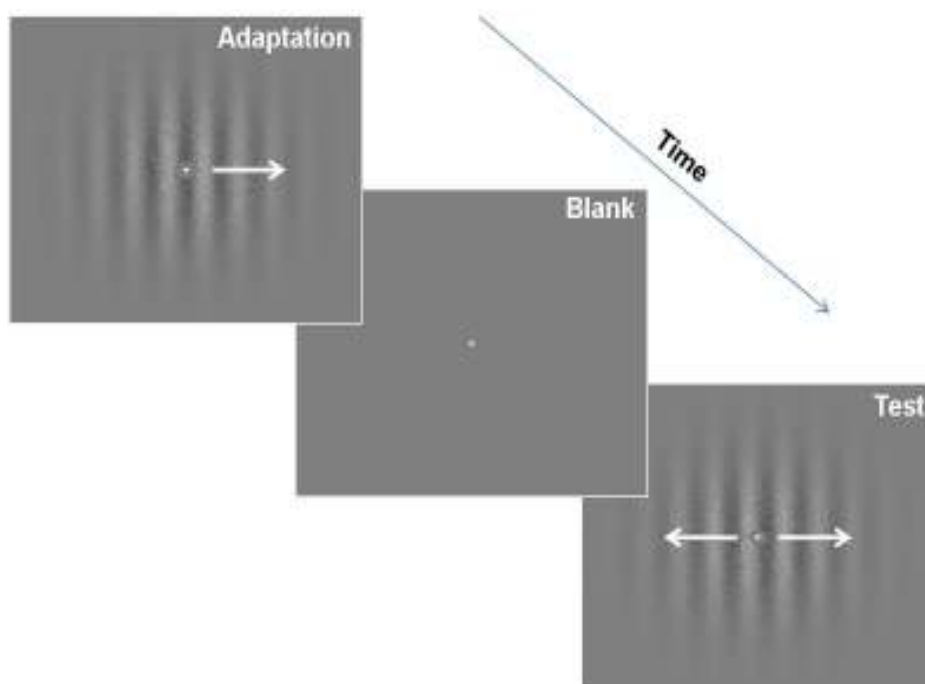
matched first order and second order Gabors' contrast to psychophysically equate their salience. We used another variant of the minimum motion technique (Anstis & Cavanagh, 1983) to estimate the required level of contrast. Subjects fixated a point at the centre of the screen. First- and second-order Gabors were presented at the centre of the screen and interleaved in a six-frame sequence (80 ms per frame), with first-order Gabors presented in odd frames and second-order Gabors presented in even frames. Each first-order Gabor's sine wave carrier was shifted by 90 deg (i.e. quadrature phase) on each appearance, and each second-order Gabor's sine carrier was shifted a corresponding distance in the opposite direction on each appearance. We then manipulated the contrast of the luminance-defined carrier in the first-order Gabor whilst keeping constant the contrast of the second-order Gabor. Initially the contrasts of the first- and second-order Gabors were set equal to those used in the previous phase for each subject. 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 carrier was very low or zero, the perceived motion direction of the six-frame sequence followed the second-order carrier. We measured the contrast of the first-order carrier required to null the unidirectional motion of the second-order carrier, assuming that this contrast equated the salience of first-order carriers with second-order carriers.

2.4.4 Measuring directional bias for first-order, second-order and cross-order motion

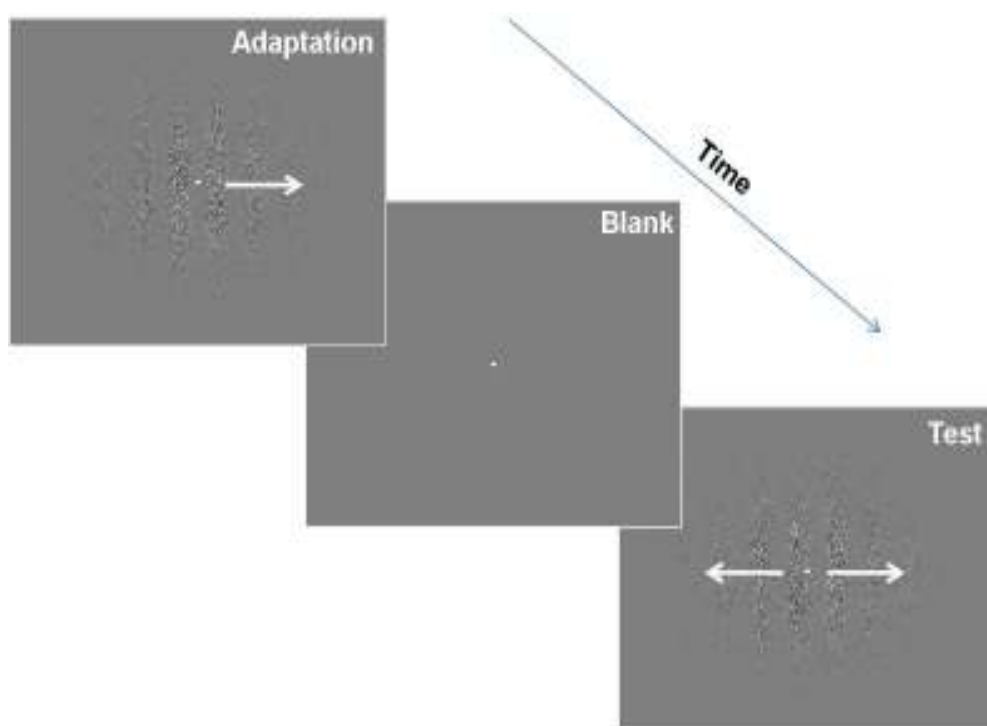
In the phase (iv) of the experiment we assessed the temporal dynamics of the visual motion priming (VMP), motion aftereffect (MAE) and perceptual sensitization (PS) employing different adaptation periods and inter-stimulus intervals (ISI). To aid fixation we used the same configuration to that was used in the previous phases of the experiment. Both directional and ambiguous stimuli were created by shifting the phase of the sine-wave carrier. To obtain directional stimuli the phase was shifted by ± 90 deg every 40 ms. The direction of motion was horizontal either to the right (+ 90 phase shift) or to the left (- 90 phase shift). A 90 deg phase

shift was chosen according to the results of Pinkus and Pantle (1997) where they showed that the visual motion priming is at maximum with this phase shift. Ambiguous test patterns were created by shifting the phase 180 deg every 80 ms. Speed of the test stimuli was equal to that of the adaptation stimulus (6.25 deg/s). 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 7.1). 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) x 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) x 4 (adaptation durations) x 6 (ISIs). Twenty trials were performed for each condition, and the order of conditions was randomized across trials.

A



B



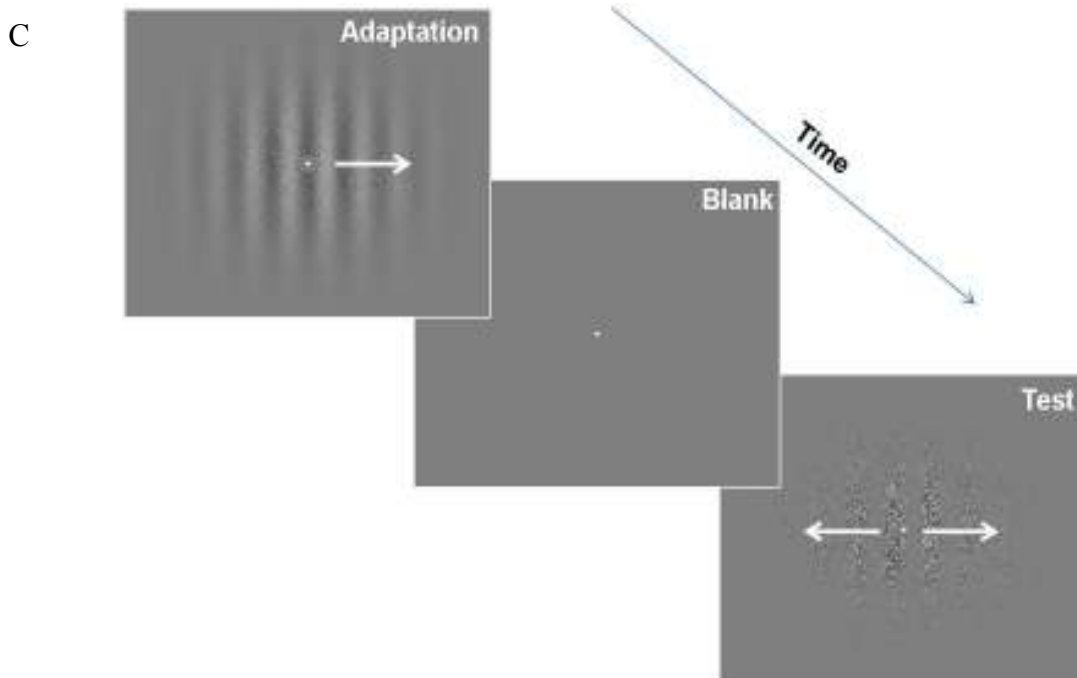


Figure 7.1. Trial sequence for (A) first-order stimuli, (B) second-order stimuli and (C) cross-order stimuli (the picture shows only the case in which adaptation is a first-order drifting Gabor patch and test is a second-order drifting Gabor patch. However, in the experiment we used also the reciprocal condition). For all the Experiments the adaptation stimulus was always directional apparent motion obtained by shifting the phase of the sinewave carrier 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 sinewave carrier by 180 deg. The duration of the test stimulus was always constant (80 ms x 4 frames = 320 ms). For illustrative purposes the Gabors patches reported here have sinusoidal carriers with exaggerated contrast.

3. Results

A repeated measures ANOVA did not show a main effect of the motion order ($F_{(1,7)} = 0.510$, $p > 0.05$). This means that the time courses of the directional biases found for first- and second-order

moving stimuli (Figure 7.2 and 7.3) are very similar. For this reason we analyzed separately the results obtained for first- and second-order motion cues. In particular, we used both a repeated measures ANOVA in order to test the significance of main effects and interactions, and also a series of one-sample t-tests to assess if each condition was significantly different from chance level.

3.1 First-Order Motion

Figure 7.2 shows the results obtained for first-order motion. We plotted the proportions 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 measured ANOVA conducted only on the results obtained with first-order motion patterns showed a main effect of the adaptation duration ($F_{(3,7)} = 20.05, p < 0.01$), a 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 pointed out a significant difference between adaptation at 80 ms 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. Moreover, there were no significant difference between the longer adaptation durations (160, 320, and 640 ms) across all the ISIs tested. To further distinguish if 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. Multiple one-sample t-tests were corrected using the False Discovery Rate procedure (Benjamini & Hochberg, 1995; Benjamini & Yekutieli, 2001). 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 toward the direction of the adaptation stimulus (84% of response in the same direction) ($t_{(7)} = 11.26, p < 0.01$), resulting in a rapid motion priming. In the first-order condition

we did not find any other priming effect, though there was a weak tendency toward facilitation for longer ISIs of 2 or 5 s (Perceptual Sensitization), but only for an adaptation duration of 320 ms.

Upon increasing adaptation duration we found that the perceived direction of the ambiguous test pattern was biased toward the opposite direction to that of the adapting stimulus (rapid motion aftereffect). 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 inter-stimulus interval ($t_{(7)} = -4.66$, $p = 0.002$). However, adapting for 640 ms produced a bias toward the opposite direction of the adapting stimulus after 120 ms (15%) ($t_{(7)} = -7.13$, $p < 0.001$). For any of the adaptation durations used we did not find any significant directional bias with ISIs longer than 1 second.

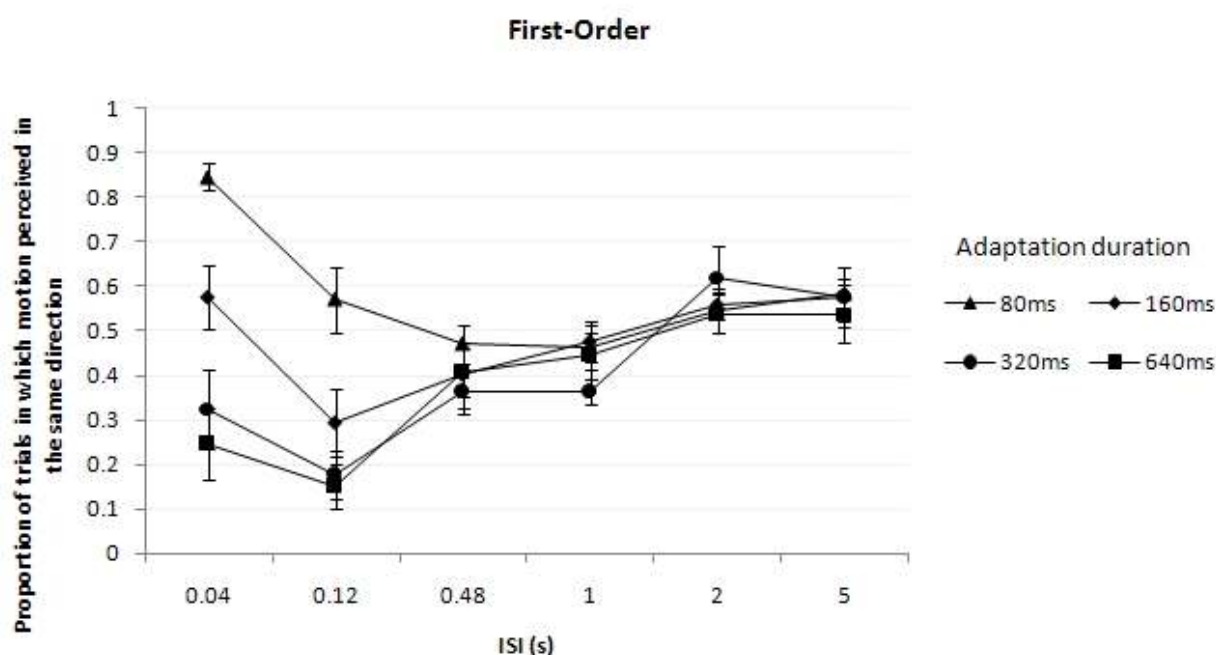


Figure 7.2. Results from Experiment 1 (first-order moving patterns; $N = 8$). For each adaptation duration the proportion of trials in which observers judged the test stimulus as drifting in the same direction as the adaptation stimulus is shown as a function of the inter-stimulus interval duration (ISI). 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 $\pm$ SEM.

3.2 Second-Order Motion

Figure 7.3 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 measured ANOVA conducted only for second-order patterns showed, a main effect of the adaptation ($F_{(3,7)} = 15.48$, $p < 0.01$), a 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 ISI 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 ($p < 0.05$). We did not find any significant difference 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 toward the same or different direction 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 toward the direction of the adaptation pattern ($t_{(7)} = 3.28$, $p < 0.05$) (73% of responses in the same direction) (rapid priming). Moreover, we obtained a significant bias toward adapting direction at 80 ms after 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) (Perceptual Sensitization). Adapting for 160 ms biases the perceived direction of the test pattern toward the direction of the adapting stimulus, but only after 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) (Perceptual Sensitization). 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%) ($t_{(7)}=-3.96$, $p = 0.005$), 120 ms (21%) ($t_{(7)}=-5.49$, $p = 0.01$) and 480 ms (35%) ($t_{(7)}=-3.24$, $p < 0.05$). 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%) ($t_{(7)}=-4.77$, $p = 0.002$) and 120 ms (21%) ($t_{(7)}=-5.40$, $p = 0.001$).

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, suggesting that the differences obtained between first- and second-order motion are 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 toward 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 toward the opposite direction to that of the adaptation pattern, resulting in rMAE. These directional biases arose and decayed rapidly within 1 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.

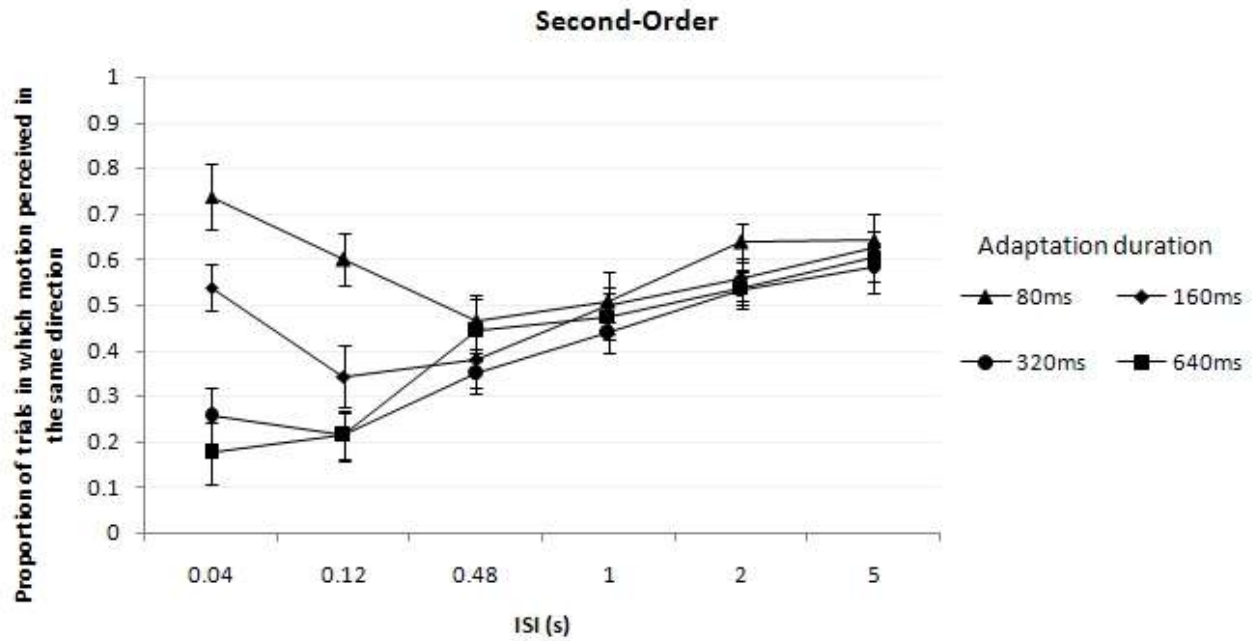


Figure 7.3. Results from Experiment 2 (second-order moving patterns; $N = 8$). For each adaptation duration, the proportion of trials in which observers judged the test stimulus as drifting in the same direction as the adaptation stimulus is shown as a function of the ISI duration. The results are shown 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 $\pm$ SEM.

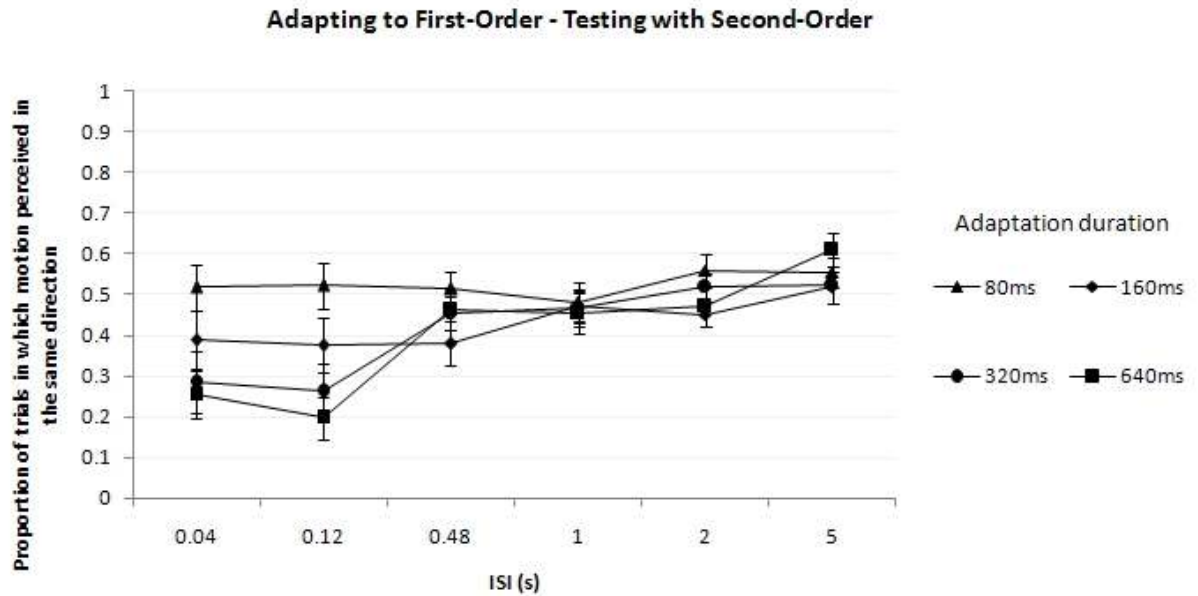
3.3 Cross-Order Motion

Since the results for first- and second-order motion were similar, in the cross-order condition we tested if a single mechanism or two distinct mechanisms can account the effects obtained presenting the two motion cues separately. The results obtained in the cross-adaptation condition are shown in Figure 7.4. A repeated measures ANOVA did reveal a significant effect of the motion order used for adaptation ($F_{(1,11)} = 3.99$, $p > 0.05$). Thus, we analyzed 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 7.4A) 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 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 ($p < 0.05$). For the 480 ms ISI we found a significant difference between the adaptation durations at 80 and 160 ms ($p < 0.05$). We did not find any other significant difference between adaptation periods for the other ISIs used. We also conducted one-sample t-tests. Adapting to first-order and testing with second-order motion we found only rapid forms of motion aftereffects, in particular when: (i) adapting at 320 ms and after an ISI of 120 ms (26% of same responses) ($t_{(11)} = -3.42$, $p < 0.001$), (ii) adapting at 640 ms and after an ISI of 40 ms (25% of same responses) ($t_{(11)} = -4.11$, $p < 0.01$) and (iii) adapting at 640 ms and after an ISI of 120 ms (19% of same responses) ($t_{(11)} = -5.68$, $p < 0.001$).

The same statistical analyses were conducted for the condition in which we adapted to second-order and tested with first-order (Figure 7.4B). In such case 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. Thus, from the cross-adaptation condition it emerges that 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.

A



B

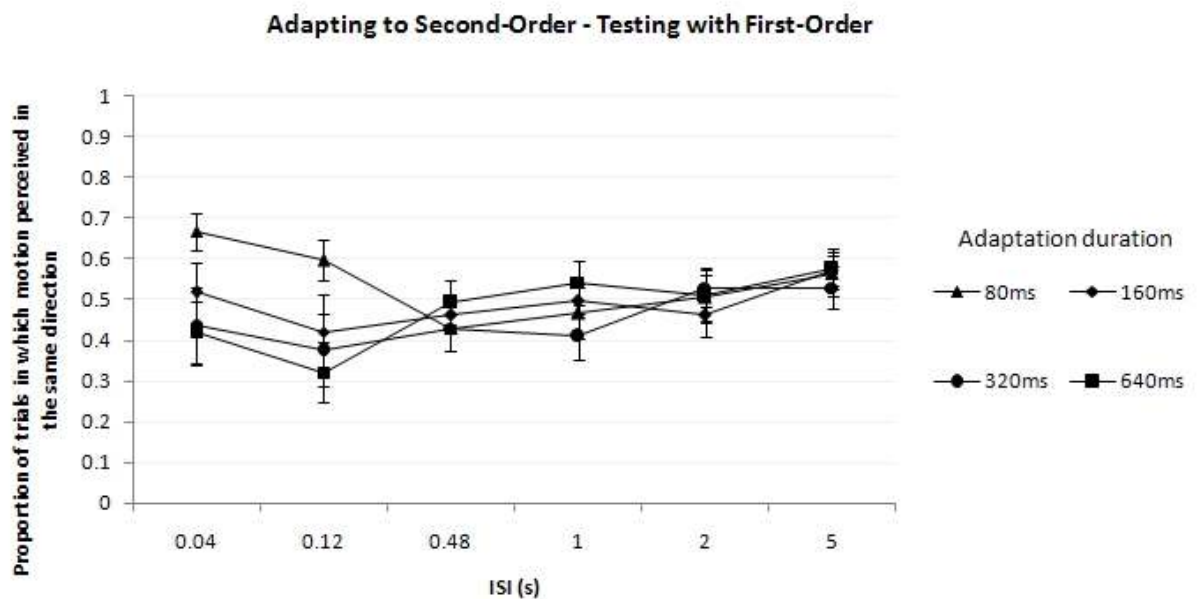


Figure 7.4. Results from Experiment 3 (cross-order adaptation; $N = 12$). As in Experiment 1 and 2, for each adaptation duration, the proportion of trials in which observers judged the test stimulus as drifting in the same direction as the adaptation stimulus is shown as a function of ISI. The results 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 $\pm$ SEM.

4. Discussion

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 toward the same direction to that of the adaptation pattern, but only after an ISI of 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), the perceived direction of the test pattern was biased toward the opposite direction of the adaptation pattern. Thus, rVMP and rMAE occur with the same stimulus configuration, producing two opposite effects due to a slight change in adaptation duration. An interesting finding was that a short adaptation worked as prime, whereas a longer adaptation had an opposite effect. We found that these effects arise and diminish within 1 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 toward the direction of the adaptation pattern, resulting in facilitation that took time to arise (PS). In our experiment we also used longer ISI durations, even though for first-order motion we did not obtain any significant effect despite a weak tendency in such direction. However, for second-

order we obtained perceptual sensitization for the shorter adaptation duration (80 and 160 ms) and for the longer ISIs (2 and 5 seconds), though these effects were very weak in comparison to those obtained by Kanai and Verstraten (2005). This is probably due to the fact that we randomized all the conditions, perhaps masking the effect.

At which neural locus/loci do these effects take place? In a subsequent experiment Kanai and Verstraten (2005) found that both rVMP and rMAE are absent after adaptation to a counterphase flickering pattern (i.e., to energy-balanced motion). The reasoning behind using ambiguous motion during adaptation 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 within 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 et al., 1998 for a review), and the motion priming studied by Campana and colleagues (2002, 2006). 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 second-order motion. 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 pointed to 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 (Leventhal et al. 1998; Barraclough et al. 2006) (see Chapter 1 – Section 5 for more details). Thus, first- and second-order rVMP and rMAE might reflect fast adaptation at the earlier stages of motion analysis such as V1, V2 and V3. In addition, some electrophysiological studies suggested that in the case of 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; Chung, Li, & Nelson, 2002; Chance et al., 1998).

What is the functional role and the underlying mechanism of brief adaptation? A study of Greenlee et al. (1991) investigated the time required for recovery from contrast adaptation. In particular, they adapted observers to first-order gratings flickering at 5 Hz, with different durations (ranging from 1 second to 1000 seconds) of different contrast values. They found that time to recovery depended on adaptation duration and not on contrast of the adaptation stimulus (Figure 7.5). In particular, increasing adapting contrast increased the initial threshold elevation but did not increase significantly 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.

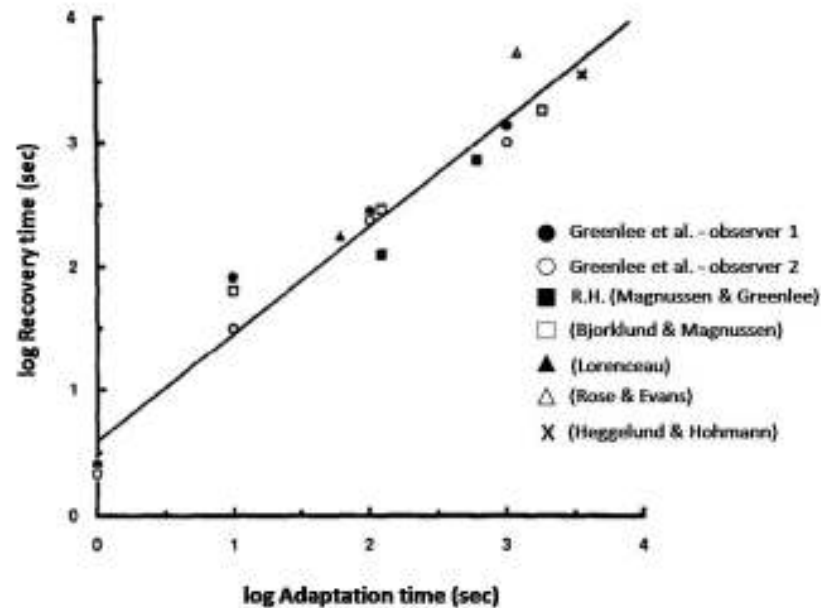


Figure 7.5. Log recovery time as a function of log adapting time. The different symbols refer to the results obtained in different studies in which were tested the recovery time of adapted gratings of various contrast values as a function of adaptation duration. Within the framework of the contrast gain control mechanism, the buildup and recovery from adaptation is represented by a power function of time (since in a log-log plot a linear function is a power function) (Adapted from Greenlee et al., 1991).

The authors 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 can adjust their gain to the prevailing contrast level. In an earlier 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, and so increases the slope (i.e., increase 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 and colleagues (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 number of channels, the activity of these channels might vary due to the presence of errors in the visual system for example. 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 (e.g., motion direction), the initial rise in the activity and the persistence of this enhanced activity of a certain channel would lead 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 own past activity averaged across time. Therefore, based on 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, indeed, could concur in originating and maintaining a “record” of the past activity in the channels that influences, in our case, 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. However, a different mechanism could account for rVMP. It is possible that using very short adaptation duration (e.g., 80 ms) the short-term gain control mechanism is not able to set-in and the rapid motion priming could be based exclusively on the

activity of low-level energy units (Pinkus & Pantle, 1997). Consider Figure 2.4 (Chapter 2), any directional imbalance (DI) in the outputs of motion detectors which is produced by a single motion step (i.e., only one shift in phase, as in the case of the shorter adaptation period used in this experiment) could be shortly delayed for tens of ms (i.e., 40 ms) by the second-stage filter (F2) and then integrated with the balanced output produced by the ambiguous test stimulus. The integrated opponent energy (D2) would cause the ambiguous test pattern to be seen in the same direction as the priming step. However, this is valid for a first-order motion step but for a second-order motion step a rectification or a kind of non linear processing is necessary before motion energy extraction. In this experiment we showed that also a very brief adaptation to second-order motion is able to bias the perceived motion direction of an ambiguous pattern presented after a very brief ISI, although it is not clear exactly which mechanisms are involved.

Kanai and Verstraten (2005) argued that a later stage of motion analysis seems 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) and Huang et al. (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 to 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). On the other hand, shorter ISIs can block or interfere with the building of such episodic representation. Moreover, Campana et al. (2002, 2006) using TMS found that motion priming with ISI of 500 ms 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. 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 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 that rMAEs transfer to second-order stimuli, although these rapid motion aftereffects were weaker than that obtained in the within-order conditions. On the contrary, second-order motion did not influence the processing of first-order motion. We did not observe either rVMP, rMAE or PS when adapting to second-order and testing with first-order. Schofield, Ledgeway and Hutchinson (2007) found similar interactions using dynamic MAE (see Chapter 3 – Section 2) and employing longer adaptation durations. Specifically, 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 when the adaptation and test patterns were of the same type. In addition, these MAEs were tuned for spatial frequency. 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. There was little or no transfer from second-order to first-order patterns. Our results are reliable because we matched for salience first- and second-order motion stimuli, furthermore we used dynamic test patterns which are generally considered to be more sensitive than static test patterns to measure the MAE, and 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 of first-order and second-order motion systems. First-order motion system operate at both low- and high-levels of motion analysis, and appear 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 (Edwards & Badcock, 1995). The findings of this experiment support the presence of such hierarchical organization and the fact that first-order motion influences the perception of second-order motion but not vice-versa; however, first-order motion influences second-order 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. Thus, in agreement with Edwards and Badcock (1995) it is possible that second-order motion detectors receive weak first-order motion signals at different levels of motion processing.

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 are 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) (Edwards & Badcock, 1995). Using random dot

kinematograms, Edwards and Badcock (1995) found that first-order noise dots impaired the ability to extract second-order motion, whereas second-order noise dots had no effect on the extraction of first-order motion. The authors argued that the second-order motion system is also sensitive to first-order motion and this reflects the operations of second-order local motion detectors. Moreover, their findings are indicative of separate processing for first-order and second-order motion at the level of global motion extraction. Thus, 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. In addition, the task and the stimulus configuration that we employed did not permit us to tap much higher-level motion detecting mechanisms and neural substrates where first- and second-order motion are integrated, but allowed investigation of low-levels (V1, V2/V3) and an intermediate level (MT) of motion processing.

APPENDIX

The Maximum Likelihood Procedure

The MLP procedure is composed of two independent processes: the *maximum likelihood estimation* and the *stimulus selection policy*.

Maximum likelihood-estimation. In the ML procedure, prior to beginning an experiment the experimenter constructs an hypothesis. In our case the hypotheses are arrays of contrast values that we selected for first- and second-order stimuli (i.e., each contrast value represent a psychometric function). Each of these functions has the same fixed slope (β), false alarm rate / chance level (γ) and attentional lapse rate (λ), but differs in the midpoint (α).

After collecting the subject's response, the procedure selects the hypothesis having the highest likelihood to resemble to the actual subjects' psychometric function by means of the following function:

$$L(H_j) = \prod_{i=1}^n H^C(x_i)[1 - H(x_i)]^I \quad (1)$$

where $L(H_j)$ is the likelihood of the j^{th} hypothesised function, i is the number of trials, the exponents C and I are, respectively, equal to 1 and 0 when the response is *yes* (or correct) and 0 and 1 otherwise.

Once the likelihood of each hypothesis has been calculated the ML procedure selects the highest likelihood hypothesis. The likelihood of the hypotheses is calculated trial by trial. Thus, after the first trial a ML estimate is returned by the procedure, although it may be highly inaccurate. The

more the trials, the more accurate the estimate becomes. Therefore, the best estimate is that returned by the last trial.

Stimulus selection policy. Once the most likely hypothesis has been found the next stimulus is set at threshold level (i.e., at p-target) (Simpson, 1989). Even after the first trial, the ML procedure has enough information to select the threshold level. This is because the most likely hypothesis is also the hypothesis containing the most likely subject's threshold. Thus the threshold level can be calculated by means of the inverse function of the most likely hypothesis function. In practice, the level of the next stimulus will be the inverse of the most likely hypothesis at p-target, therefore:

$$\Psi^{-1}(p_t) = \alpha_j - \frac{1}{\beta} \ln \left(\frac{1 - \lambda - \gamma}{p_t - \gamma} - 1 \right) \quad (2)$$

where p_t is p-target.

Green (1990, 1993) point out the presence of an optimal p-target. This particular p-target (*sweetpoint*) optimises the estimate of the subject's threshold. This is because the variance associated to the estimate of this particular p-target is smaller than the variance associated with any other possible p-target. The variance of the threshold estimate associated with any p-target is equal to the binomial variance, $\Psi(1-\Psi)$, divided by the slope of the psychometric function squared, therefore:

$$\sigma^2 = \frac{\Psi(1-\Psi)}{\Psi'^2} \quad (3)$$

where Ψ'^2 is the derivative of the psychometric function slope squared. The best possible p-target is the minimum of the distribution resulting from the above ratio. In the case of the logistic function the sweetpoint (p_{sw}) can be calculated analytically as follows (Green, 1993):

$$p_{sw} = \frac{2\gamma + 1 + \sqrt{1 + 8\gamma}}{3 + \sqrt{1 + 8\gamma}} \quad (4)$$

If we assume that the subject does not produce any attentional lapses the sweetpoint depends exclusively on γ .

The major advantage of the ML is its speed. Green (1993) claimed that twelve trials of ML are sufficient for a reliable threshold estimate. Moreover, another advantage of the ML procedure is the possibility to track a point of the psychometric function (i.e., p-target). This is particularly interesting when the experimenter needs to replicate the results of a study targeting a specific point of the psychometric function.

However, the ML method has disadvantages. The first is that both the shape and slope of the hypothesised psychometric functions are determined a priori by the experimenter. These parameters are unknown and might not coincide with the “true” ones. Green ran several stimulations evaluating whether the mismatch between the “true” subjects’ psychometric function and the psychometric function hypothesised by the procedure affects the threshold estimation. He found that (i) a shape mismatch (comparing logistic and Gaussian functions) does not have evident effect on the threshold estimation, and that (ii) a slope mismatch can affect the threshold estimates for example, by increasing the estimate’s variance (Green, 1990, 1993). Moreover, the experimenter might not know in advance the rate of attentional lapses (λ) or false

alarm tendency (γ). In three papers, Green and colleagues (1993, 1995; Gu & Green, 1994) investigated whether the lack of knowledge of these two parameters (i) affects the threshold estimate and (ii) whether these two parameters can be estimated by ML procedure together with the subject's threshold. Subjects' lapses of attention affect much the threshold estimate when they are numerous (e.g., 20% of the responses given by the subject) and moderately when they are few 1-5% (Green, 1995). In particular, the effect of lapses of attention is large in the first five trials but almost negligible in the later ones (Gu & Green, 1994).

To summarize, the most important advantages of the ML procedure are its speed and the possibility of tracking different p-targets. On the other hand, the disadvantages are that some of the parameters of the hypothesized psychometric functions are unknown and that the threshold estimation might be affected by the false alarms and by the attentional lapses.

Chapter 8

General Discussion

The Experiments outlined in this Thesis were developed to further investigate the perception of first-order and second-order motion. To this purpose we employed different experimental paradigms such as visual motion priming (VMP), motion-induced position shift (MIPS) and motion aftereffect (MAE). Our goal was to better understand how first-order and second-order motion are integrated or combined and to infer at which level along the motion processing hierarchy such integration occurs, for which we employed different cross-order conditions. Taken together our results suggest that first-order and second-order motion are analyzed separately from low-levels (V1, V2 and V3) of motion analysis up to the motion integration level MT. We provided some evidence regarding the presence of cross-order effects in the motion processing pathway, though these effects are very weak and small compared to those obtained in the within-order conditions (i.e., when first-order and second-order motion are presented separately). Further suggesting some degree of separation between a motion system that primarily encodes first-order motion and a system that encodes mostly second-order motion.

In the first Experiment (see Chapter 5) we used a repetition priming paradigm to investigate the implicit short-term memory mechanisms for first- and second-order motion cues. We found that priming for motion direction exists with first-order and second-order motion when presented separately and it is also sensitive to spatial position (i.e., we found a significant interaction between priming for motion direction and spatial position). Faster reaction times were found when both motion direction and spatial position were repeated. Moreover, we found priming for

motion direction in the cross-order condition (i.e., when first-order motion primed second-order motion and vice versa) although the effect size was about half of that found in the two within-order conditions, and no significant interactions between motion direction and spatial position were found in this case. These data suggest that priming for first-order and second-order motion may be served by different neural circuits in the same retinotopically organized neural structures. Indeed, in the within-order conditions we found priming for motion direction as well as interaction between motion direction and spatial position. In addition, the results obtained in the cross-order condition suggest that the neural locus in which the same neurons hold a unique representation for first- and second-order motion signals is not position sensitive. This suggests that first-order and second-order motion signals could be pooled at a motion analysis level in which the retinotopic organization is completely lost or it is very coarse (e.g., MST). Overall, these results suggest also that the neural substrate for priming of motion direction may change depending on task demands and stimulus characteristics. Whereas when first- and second-order motion is presented separately priming can be based on the activity of retinotopically organized areas such as MT, but when the two kinds of motion are interleaved across trials, the neural locus mediating priming may shift to higher visual areas, where the retinotopical organization is lost or at least is very coarse.

Thus, the specific level of representation triggering the priming effect could be dependent not only on the kind of feature that is primed, but also on the task or the context. This short-term implicit memory, which can be viewed as a pre-activation for a given feature or ensemble of features, could be held in multiple sites along the visual pathways, as suggested by a recent fMRI paper that revealed the neural correlates for priming of pop-out (Kristjansson, Vuilleumier, Schwartz, Macaluso, & Driver, 2007), and the specific stimulus and task requirement could trigger the locus where the retrieval occurs.

The results of the first experiment suggest the presence of partially separate and independent memory stores for the two motion detecting-systems up to a certain level of motion processing, converging into common mechanism and representation at higher levels of the visual hierarchy. Given the dependence of priming for both first- and second-order motion upon spatial position, in the second experiment (see Chapter 6) we further investigated the issue of how the two types of motion encode the spatial position. In particular, we assessed if a single and common mechanism is responsible for encoding and assigning the spatial position of first- and second-order moving patterns, or two distinct and separate mechanisms encode and assign the location. To investigate this we measured the motion-induced position shift for first- and second-order moving stimuli presented separately and in a cross-order condition in which first- and second-order stimuli were presented within the same trial. We found that both first- and second-order moving objects shift the perceived position, although with different spatiotemporal tunings, further suggesting distinct motion-detecting mechanisms for these two motion cues. However, in the cross-order condition when first- and second-order were matched for salience we did not obtain any significant positional shift, clearly suggesting that first- and second-order motion mechanisms independently encode and assign the spatial position of a moving object.

A large number of recent papers have investigated the properties of visual processes that mediate global operations across space, such as the detection of a virtual spatial contour linking a series of Gabor patches (Field, Hayes, & Hess, 1993). Field et al. (1993) proposed a model of global integration based on ‘association fields’ which link together information from different local spatial filters or receptive fields. Such a process could be implemented by long-range lateral connections between cortical cells with widely separated retinal receptive fields. The experimental task employed to measure a motion induced position shift also requires the subject to integrate information across space by linking together two Gabor patches and extracting the orientation of a virtual line joining them. Important differences have been reported between

static first- and second-order Gabors in tasks requiring global interactions, which are consistent with our position shift results. Ellemberg, Allen, and Hess (2004) found weaker lateral spatial interactions between second-order Gabor patches compared to first-order Gabor patches. In a task involving orientation discrimination of Gabor patches, Allen, Hess, Mansouri, and Dakin, (2003) found that subjects were unable to combine information between first-order and second-order Gabors. They concluded that there are separate global integration mechanisms for first-order and second-order attributes. These results are consistent with our failure to observe a cross-order position shift since, in order to judge the relative positions of first-order and second-order patches it is necessary to integrate information between them. Huang and Hess (2007) recently studied collinear threshold facilitation with first- and second-order Gabor patches. In this paradigm, the detectability of a central target patch is improved by the presence of collinear flanking patches. Huang and Hess (2007) found weaker facilitation when both target and flanker patches were second-order than when both patches were first-order, but no facilitation at all when one patch was first-order and the other was second-order. They favoured an account of facilitation involving long-range interactions that occur only between patches that match in order. Their results are consistent with the pattern of results we obtained.

Despite the involvement of apparently distinct mechanisms for first- and second-order motion stimuli, our first two experiments do not allow us to conclude if the stage at which location is coded is the same, or different for first- and second-order motion. Although, the finding that priming for motion direction is position sensitive for both first-order and second-order and the similarity of results obtained in terms of reaction times and accuracy, suggests the involvement of the same neural substrate/s that maintain/s a retinotopical organization. Recent studies point out that the stage at which motion could strongly influence perceived position is situated at the level of area MT (Ashida et al., 2007; McGraw, Walsh, & Barrett, 2004). Using a motion adaptation paradigm McGraw et al. (2004) (see Chapter 3), found that area MT is involved in

modulating the positional representation of objects presented after the adaptation period. They disrupted the MT cortical activity using TMS immediately after motion adaptation. When TMS was delivered to MT the perceived misalignment of the test stimulus was greatly reduced. On the other hand, disruption of V1 had no effect on the perceived position after motion adaptation. This result demonstrates that the locus at which motion and positional information interact is situated in MT rather than in V1/V2. Similar findings were found by Campana and colleagues (2002, 2006) with motion priming as they showed that priming for motion direction relies on the activity of area MT. Delivering TMS over MT gave a significant increase in reaction time, whereas TMS over V1/V2 did not significantly influence the performance. However, these results are based only on first-order motion patterns. Using fMRI, Ashida and colleagues (2007), examined with motion adaptation whether a single and common mechanism is responsible for the detection of first- and second-order motion, or whether two separate but co-localized mechanisms exist within the same cortical area. The results showed direction-selective adaptation independently for each type of motion in area MT. Similar findings were also found in area V3A. Moreover, they did not find cross-order adaptation between first-order and second-order motion patterns. The results provide strong evidence for separate neural populations responsible for detecting first- and second-order motion that whilst co-existing in the same area, encode and assign the position of moving objects independently. Consistent with this perspective, Edwards and Badcock (1995) provided psychophysical evidence regarding the independence of first- and second-order motion systems at the level of MT with respect to global-motion pooling. They showed that adding a second-order motion signal consisting of contrast-modulated dots equal in strength and moving in an opposite direction (i.e. transparent motion) to a first-order global-motion signal consisting of luminance-defined dots had no effect on the extraction of the first-order global-motion signal, while adding a first-order motion signal to a second-order global-motion signal effected the extraction of the second-order global-motion

signal. These results propose a system that responds only to first-order motion, and an independent system that encodes both first- and second-order motion. Moreover, these motion systems appear to remain separate up to and including the level at which global-motion signals are extracted.

The dissociations found between the tuning for first- and second-order moving patterns and the results from cross-order motion suggest that object position is not assigned by a single, common mechanism. Rather, it seems that multiple channels and motion processing streams are involved in the assignment of an object's location. Psychophysical, TMS and fMRI results (Campana, Cowey, & Walsh, 2002; Cowey et al., 2006; McGraw et al., 2004; Ashida et al., 2007) support the idea that different mechanisms exist for the detection and position assignment of different types of motion, and that they could be co-localized in the same cortical area. Thus, there seem to be distinct and separate motion-detecting mechanisms for first- and second-order motion that independently encode many features of a moving stimulus (i.e., spatial frequency, temporal frequency, spatial position and so on).

The findings obtained in the third experiment (see Chapter 7) support the theoretical framework outlined above. In the third experiment we used a paradigm developed by Kanai and Verstraten (2005) to attempt to tap low-level (e.g., V1, V2 and V3) and intermediate levels (e.g., MT) of motion analysis. In particular, the authors showed that, depending on both the duration of the adapting stimulus and the duration of the adaptation-test blank interval, the perceived direction of an ambiguous test pattern is biased towards the opposite direction of the adaptation pattern (rapid motion aftereffect - rMAE), or in the same direction (rapid visual motion priming - rVMP). Moreover, they showed that using greater adaptation durations and adaptation-test blank intervals longer than 1 second, the perceived motion direction of the test pattern is biased toward the same motion direction. We argued that very brief adaptation durations could selectively tap

the response of low-level first- and second-order motion detectors, whereas longer adaptation and ISI durations could reflect higher-level activity. In essence, in the third experiment assessed if rVMP, rMAE and the Motion Priming obtained for longer ISI (Perceptual Sensitization - PS) exist also within the second-order motion domain. We found that rVMP, rMAE and PS had similar time courses for first-order and second-order motion patterns when presented separately, though with some small differences. For example, we found PS only for second-order motion and not for first-order, even if, in the case of first-order motion, there was a weak tendency in direction of facilitation for the adaptation period at 320 ms and for the longer ISIs (i.e., 2 and 5 s). Moreover, the rVMP and rMAE were slightly weaker for second-order than for first-order motion, but the analysis of variance (ANOVA) did not point out any significant effect of order. Instead, in a cross-order adaptation condition (i.e., adapting to first-order and testing with second-order and vice versa) we found asymmetric transfers between first- and second-order motion. The logic behind the cross-order condition was to assess if a single mechanism could explain the results obtained presenting first- and second-order motion separately. We found that first-order motion influenced (although less than in the within-order conditions) the processing of second-order motion (see Schofield et al., 2007). We found that some rMAEs induced adapting to first-order motion transferred to second-order stimuli, whereas second-order motion did not influence the processing of first-order motion. Indeed, we did not observe any rVMP and rMAE when adapting to second-order and testing with first-order. These findings further suggest that despite the presence of similar time courses of early and late adaptation effects for first- and second-order motion, the mechanisms underlying the perception of these two classes of stimuli remains rather separate from the lower levels of motion analysis up to and including the motion integration level (i.e., MT) (Edwards & Badcock, 1995). However, under certain conditions, there is some ‘cross-talk’ effects between first- and second-order systems. As discussed in Chapter 7, the asymmetric transfer between first-order and second-order motion could be due to

the hierarchical organization of first-order and second-order motion systems. The first-order motion system seems to operate from the lower levels of motion analysis to the higher levels, influencing the perception of second-order motion, whereas second-order motion system appears to operate mostly at intermediate- and high-levels of motion processing and does not interfere with the processing of first-order motion (Edwards & Badcock, 1995). The findings of the latter experiment support the presence of such hierarchical organization and the fact that first-order motion influences the perception of second-order motion but not vice-versa. Thus, it is possible that second-order motion detectors receive weak first-order motion signals at different levels of motion processing (Edwards & Badcock, 1995).

However, the cross-order effects obtained are always weak and they are not comparable with the effects of first- and second-order stimuli when presented separately. Our results support the notion that these two motion cues are processed by different mechanisms and distinct neural populations, but probably laying in the same cortical areas at low- to middle-levels of the “motion stream”, and are integrated at a later stage of motion processing (e.g., MST). Further research is necessary to assess more directly the locus at which first-and second-order motion are integrated.

The majority of current models of first-order and second-order motion perception (e.g. Wilson, Ferrera & Yo, 1992) include two separate pathways for first-order and second-order motion, one encoding first-order signals and the other encoding second-order motion signals. The data outlined in this Thesis supports the model of Wilson et al. (1992; see Chapter 1) (Figure 8.1). In this model the image is initially filtered by orientation-selective and spatial frequency-selective filters. The information is subsequently passed to two different streams. In the case of first-order information, the local motion energy contained within the image is simply extracted using, for

example, Reichardt-like detection units. With respect to second-order motion, a rectification stage follows the initial filtering of the image. The rectification is essential to turn second-order information into first-order information and is followed by a second stage of orientation-selective and spatial-selective filtering, before the local motion energy is finally extracted using always, for example, Reichardt-like detection units. First-order and second-order local motion signals are then combined in a spatiotemporal integration stage to compute the net direction of image motion.

The findings of the experiments outlined in this Thesis are easily interpreted and explained within the framework of such a model, in which first-order and second-order motion signals are encoded separately from the earlier stages of visual processing. The two motion streams or pathways seem to have preferential selectivity to different spatial and temporal frequencies, and are apparently able to encode different attributes of a moving stimulus such as position. Another important aspect of this model, again supported by our data, is that the neural responses to the two classes of motion can be subsequently pooled at higher levels along the visual hierarchy. According to our data, it is possible that first-order and second-order signals are pooled at a motion analysis stage in which the retinotopical organization is lost. A similar stage would analyze more complex motion patterns such as optic flow, rotational or expanding and contracting patterns (e.g., MST) (see Chapter 1, Section 3.3.3). The two parallel motion streams can be implemented on the same cortical areas but involving distinct and separate neural circuitries (see Ashida et al., 2007). First-order and second-order motion signals seem to remain separate from low-levels (V1, V2 and V3) up to and including area V5/MT.

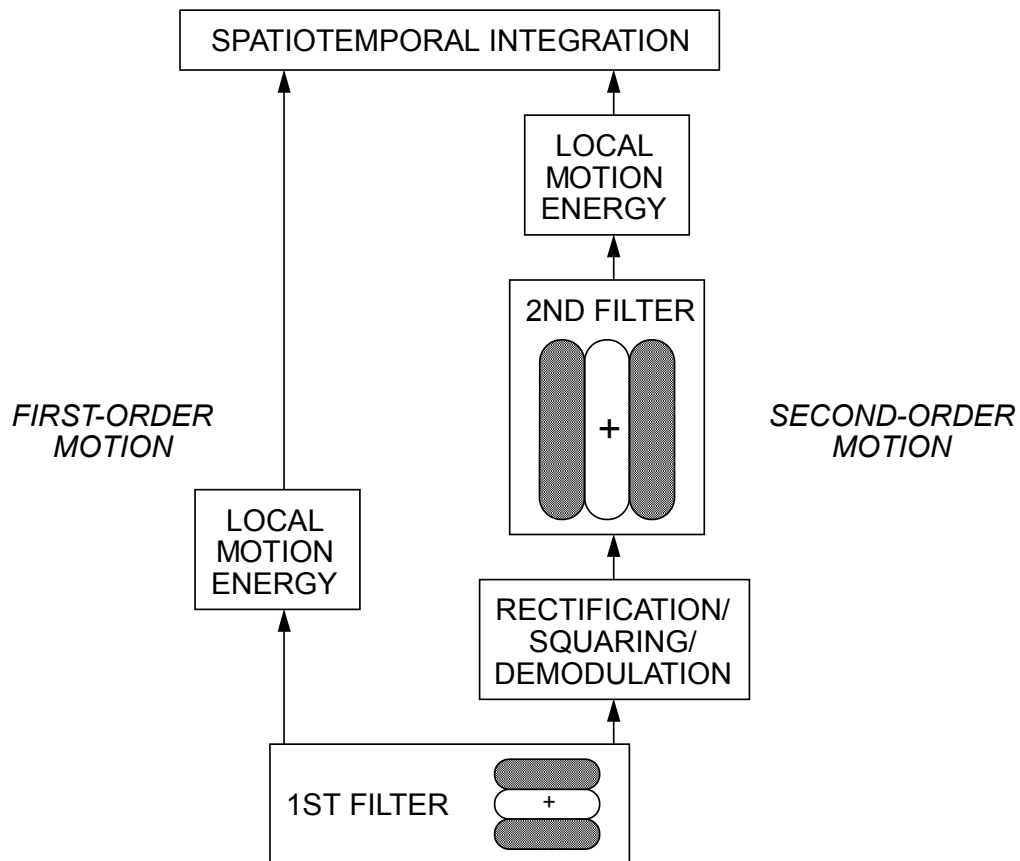


Figure 8.1. Generic model of first-order and second-order motion processing outlined by Wilson et al. (1992). The image is filtered with orientation-selective and spatial frequency-selective filters before branching off into two separate streams. For first-order (luminance-defined) motion, the local motion energy contained within the image is simply extracted using Reichardt-like detection units. For second-order motion, a rectification stage follows the initial filtering of the image. The rectification stage turns second-order information into first-order information and is followed by a second stage of orientation-selective filtering at a different spatial scale, before the local motion energy is finally extracted. The local first-order and second-order motion information is then pooled for spatiotemporal integration (Chubb & Sperling, 1988; Wilson, Ferrera, & Yo, 1992; Baker, 1999) (Taken from Hutchinson, 2005).

The data of the third experiment (see Chapter 7) suggest the presence of similar low-level and high-level mechanisms that encode first- and second-order characteristics. However, further studies are necessary to explore at which level are present second-order motion detectors. Currently no cells have been identified that respond solely to second-order motion. As discussed previously (Chapter 1 - Section 4.3) this is because neurons that respond to second-order motion have been probed and selected using luminance bars or first-order drifting gratings. Therefore, it would be beneficial to use second-order drifting gratings in order to locate cells that respond selectively to second-order motion. The response properties of such cells could provide reliable information about the extraction of second-order motion, and possibly the selectivity of such ‘extraction’ neurons (Hutchinson, 2005). Moreover, it would also be worthwhile examining whether neurons that respond to one type of second-order motion respond to other types of second-order motion and, if so, compare their response properties. The model of Wilson et al. (1992) can account for a wide range of psychophysical data. Indeed, a number of studies and our results conclude that first-order and second-order motion are encoded separately, or at least with some degree of separation, in the initial stages of visual processing. However, the model of Wilson et al. (1992) does not incorporate recent discoveries concerning second-order motion perception. For example, it assumes that the stage at which first-order and second-order motion are extracted (i.e. the motion energy stage, see Figure 8.1), the motion sensors are identical. However, it has been shown that first-order and second-order motion mechanisms exhibit different spatiotemporal sensitivity, different direction selective properties, and therefore, different velocity sensitivity (Ledgeway & Smith, 1997; Ledgeway & Hess, 2002; Bressler & Whitney, 2006). These studies highlight that the mechanism(s) which extract/s motion from second-order images may have many different response characteristics to those that encode first-order motion. Thus, more studies are required to further understand the response properties of the second-order detectors. In addition, more research is necessary to investigate at which level

integration occurs, and also how first-order and second-order motions are integrated. Integration could occur, for example, through a vector summation or a winner-takes-all mechanism (Hutchinson, 2005). The data presented in this thesis indicate a possible involvement of area MST in the combination of first- and second-order motion. Nevertheless, the development of an experimental design that taps that level of motion processing is necessary to obtain a greater understanding of the combination mechanism itself.

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