the neural correlates of the jitter illusion

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Papers and proceedings arising from this research

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To my parents, Tony and Judy, who still provide the best education – in every sense of the term – possible. To my sister Amy, whose love and support is so very important to me. And to Rick, whose ideas, friendship and love I treasure.

To Rita, Betty, Margaret and Alec, whose unconditional love (whilst not always warranted) has been a source of such comfort. And finally to Anne, Laura, Sarah and all the other exciting minds to which I consider myself so lucky to have been exposed – may it always be so.

abstract

The work that follows introduces a new visual illusion. The ‘jitter’ illusion arises in response to single brief presentations of *stationary* Glass patterns composed of decrement- and increment-defined dot-pairs. Remarkably, the perceptions that arise are of coherent global motion in trajectories that are consistent with the spatial configuration of the Glass patterns; patterns configured according to concentric functions give rise to perceptions of motion in concentric trajectories, those configured according to radial functions give rise to perceptions of motion in radial trajectories, and so on. The aim of the work that follows was to develop a model of the neural correlates of this illusion. An additional aim was to explore the implications of such a model for developing a broader understanding of the means by which coherent visual perceptions arise.

Experiments were conducted under the working hypothesis that the jitter illusion is mediated by activity that arises within the magno-cellular (M-), and not the parvo-cellular (P-) pathway of the visual system. It is argued that a model based entirely on M-pathway activity can effectively account for the illusion if two critical conditions are met. The first is that the model must propose the mechanism by which presentations of *stationary* Glass patterns stimulate activity in the *motion*-sensitive cells of the M-pathway. The second is that it must propose plausible mechanism(s) by which the ensuing M-pathway activity gives rise to perceptions of coherent global motion. Experiments reported in chapters 3 and 4 address the first of these conditions. Data from these experiments suggest that abrupt changes in luminance introduced at the onset and offset of stationary Glass patterns (and *not* eye-movements) mediate the M-pathway activity on which the illusion is based. Experiments reported in chapters 5 through to 8 address the second condition. In chapters 5 and 6, the data suggest that the patterns of Off- and On-channel responses elicited by *individual* Glass pattern dot-pairs somehow stimulates cells that act as ‘local’ motion detectors. In chapters 7 and 8, models of the means by this occurs were tested. The resulting data rule out the possibility that the stimulation is a product of a processing asynchrony in the M-pathway Off- and On-channels. Instead, they are consistent with a model based on the *diphasic temporal impulse-response functions* attributed to cells that make up the M-pathway. Based on its ability to satisfy each of the stated conditions, the so-called

diphasic TIRF model is presented as a plausible account of some of the neural correlates of the jitter illusion.

The implications of the diphasic TIRF model are discussed in relation to both the jitter illusion and to visual processing more generally. One of the critical (and novel) implications of the model is that under some circumstances, M-pathway mechanisms ‘extract’ structural information from static visual images that P-pathway mechanisms cannot. On this basis, it is argued that both the jitter illusion and the diphasic TIRF model offer valuable insights into some of the means by which light-induced activity within the human visual system gives rise to coherent global perceptions.

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CHAPTER 1
general introduction

Visual perceptions are a product of the cascade of neural activity elicited when light energy falls upon the retina. Interestingly, the activity on which these perceptions are based arises in a number of different 'streams' within the human visual system. These streams, usually referred to as pathways or channels, are both functionally and structurally distinguishable; evidence suggests that the cell populations of which they are composed are exquisitely sensitive to different visual cues (Schiller 1982; Schiller, Sandell & Maunsell 1986; Schiller, Logothetis & Charles 1990(a) and (b)) and retain a degree of anatomical independence throughout the visual system (Livingstone & Hubel, 1987 & 1988). As a consequence of this, one of the key questions currently facing vision scientists is how patterns of neural activity elicited across the different pathways and channels are integrated such that coherent 'global' visual perceptions arise. To that end, research within the field of vision science often focuses on determining the neural correlates of *particular* visual perceptions – the rationale being that through the identification of these correlates in particular cases, more general principles about how light-induced activity within the human visual system gives rise to coherent global perceptions may emerge.

Relative to other types of visual perception, visual illusions are unique in that they arise when the visual system's interpretation of information contained within the visual scene is not consistent with objective measures of that information. In the case of the Muller-Lyer illusion, for example, subjective experiences of length are often inconsistent with objective measures. One consequence of this unique characteristic is that investigations into the neural bases of visual illusions can expose properties of visual system processing *that may not otherwise be apparent*. That is, through the process of identifying the neural correlates of some visual illusions, novel insights into the neural activity underlying coherent global perceptions can arise.

With that in mind, the work that follows was aimed at identifying the neural correlates of a *new* visual illusion – dubbed the 'jitter' illusion for reasons that will be outlined below. In the chapters that follow the experiments on which this identification was based will be discussed in detail, as will the characteristics (and merits) of the resulting model of the neural bases of the illusion. In line with the above discussion, an additional and critical issue that will be addressed is the broader implications of this model for deriving more general principles about how light-induced neural activity within the visual system gives rise to coherent perceptions of the visual world.

Glass patterns

Glass patterns (first described by Leon Glass in 1969) are a class of stimuli that are composed of two sets of dots, each of which is simultaneously presented on a uniform background. Of these sets, one is made up of dots that are positioned randomly within a specific stimulus area. The other is made up of dots that are positioned, each with respect to one of the random dots, according to a universal function (Glass 1969). In the case of Glass patterns that are generated according to a concentric function, for example, the partner of each random dot is assigned a spatial position based on a concentric function (see Figure 1.1). In this way, a number of different types of Glass patterns can be constructed. In the work that follows these types will be referred by the functions used in their construction – patterns constructed using a concentric function will be referred to as 'concentric' Glass patterns, those constructed using a radial function will be referred to as 'radial' Glass patterns, and so on.

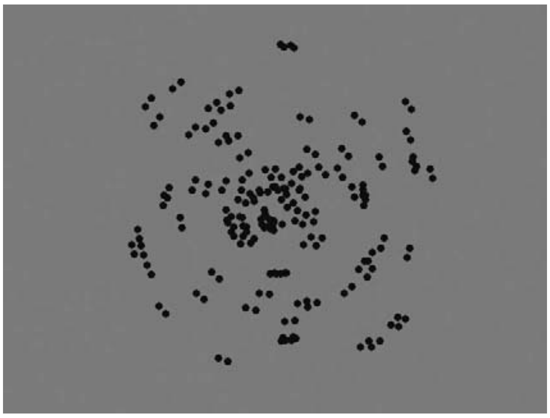

Figure 1.1: Glass patterns are composed of two sets of dots presented simultaneously. For every random dot a partner is generated and positioned according to a universal function. In the case of this 'concentric' Glass pattern, partner dots were positioned according to a concentric function.

The types of dots of which Glass patterns are composed play a critical role in the perceptions to which the patterns give rise. It is well documented that patterns composed entirely of decrement-defined dot-pairs (pairs in which each dot is *darker* than the background) and patterns composed entirely of increment-defined dot-pairs (pairs in which each dot is *lighter* than the background) give rise to perceptions of striking global form that is consistent with the function used to generate the pattern (Glass 1969; Anstis 1970; Dakin 1997). That is, concentric Glass patterns give rise to strong perceptions of concentric structure, radial Glass patterns give rise to strong perceptions of radial structure, and so on (see Figures 1.2(a) and (b)). It has also been well documented (Anstis 1970; Glass & Switkes 1976; Earle 1991) that patterns composed of decrement- and increment-defined dot-pairs (pairs in which one dot is *darker* and the other *lighter* than the background) do *not* give rise to equivalent perceptions. While these patterns do appear ordered, they do not elicit strong perceptions of a structure that is consistent with the function used in their construction (see Figure 1.2(c)).

(a) **(b)** **(c)**

Figures 1.2(a), 1.2(b) and 1.2(c): The perceptions that arise in response to (in this case concentric) Glass patterns are determined by the dot-pairs of which the patterns are composed. Inspection of Figures (a) and (b), in which patterns are composed of decrement-defined dot-pairs and increment-defined dot-pairs respectively, demonstrates that such patterns give rise to coherent, ‘structured’ perceptions. Inspection of Figure (c), on the other hand, illustrates that patterns composed of decrement- and increment-defined dot-pairs do not.

Several models of the neural activity arising in response to Glass pattern presentations can account for the qualitatively different perceptions that are elicited by the patterns represented in Figure 1.2 (see Prazdny 1986; Wilson, Wilkinson & Asaad 1997; Wilson & Wilkinson 1998). These models propose that coherent, ‘structured’ global perceptions only arise when individual dot-pairs stimulate orientation-sensitive cells found early in the visual system. According to the models, this is only possible when the dots of which each pair is composed stimulate excitatory activity in cells *associated with the same visual channels*. Independent evidence suggests that decrement dots stimulate excitatory activity in cells associated with one channel, while increment dots stimulate excitatory activity in cells associated with another (Schiller 1982; 1992 - see chapter 5 for a detailed discussion of the Off- and On-channels). On this basis, the models successfully predict that Glass patterns composed of decrement-defined *or* increment-defined dot-pairs will elicit coherent 'structured' perceptions, but that patterns composed of decrement- *and* increment-defined dot-pairs will not. The neural bases of the perceptions that arise in response to this final type of Glass pattern are of particular relevance to the work that follows, because it is presentations of these patterns that give rise to the jitter illusion.

The jitter illusion

The jitter illusion is a term that refers to perceptions of *coherent global motion* that arise in response to single, brief presentations of *stationary* Glass patterns. These perceptions of illusory 'jitter' motion were unexpectedly found to arise when uniform grey fields are presented before and after Glass patterns composed of decrement- and increment-defined dot-pairs (see Figure 1.3). The perceptions have a number of notable features. The first is that they arise briefly and only at the onset and offset of each Glass pattern presentation – at longer presentation durations the motion perceptions are interspersed by 'steady' perceptions of the stationary Glass pattern (note that the term 'the jitter illusion' refers only to the illusory *motion* perceptions that arise). The second is that their structure is always consistent with the function according to which a Glass pattern was constructed. That is, under the conditions described above, presentations of concentric Glass patterns elicit perceptions of motion in concentric trajectories (the patterns appear briefly to move clockwise or counter-clockwise at stimulus onset and offset), presentations of radial Glass patterns elicit perceptions of motion in radial trajectories (the patterns appear briefly to move inward or outward at stimulus onset and offset), and so on. These features, in combination with the conditions under which the illusion arises, provide some clues as to the relative role of the so-called form- and motion-processing pathways in generating the illusion. For this reason, some of the properties of these pathways will be discussed below.

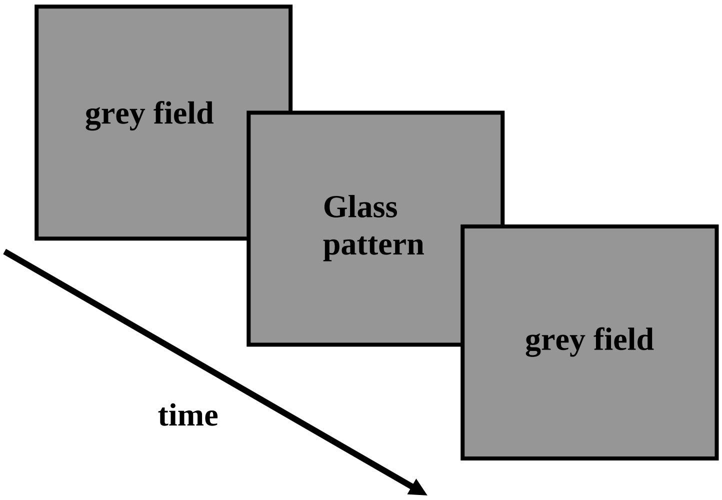

Figure 1.3: A graphical representation of the sequence of frames that gives rise to the jitter illusion. Uniform grey fields equivalent in luminance to the background of the Glass pattern are presented before and after the Glass pattern. Note that the black outline has been used here for the sake of representation only. The effect arises when the frames are presented consecutively.

Role of the parvo- and magno-cellular pathways

It has already been established that the visual system is made up of a number of pathways tuned to respond to particular visual cues. There is evidence that the tuning of two of the major pathways – the parvo- (P-) and magno- (M-) cellular pathways – is such that they preferentially respond to cues that delineate *form* and *motion* within the visual scene respectively (Livingstone & Hubel 1987 & 1988). These pathways, also known as the form- and motion-processing or colour-opponent and broad-band pathways (see below for an explanation), are first distinguishable in the visual system at the retinal level. From there they remain relatively independent throughout the lateral geniculate nucleus and into the cortex, and extend through the cortex on a path that incorporates the inferior temporal area in the case of the P-pathway, and the middle temporal area in the case of the M-pathway (Schiller & Logothetis 1990; Baloch, Grossberg, Mingolla & Nogueria 1999). A cursory analysis of the jitter illusion suggests *both* pathways are involved in its generation; the fact that the illusion arises in response to presentations of stationary ‘form’ stimuli suggests the involvement of the P-pathway, whilst the fact that the illusion is one of motion suggests the involvement of the M-pathway. However, a more in-depth analysis casts some doubts over the plausibility of this suggestion.

The cells that make up the P-pathway have a number of tuning characteristics that render them suitable for processing stationary, ‘form’ objects that arise within the visual scene. Firstly, there is evidence that P-pathway cells are *most effectively* stimulated by static or slow-changing visual presentations (see Ohtani, Ejima & Nishida 1991; Baloch et al 1999). That is, their tuning characteristics are such that they preferentially respond to presentations of stationary objects. Secondly, at the retinal level the neural architecture of the P-pathway is such that the cells are tuned to process both colour and luminance variations within the visual scene (Schiller & Logothetis 1990; Schiller, Logothetis & Charles 1990(a) & (b)). In fact, as a result of the colour-processing capabilities of the P-cells, the pathway is also known as the colour-opponent pathway. This dual sensitivity allows the cells to process both luminance- and colour-defined characteristics of objects presented in the visual scene. Thirdly, in most cases the cells respond in a *sustained* fashion to appropriate visual stimuli (Schiller & Logothetis 1990; see Figure 1.4). This means that activity within the P-pathway cell population can be maintained for the duration of a stimulus presentation, thereby facilitating the processing of a stationary visual image over extended periods. Each of these characteristics contributes to the effectiveness of P-pathway cells in processing the cues that delineate stationary visual stimuli such as those that give rise to the jitter illusion.

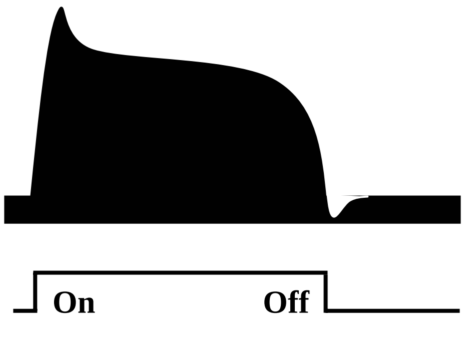

Figure 1.4: The sustained response profile characteristic of cells that make up the P-pathway. Excitation is generated by the onset of certain visual stimuli and may not return to baseline until after stimulus offset.

The population of cells that makes up the M-pathway, on the other hand, is tuned to respond to cues that signify the movement or motion of objects within the visual scene. Again, a number of the response characteristics of the M-pathway cells facilitate this type of processing. Firstly (and in contrast to the cells of the P-pathway), there is evidence that M-pathway cells are most effectively stimulated by rapid or abrupt changes to the visual environment (Ohtani, Ejima & Nishida 1991; Baloch et al 1999) – the types of changes that are often characteristic of moving objects. Secondly, the structure of the M-pathway is such that signals are transmitted to the cortex very quickly; the first 7-10 milliseconds of stimulus-generated cortical activity have been attributed to the M-pathway (Sestokas & Lemkuhle 1986; Maunsell & Gibson 1992). In addition to this, it has been demonstrated that most M-pathway cells have a *transient* response profile, meaning that suitable visual events elicit a very rapid cellular response that also (rapidly) returns to baseline (see Figure 1.5). In combination, these characteristics also facilitate the processing of rapidly changing visual scenes. Finally, the cells of the M-pathway are exquisitely sensitive to changes in luminance (contrast) within the visual scene (Schiller & Logothetis 1990; Schiller, Logothetis & Charles 1990(a) & (b)). In fact, there is evidence (Schiller & Logothetis 1990) that the cells of the M-pathway are *much more sensitive* to such changes than those that make up the P-pathway. This sensitivity is the result of ‘broad-band’ connections between the photoreceptors and the earliest M-pathway cells. In this way a number of response characteristics facilitate the motion-sensitivity of the cells that make up the M-pathway.

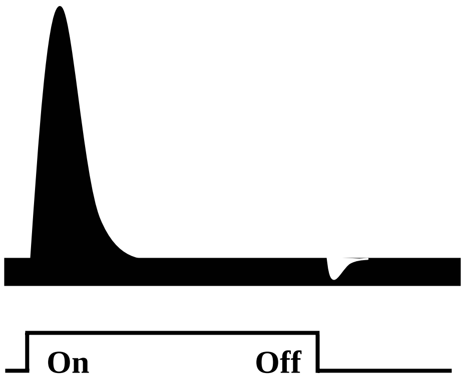

Figure 1.5: The transient response profiles characteristic of M-pathway cells. Excitation is generated by the onset of a visual stimulus before rapidly returning to baseline firing.

As noted, the characteristics described above provide grounds for suggesting the involvement of both P- and M-pathway cell populations in giving rise to the jitter illusion. Providing additional support for that view is the explanation of an apparently similar visual illusion. The illusion, first described by Ross and his colleagues (and referred to here as the Ross effect) arises in response to rapid presentations of successive stationary Glass patterns, all of the same type and all composed of either decrement-defined *or* increment-defined dot-pairs (Ross, Badcock & Hayes 2000). Ross and his colleagues demonstrated that such presentations reliably elicit coherent motion perceptions. Indeed, similar to the jitter illusion it was reported that the structure of the motion perceptions that arise is consistent with the function used to generate each of the Glass patterns involved; a sequence of concentric Glass patterns gives rise to perceptions of motion in a concentric trajectory, a sequence of radial Glass patterns gives rise to perceptions of motion in a radial trajectory, and so on. Ross and his colleagues showed that their effect arises in spite of the fact that the presentations on which it is based contain *no coherent velocity signals*. This, in combination with the fact that the effect arises in response to presentations of Glass patterns that are composed of decrement- *or* increment-defined dot-pairs (patterns that elicit perceptions that are consistent with the function used in their construction – see above), led Ross and his colleagues to propose that P-pathway activity must somehow contribute to the generation of the effect. That is, they suggested that the only possible source of the 'structural' component of the motion perceptions was via P-pathway activity. Taking this and the fact that the effect is one of motion into account, Ross et al proposed that their effect is a product of *interactive* P- and M-pathway processing (see Ross et al 2000).

However, in spite of the similarities between the jitter illusion and the Ross effect there is a significant problem associated with proposing a similar account of the neural activity on which the jitter illusion is based. While it is the case that both the jitter illusion and the Ross effect arise in response to presentations of stationary Glass patterns, and that in each case these presentations do *not* contain coherent velocity signals (see Ross et al 2000), one critical difference between them is that the jitter illusion arises in response to presentations of Glass patterns composed of *decrement- and increment-defined dot-pairs*. Evidence suggesting that P-pathway activity does not 'extract' the structure of such patterns has already been reported (see above). This means that the rationale used to support P-pathway involvement in generating the Ross effect does *not* apply in the case of the jitter illusion. That is, the argument that the 'structural' component of the motion perceptions must arise on the basis of P-pathway activity has, in the case of the jitter illusion, little currency.

One consequence of the argument outlined above is that the *only* basis upon which to suggest P-pathway involvement in generating the jitter illusion is the observation that the illusion arises in response to presentations of stationary visual stimuli. This has an important implication for developing a model of the neural correlates of the jitter illusion: it suggests that a model based *entirely* on M-pathway activity would be sufficient provided that two conditions were met. The first of these is that the model would need to account for the means by which activity in M-pathway cells, known to selectively respond to moving stimuli, arises in response to presentations of stationary Glass patterns. The second is that it would need to propose some plausible mechanism(s) by which the activity thus generated gives rise to perceptions of coherent global motion. The challenge addressed in the work that follows was whether such a model could be constructed.

Things to come

In the chapters that follow a series of experiments relating to the jitter illusion will be described. Each experiment within the series was designed to address a specific question relating to the mechanism(s) by which presentations of stationary Glass patterns might give rise to perceptions of coherent global motion. For the reasons outlined above, the experiments were conducted under the working hypothesis that the illusion is a product of neural activity that arises entirely within the M-pathway of the human visual system. To that end, the general aim of the initial experiments was to identify the means by which M-pathway activity arises in response to presentations of *stationary* Glass pattern stimuli, and the aim of all subsequent experiments was to determine the mechanisms by which the activity thus generated gives rise to perceptions of coherent global motion. On the basis of all the resulting data, a model of the neural correlates of the jitter illusion was developed. A detailed description of the model will be provided in chapter 8, as will a discussion of its psychophysical and physiological plausibility as an account of the jitter illusion. Fittingly, discussion in the final chapters will focus on the implications of this model for developing a more general understanding of the means by which light-induced activity within the visual system gives rise to coherent, global visual perceptions.

CHAPTER 2
general methods

Equipment

The MatLab language (MatLab version 2.1.10) was used to develop a standard set of functions, each of which was designed to generate the coordinates of the dots of a specific type of Glass pattern. The functions incorporated a random seed that ensured each pattern was unique, and were written such that output was in text format. The resulting coordinate files were then teamed with purpose-written C-language control files that specified stimulus parameters such as luminance values and presentation durations for each experiment.

RUNSTIM (version 2.1.10) software was used to convert the information contained within the coordinate and control files into stimulus presentations. RUNSTIM is a piece of software purpose-built for use in psychophysical experimentation. One feature of this software is that it provides precise control over stimulus presentation durations. This is achieved in a number of ways. Firstly, the software allows users to specify (within a certain range) the required monitor refresh rate. The advantage of this is that it eliminates the timing problems that arise when refresh rates are incompatible with presentation durations. Secondly, the software runs from the MS-DOS platform (the real DOS platform, not an emulated version). This avoids timing problems that arise as a consequence of background Windows ‘housekeeping’ duties. A built-in RUNSTIM function tests for timing inaccuracies in the monitor frame rate, and thus serves as a final safeguard for ensuring accurate presentation durations.

Stimuli were displayed on a 100 Hz, Sony E200 CRT flat-screen monitor using a Celeron 533MHz CPU. The monitor was checked and calibrated regularly to ensure the integrity of luminance values. Subject responses were recorded using a normal computer keyboard.

Stimuli

Across the different experiments stimuli had a number of common features. All were presented on a uniform grey background the luminance of which was 18cd/m^2. On this background, the dots of which each stimulus was composed were generated to fall within a circular stimulus area that subtended 18.7 degrees of visual angle when subjects were seated for testing. Unless otherwise specified, stimuli were composed of 200 dots. Each dot subtended 12 arc minutes of visual angle. For patterns defined by pairs of dots, the distance between dots within each pair (the intra-pair distance) was 21 arc minutes of visual angle. The dots of which each pattern was composed were defined in one of two ways. They were either uniformly darker than the background (decrement dots) or uniformly lighter than the background (increment dots). In most cases decrement dots were assigned a luminance of 6cd/m^2, and therefore yielded Michelson contrast values (L_{max} – L_{min}/L_{max} + L_{min}) with the background of 0.5. Similarly, increment dots were assigned luminance values of 54cd/m^2 and so yielded Michelson contrasts of 0.5.

. **(a)** **(b)**

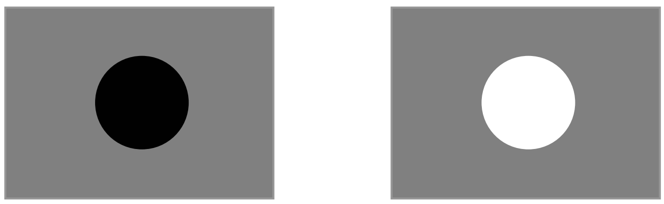

Figure 2.1: Glass patterns were composed of (a) decrement and (b) increment dots. Each dot subtended 12 arc minutes of visual angle.

Glass patterns were constructed according to concentric, radial or linear functions. The dots of which each pattern was composed were generated in two phases. During the first phase, dots were assigned a spatial position in a truly random fashion. That is, individual dots could occupy any position within the stimulus area and overlap was possible. In the second phase, partner dots were positioned according to a universal (concentric, radial or linear) function. In instances where the positioning of the initial random dot was such that the partner dot fell beyond the perimeter of the defined stimulus area (in the case of radial and linear patterns), the position of each dot was re-calculated until this was no longer the case. This was done in order to ensure homogeneity of density across pattern types. Glass patterns were also configured such that intra-pair distance was held constant irrespective of the degree of eccentricity from the pattern's point of origin (see Figure 2.2).

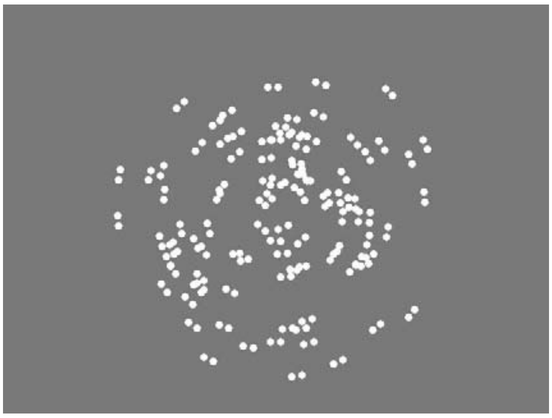

Figure 2.2: Example of a (concentric) Glass pattern in which intra-pair distance was held constant irrespective of the degree of eccentricity from the origin. This strategy eliminated confounds introduced by changes in salience occurring as a result of varying intra-pair distance (Caelli & Julesz 1979).

Non-Glass pattern stimuli were constructed in one of two ways. Either the individual dots of which each pattern was composed were positioned in a truly random fashion, or the dot-pairs of which the patterns were composed were assigned random positions and random orientations. Whilst the former controls for both the global configuration and the pairing of dots per se, the latter controls only for the overall configuration of the dot-pairs (be it concentric, radial or linear). In each case, the patterns were designed to be identical to Glass patterns in every respect other than their global configuration (see Figure 2.3).

(a) **(b)**

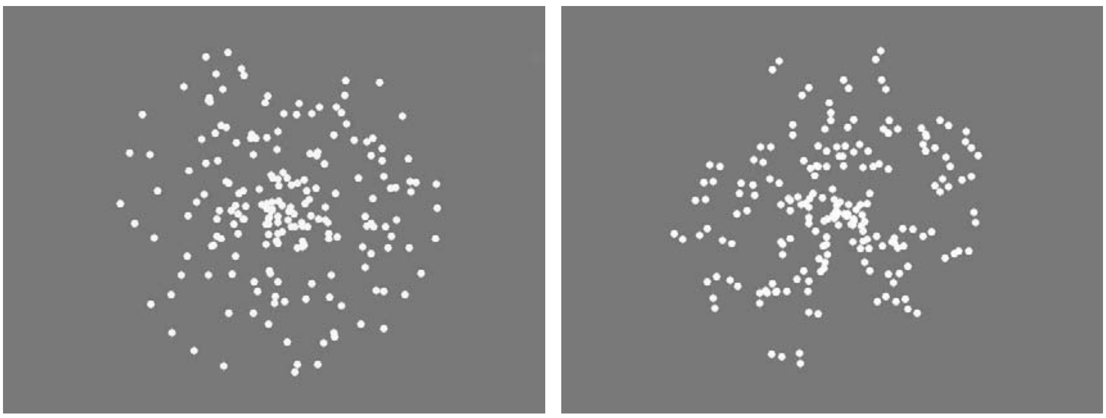

Figure 2.3: Non-Glass pattern stimuli consisted of randomly positioned individual dots (a), and dot-pairs in which position and orientation was randomly assigned (b). In all respects other than their global configuration these patterns were identical to Glass patterns (see Figure 2.2).

Subjects

Observers consisted of the author (subject AB), one other investigator (subject vdZ), and several trained but naive psychophysical observers who participated in return for course credit, payment or for the sheer joy of it. The inexperienced observers were naïve to the aims of each experiment. All subjects had normal or corrected-to-normal vision.

Design and procedures

Subjects were tested individually in a light-attenuated room. A chin rest was positioned such that the stimuli were viewed from a distance of 57 centimetres. Subjects were instructed to place their chins on the rest and their hands on the keyboard. A 2AFC paradigm was employed such that subjects were instructed to report whether each stimulus presentation gave rise to the perception of ‘coherent global motion’ or not. Responses were recorded by means of a key-press; affirmative ‘motion’ responses were registered by pressing the ‘m’ key, and negative responses were registered by pressing the ‘z’ key. The responses were recorded in data files that were compatible with Microsoft Excel software. Microsoft Excel macros were written to process the data.

Stimulus presentations, unless otherwise specified, were 100 milliseconds in duration. Uniform grey fields presented after each Glass pattern presentation marked the inter-stimulus interval (ISI). The luminance of this field was equivalent to the luminance of the background of the dot-patterns. The ISI for each experiment was 2000 milliseconds in duration. During this time subjects were required to register a response to the preceding stimulus (see Figure 2.4). The method of constant stimuli was used such that stimuli were presented in a randomised order within each block. The blocks consisted of equal numbers of control and test stimuli. Blocks were presented more than once so mean responses for subjects in each condition were calculated as an average across blocks. Unless otherwise stated, all patterns were presented using abrupt (square-wave) stimulus onset and offset profiles.

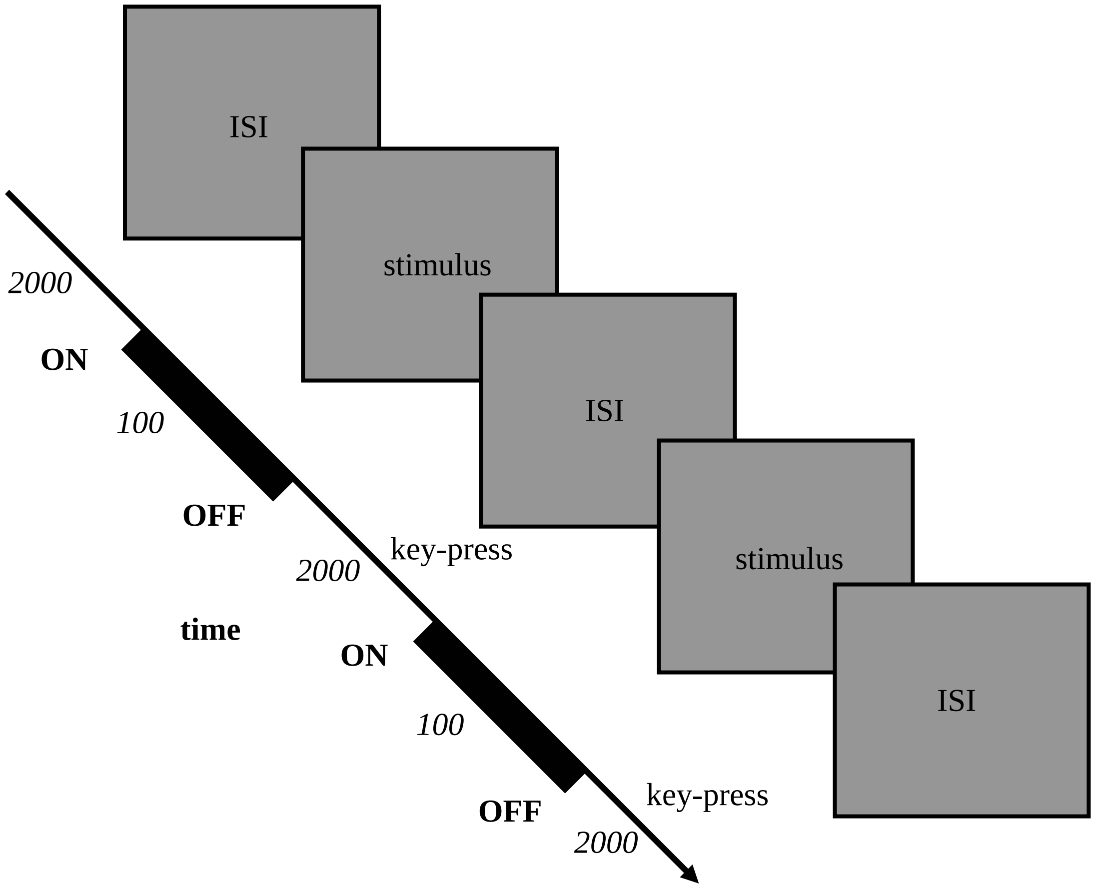

Figure 2.4: Diagrammatic representation of the experimental procedure. Stimuli were presented for 100 msecs and were followed by ISIs that lasted 2000 msecs. The onset and offset profile of each stimulus was square-wave, and subjects made key-press responses to each stimulus during the subsequent ISI.

Results

Unless otherwise indicated, data for each experiment represent the mean proportion of affirmative ‘motion’ responses registered by individual subjects or the group in each condition. Mean proportions of 1 indicate that affirmative responses were registered for every trial, whilst mean proportions of 0 indicate that affirmative responses were not recorded in response to a single trial. The mean proportion value of 0.5 has been marked on most graphs. It was expected that this proportion would be recorded only in the event that subjects were on average making random responses to the stimuli.

Checks and balances

Checks were undertaken in order to establish that the jitter illusion is not an artefact of the methods used to present the Glass pattern stimuli. The display software was tested first. Both RUNSTIM and Apple QuickTime software were used to present stimulus sequences. The illusion was reliably elicited in each case, constituting evidence that the jitter illusion is not a product of software-based presentation asynchronies. The monitors used to present the stimuli were also tested. LCD and CRT monitors were used, and again the illusion arose reliably in each case. This ruled out the possibility that illusion arises as a result of monitor-based presentation asynchronies. Finally, a recording cathode ray oscilloscope was used to measure the speed at which decrement and increment dots are displayed (using RUNSTIM) on CRT monitors. This technique confirmed that no systematic presentation asynchronies are involved in the presentation of the stimulus sequences. On the basis of this evidence, it was concluded that the data reported in the chapters that follow do not reflect equipment-based artefacts, but rather the psychophysical correlates of perceptual events.

CHAPTER 3
the role of eye-movements in stimulating M-pathway activity

The observation that the jitter illusion is elicited by presentations of *stationary* Glass patterns poses a problem for any model that attributes its generation to activity that arises within the M-pathway. That is, it raises the question of exactly how such presentations stimulate activity within the *motion-sensitive* cells that make up the M-pathway. Accounts of other motion-from-form illusions suggest one possible means by which this is the case. The escalator (Fraser & Wilcox 1979), peripheral drift (Faubert & Herbert 1999) and Pinna/Brelstaff (Pinna & Brelstaff 2000) motion illusions all arise in response to presentations of stationary luminance-defined stimuli. In each case the *nature* of the perceptions, along with the *conditions* under which they arise, are consistent with the notion that transients introduced through the execution of *eye-movements* mediate the M-pathway activity on which they are based. This raises the possibility that in the case of the jitter illusion, M-pathway activity arises via the same mechanism. The general aim of the experiments reported in this chapter was therefore to determine whether eye-movements elicit the M-pathway activity on which perceptions of illusory 'jitter' motion are based.

Several features of the escalator, peripheral drift and Pinna/Brelstaff illusions (Fraser & Wilcox 1979; Faubert & Herbert 1999; Pinna & Brelstaff 2000) suggest their generation is linked to the execution of eye-movements. In each case, *prolonged* stimulus presentations (in the order of several seconds at least) are required to elicit perceptions of illusory motion. This is consistent with evidence indicating that the latencies involved in generating smooth-pursuit eye-movements and saccades are *at least* 130 milliseconds (Robinson 1965; Leigh & Zee 1985) and 200 milliseconds (Leigh & Zee 1985) respectively. That is, it suggests that the illusions only arise in response to prolonged presentations of the stimuli precisely because these presentations allow sufficient time for eye-movements to be made. An additional feature of each of the motion-from-form illusions is that the motion perceptions arise *sporadically*. This suggests that eye-movements, executed throughout the course of each stimulus presentation, serve to 'refresh' (Faubert & Herbert 1999) the effect. In fact, in the case of the escalator illusion motion perceptions can be deliberately elicited by making eye-movements between external markers (see Figure 3.1).

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Figure 3.1: A concentric representation of the stimulus that elicits perceptions of the escalator illusion (Fraser & Wilcox 1979). Perceptions of motion can be deliberately elicited by making eye-movements between the markers positioned to the left of the pattern.

The possibility that eye-movements mediate M-pathway responses to each of the stationary motion-from-form stimuli mentioned above is based on the observation that the execution of eye-movements effectively introduces transients to the luminance composition of the visual scene (Leigh & Zee 1985; Faubert & Herbert 1999). That is, the execution of eye-movements (across a non-uniform field) results in an *abrupt change* to the pattern of light energy falling onto the retina. As discussed earlier (see chapter 1), such a change is precisely the type of stimulus to which the cells that make up the M-pathway are sensitive. It is also worth noting that in some cases, the same principles apply when the viewer's head or the stimulus itself is moved during viewing. That is, head or stimulus movements can also introduce transients that elicit activity in cells that make up the M-pathway. Consistent with this, it was initially reported that in order to perceive the Pinna/Brelstaff illusion movements of the head or the stimulus itself were required (Pinna & Brelstaff 2000).

The suggested link between eye-movements and the abovementioned motion-from-form illusions withstands evidence that the movements do *not* determine the direction in which a pattern appears to move. Fraser & Wilcox (1979) reported that their illusion could *not* be mediated by the execution of eye-movements because neighbouring patterns can simultaneously appear to move in opposing directions. Indeed, this finding does suggest that eye-movements do not determine the direction of the global motion perceptions that arise. However, from this it does not necessarily follow that the movements do not elicit the neural activity on which the perceptions are based. That is, it is entirely possible that the movements are a necessary but not sufficient condition for the illusions to arise - that their role is to stimulate M-pathway cells and *subsequent* M-pathway processing determines the nature of the motion perceptions that arise.

The role of eye-movements in generating other motion-from-form illusions has implications for the neural correlates of the jitter illusion. That is, as in the case of other motion-from-form illusions it is possible that eye-movements (head and stimulus movements are precluded by the conditions used during testing – see chapter 2) executed during some Glass pattern presentations elicit the M-pathway activity on which the jitter illusion is based. The specific aim of the experiments reported in this chapter was to determine whether this is the case. To that end, the duration of Glass pattern presentations was manipulated. In line with evidence suggesting that the shortest latency associated with the execution of an eye-movement is 130 milliseconds (see above), it was predicted that the illusion would only arise in response to presentations of at least that duration. Shorter presentations do not allow sufficient time for eye-movements to be executed, and therefore should not give rise to the jitter illusion.

Methods.

Stimuli

In the experiments that follow, three independent variables were manipulated. The most important in terms of the hypothesis was the duration of the Glass pattern presentations (see below). The remaining two independent variables were designed to test some of the broad stimulus conditions under which the illusion arises. First, the signal composition of the Glass pattern stimuli was manipulated. Preliminary results (see description in chapter 1) suggested the illusion only arises in response to patterns composed of decrement- *and* increment-defined dot-pairs. In order to formally establish this to be the case, the stimuli used here were defined in one of three ways; they were composed entirely of decrement-defined dot-pairs (condition dec/dec; see Figure 3.2(a)), entirely of decrement- and increment-defined dot-pairs (condition dec/inc; see Figure 3.2 (b)), or entirely of increment-defined dot-pairs (see Figure

3.2(c)). Based on earlier observations, it was predicted that the illusion would only arise in response to patterns composed of decrement- *and* increment-defined dot-pairs.

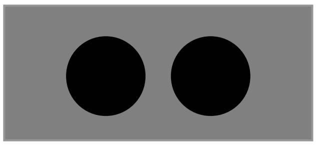


Figure 3.2(a): Decrement-defined dot-pairs, in which each dot is a luminance decrement relative to the background (condition *dec/dec*).

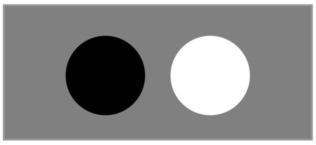


Figure 3.2(b): Decrement- and increment-defined dot-pairs, in which one dot is a luminance decrement and the other a luminance increment relative to the background (condition *dec/inc*); see also Figure 3.3.

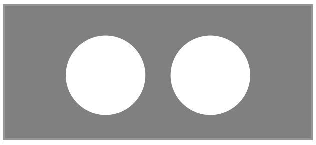


Figure 3.2(c): Increment-defined dot-pairs, in which each dot is a luminance increment relative to the background (condition *inc/inc*).

The second independent variable was the configuration of the Glass patterns used in each presentation. There is evidence that the neural processes underlying the generation of complex- and simple-trajectory motion perceptions are not equivalent (Morrone, Burr & Vaina 1995). Therefore, in order to establish whether patterns arranged according to both complex and simple functions give rise to the jitter illusion, concentric (Figure 3.3(a)), radial (Figure 3.3(b)) and linear (Figure 3.3(c)) Glass patterns were tested. With no evidence to suggest otherwise, it was expected that each type of pattern would elicit the jitter illusion.

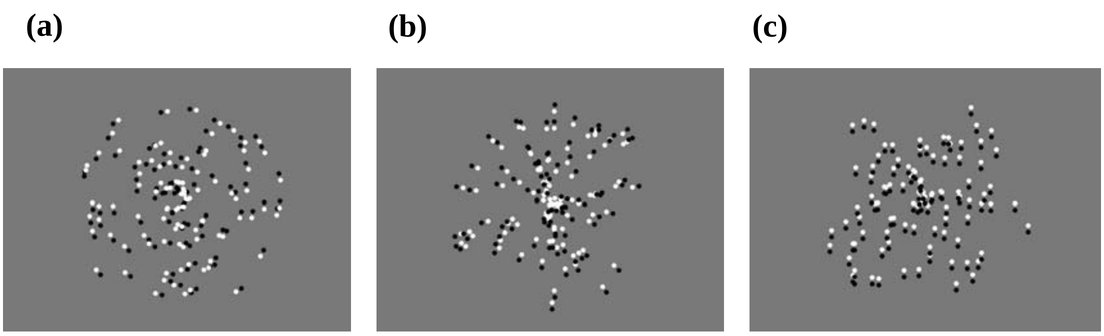


Figure 3.3: Concentric (a), radial (b) and linear (c) Glass patterns were tested. In this example each pattern is composed of decrement- and increment-defined dot-pairs. Note that none of the patterns defined in this way give rise to perceptions of a structure that is consistent with the function used in their construction – see chapter 1.

For each of the conditions, control patterns were constructed to be equivalent to test patterns in every way except for their structural composition. Each of the experiments reported in the results section was conducted using ‘random’ control stimuli - stimuli that were composed of dots that were randomly positioned within the stimulus field. In order to test for differences between responses to different types of control stimuli, an additional experiment was run using ‘dot-pair’ control stimuli or stimuli that were composed of *randomly oriented dot-pairs* (see the description provided in chapter 2).

Subjects

Subjects consisted of two experienced psychophysical observers (AB and vdZ) and two trained observers (RB and US) who were naïve to the aims of the experiment.

Procedure

The third independent variable that was manipulated was the duration of stimulus presentations. Presentations lasted 50, 100 or 800 milliseconds. If, as discussed earlier, eye-movements *are* required in order for perceptions of the illusion to arise, it was expected that only the longest of these conditions would reliably elicit the illusion. That is, based on measures of the time that is required for the execution of eye-movements, it was expected that presentations lasting 50 and 100 milliseconds would not be sufficiently long to elicit perceptions of the illusion.

Stimuli were presented in nine different blocks. Each block was arranged such that one pattern configuration (concentric, radial or linear) was presented for one of the presentation durations (50, 100 or 800 milliseconds). Within each block, 20 representatives from each of the signal composition conditions (conditions dec/dec, dec/inc and inc/inc) were presented. Thus, with controls included, each block consisted of 120 stimuli in total. The blocks were presented twice to each subject, so mean responses are based on 40 trials for each condition. As per the description provided in chapter 2, subjects were instructed to indicate whether each stimulus appeared to undergo coherent global motion or not.

Results.

Results for the control conditions are not represented in the graphs below because proportions of affirmative ‘motion’ responses to these patterns were negligible. That is, presentations of control stimuli yielded mean proportions of affirmative ‘motion’ responses that were equal or close to zero. Additionally, across experiments the data indicated no systematic differences between responses to the two different types of control stimuli; subjects consistently reported that presentations of both types of control stimuli did *not* give rise to perceptions of coherent global motion. As evidence of this, a summary of the group data for presentations of concentric Glass patterns and both types of control stimuli is represented in Table 3.4. These data represent the mean proportions of affirmative ‘motion’ responses (± standard errors) for 100 millisecond presentations of stimuli composed of decrement and increment dots. The complete set of control data can be reviewed in chapter 11.

	Means (± standard errors)
Glass pattern	0.994 (± 0.006)
Random control	0 (± 0)
Dot-pair control	0.01 (± 0.01)

Table 3.4: Group (n = 4) mean proportions (± standard errors) of affirmative ‘motion’ responses to stimuli composed of decrement- and increment-defined dots for presentations lasting 100 milliseconds (see chapter 11 for the full set of control data).

50 millisecond presentations:

Following the testing procedure involving presentations that lasted 50 milliseconds, subjects were asked to describe the perceptions to which the stimuli gave rise. They reported that some patterns appeared stationary, whilst others gave rise to perceptions of coherent global motion. They also reported that the trajectory or direction of this motion was consistent with the function used in the construction of the patterns, and that the stimuli appeared to move first in one direction and then (immediately afterwards) in the other; concentric Glass patterns appeared to move very briefly in a clockwise then a counter-clockwise direction (or vice versa), radial patterns appeared to move very briefly in an outwards direction and then an inwards one (or vice versa), and the vertically oriented linear patterns appeared to move briefly in an upwards direction and then a downwards one (or vice versa). The responses subjects recorded during the testing procedure are discussed below.

The responses of individual subjects to presentations of concentric, radial and linear Glass patterns are represented in Figures 3.5(a), 3.5(b) and 3.5(c) respectively. These data represent the mean proportions of affirmative ‘motion’ responses for individual subjects to patterns composed of decrement-defined (condition dec/dec), decrement- and increment-defined (condition dec/inc) and increment-defined (condition inc/inc) dot-pairs. The data indicate that subjects were remarkably consistent across each of the conditions tested. That is, they indicate that *every* subject recorded an affirmative 'motion' response to almost *every* presentation in the dec/inc condition (these stimuli almost always appeared to move), and a negative response to almost *every* presentation in the dec/dec and inc/inc conditions (these stimuli almost never appeared to move). This was the case across each of the different Glass pattern configurations. The small between-subject variation indicates the data can be reliably summarised across subjects. The resulting group data are represented in Figure 3.6.

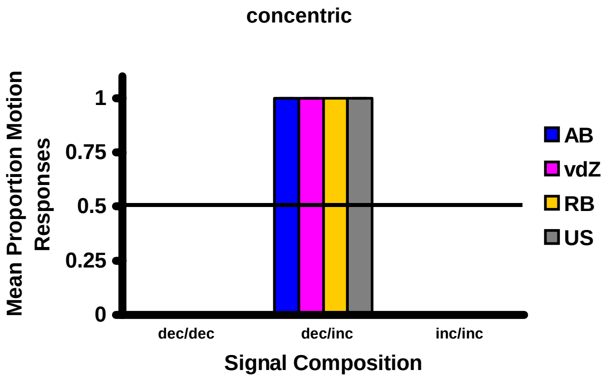


Figure 3.5(a): Mean proportion of affirmative 'motion' responses for individual subjects. Data represent the responses to concentric patterns in the *dec/dec*, *dec/inc* and *inc/inc* conditions. Error bars represent one standard error.

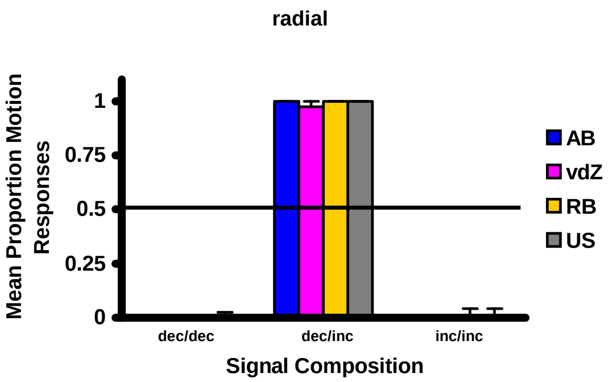


Figure 3.5(b): Results for radial Glass patterns. Other details are as per Figure 3.5(a).

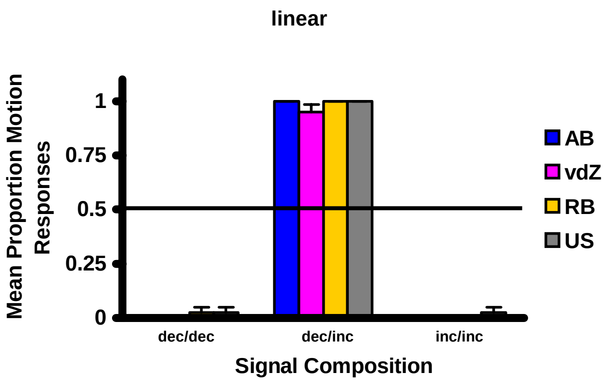


Figure 3.5(c): Results for linear Glass patterns. Other details are as per Figure 3.5(a).

The summarised or group version of the data represented in Figure 3.6 has several striking features. Firstly and perhaps most importantly, the data indicate that the illusion can be reliably elicited by presentations lasting as little as 50 milliseconds. This is confirmed by the high proportions of affirmative responses recorded in response to patterns composed of decrement- and increment-defined dot-pairs. Secondly, the data confirm that of the signal compositions tested, *only* those patterns defined in this way reliably gave rise to the illusion. In fact, the data indicate that patterns composed of decrement- and increment-defined dot-pairs elicited affirmative responses on almost every trial (the lowest mean proportion, recorded in response to linear patterns, was 0.9875 ± 0.009), while those composed of decrement- *or* increment-defined dot-pairs elicited negative responses on almost every trial (with the highest recorded proportion resting at 0.037 ± 0.015, in response to radial patterns in condition inc/inc). Finally, the data suggest that the pattern of responses recorded was consistent across different Glass pattern configurations. That is, the proportions of affirmative responses were consistent across conditions in which concentric, radial and linear patterns were presented.

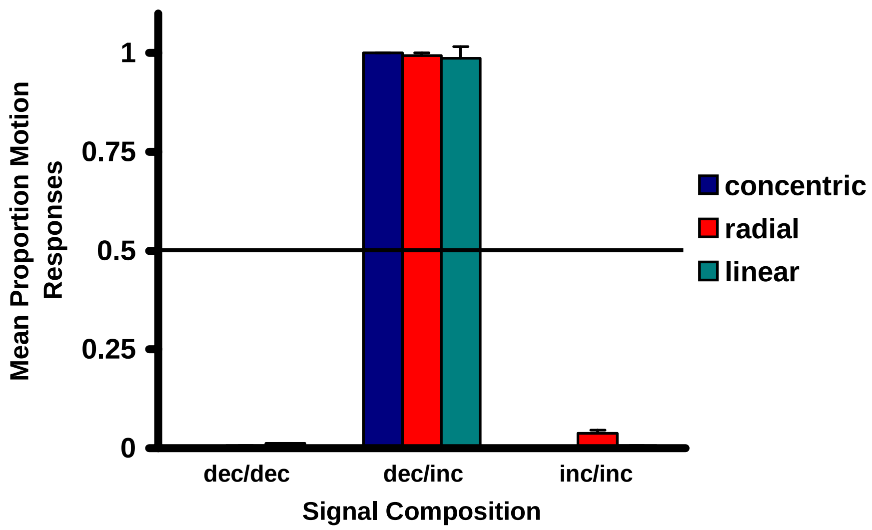


Figure 3.6: Group mean proportions of affirmative 'motion' responses for presentations lasting 50 milliseconds. The data represent group responses to concentric, radial and linear Glass patterns. Error bars represent one standard error.

100 millisecond presentations:

After the testing procedure, subjects were again asked to describe the perceptions to which stimulus presentations lasting 100 milliseconds gave rise. They reported that some Glass patterns appeared stationary, whilst others appeared to move first in one direction and then, almost immediately afterwards, in the other. Again, the trajectory of this motion was consistent with the function used to construct the Glass patterns in question. The responses recorded during the testing procedure are discussed below.

As was the case for presentations lasting 50 milliseconds, data for presentations lasting 100 milliseconds were consistent across individual subjects (see chapter 11). Consequently (and for the same reasons outlined above), the data were collapsed onto a single graph that is represented in Figure 3.7. Inspection of this figure indicates that presentations lasting 100 milliseconds also reliably gave rise to perceptions of coherent motion. Again, this was only the case for patterns composed of decrement- *and* increment-defined dot-pairs, with the *lowest* mean proportion recorded in response to these patterns resting at 0.937 ± 0.019. By contrast, the *highest* mean proportion recorded in response to patterns composed of decrement- or increment-defined dot-pairs was 0.043 ± 0.016 (recorded in response to radial patterns in condition inc/inc). Finally, consistent with the previous data, these data indicate subjects' responses were consistent across concentric, radial and linear Glass pattern configurations.

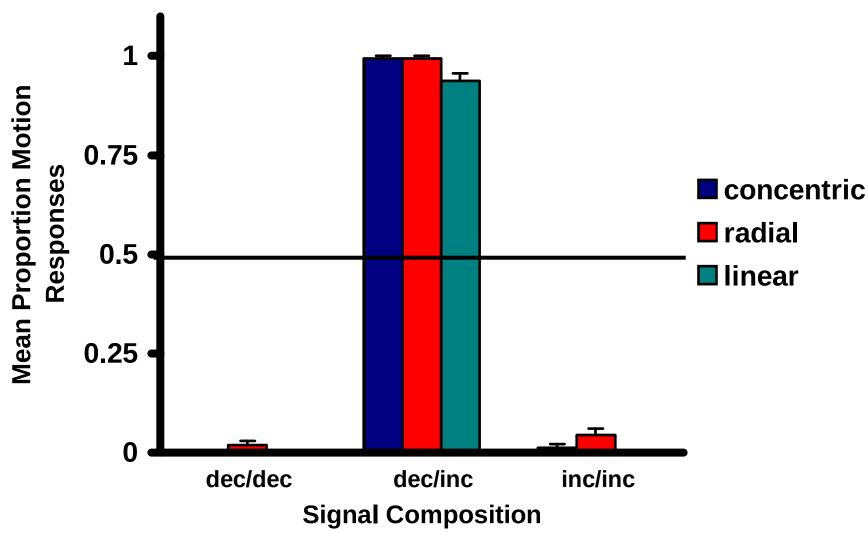


Figure 3.7: Group mean proportions of affirmative 'motion' responses for presentations lasting 100 milliseconds. The data represent group responses to concentric, radial and linear Glass patterns. Error bars represent one standard error.

800 millisecond presentations:

In the case of presentations lasting 800 milliseconds, subjects again reported that some stimuli appeared stationary, whilst others appeared to move first in one direction and then the other. They again reported that the direction in which the latter appeared to move was determined by the function according to which they were constructed. However, for these longer presentations subjects also reported that the perceptions of motion that were elicited were 'interspersed' with a brief perception of the stationary Glass pattern. That is, at durations of 800 milliseconds it became clear that the motion perceptions *arise only briefly at stimulus onset and offset*. The responses recorded during the testing procedure are discussed below.

The data for presentations lasting 800 milliseconds were again consistent across subjects and so were summarised in Figure 3.8. These data indicate that affirmative responses were only reliably recorded in response to patterns composed of decrement- *and* increment-defined dot-pairs; the lowest mean proportion recorded in response to these patterns was 0.831 ± 0.029 (in the case of concentric patterns), whilst the highest mean proportion recorded in response to patterns in the remaining conditions was 0.037 ± 0.015 (recorded in response to radial patterns in condition dec/dec). Interestingly, the data indicate that for presentations lasting 800 milliseconds the proportions of affirmative responses recorded in condition dec/inc were not as high as those recorded in response to shorter presentations. Even so, a minimum mean proportion of 0.831 (± 0.029) suggests that presentations lasting 800 milliseconds reliably gave rise to perceptions of illusory 'jitter' motion. Finally and again consistent with the previous data, the data represented in Figure 3.8 indicate that the same pattern of results was observed across presentations of concentric, radial and linear Glass patterns.

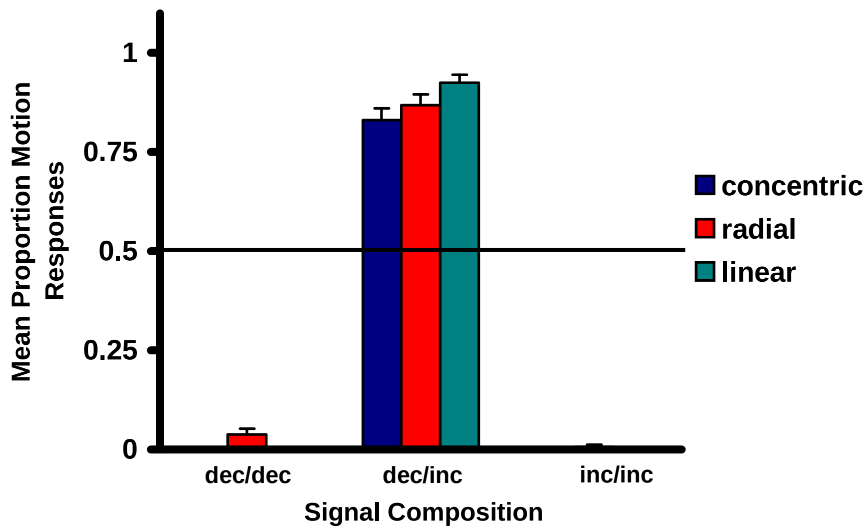


Figure 3.8: Group mean proportions of affirmative 'motion' responses for presentations lasting 800 milliseconds. The data represent group responses to concentric, radial and linear Glass patterns. Error bars represent one standard error.

Discussion:

The data presented here do *not* support the hypothesis that eye-movements mediate M-pathway responses to stationary Glass pattern presentations. On the basis of that hypothesis, it was predicted that perceptions of illusory 'jitter' motion would only arise in response to Glass pattern presentations lasting a minimum of 130 milliseconds. However, the data presented here clearly indicate that this was not the case; the illusion was reliably elicited by presentations lasting just 50 and 100 milliseconds. In fact, on the basis of the data it appears that the strongest motion perceptions arose in response to Glass pattern presentations of the shortest duration. This is evidenced by the fact that in comparison to presentations lasting 800 milliseconds, those that lasted 50 and 100 milliseconds more reliably gave rise to the illusion. On the basis of the evidence reported here, it therefore appears that the M-pathway activity on which the jitter illusion is based is *not* mediated by eye-movements.

Of course, these data do *not* exclude the possibility that the M-pathway activity on which the jitter illusion is based is elicited by eye-movements initiated *prior* to the onset of each Glass pattern. That is, it is possible that movements initiated during the ISI generate transients that stimulate M-pathway responses to the stationary Glass pattern that follows. However, this account is unlikely given the pattern of results that was observed. The data indicate that motion perceptions arose in response to almost every presentation of those Glass patterns that were composed of decrement- and increment-defined dot-pairs. This means that in order for the account to hold true, eye-movements would have to have been initiated prior to almost *every* presentation of those patterns in particular by *every* subject that was tested. This is sufficiently unlikely to suggest that neither eye-movements initiated prior to nor during Glass pattern presentations elicit the M-pathway activity on which the jitter illusion is based.

Importantly, the findings presented in this chapter also speak to some of the specific conditions under which perceptions of illusory ‘jitter’ motion arise. Firstly, the observation that motion perceptions were not reliably elicited by presentations of patterns that were composed of either random dots or randomly oriented dot-pairs (see the data presented above and in chapter 11) speaks to the significance of the Glass pattern structure in giving rise to the illusion. That is, it suggests that the unique properties of this structure somehow stimulate the patterns of neural activity upon which perceptions of coherent global motion are based. Secondly, the data indicate that of the different signal compositions that were tested, only presentations of Glass patterns that were composed of *decrement- and increment-defined dot-pairs* reliably gave rise to the illusion. Importantly, this suggests that the luminance or contrast variations defined by the dot-pairs of which a Glass pattern is composed plays a determining role in whether or not the illusion arises. The significance of both Glass pattern structure and the luminance composition of individual Glass pattern dot-pairs will be addressed in later chapters.

It is therefore the case that the main finding to arise from this chapter - that eye-movements are unlikely to mediate the M-pathway activity on which the jitter illusion is based - sets the jitter illusion apart from other motion-from-form illusions. Importantly, it rules out the possibility that models of the escalator (Fraser & Wilcox 1979), peripheral drift (Faubert & Herbert 1999) and Pinna/Brelstaff (Pinna & Brelstaff 2000) illusions can be used as templates upon which to base a model of the neural correlates of the jitter illusion. It also means that one of the critical problems facing any model that attributes the illusion to activity that arises entirely within the M-pathway remains. That is, it remains unclear how presentations of *stationary* Glass patterns stimulate the motion-sensitive cells that make up the M-pathway. One possible solution to this problem is that abrupt changes, brought about as a result of the onset and offset profiles used in Glass pattern presentations, elicit the M-pathway activity on which perceptions of illusory ‘jitter’ motion are based. This possibility is addressed in the following chapter.

CHAPTER 4
the role of stimulus onset and offset profiles in stimulating M-pathway activity

The suggestion that the M-pathway activity on which perceptions of illusory ‘jitter’ motion are based is *not* stimulated by eye-movements raises an alternative possibility; that the activity arises as a consequence of the changes in luminance defined by the onset and offset of each Glass pattern presentation. It has already been noted (see chapter 1) that the cells of which the M-pathway is composed have a number of characteristics that facilitate motion processing. One such characteristic is their exquisite sensitivity to abrupt changes to the luminance composition of the visual scene (Maunsell & Gibson 1992). Indeed, there is evidence that a single step-change in luminance, when it is of sufficient magnitude (see Maunsell & Gibson 1992), can be sufficient to elicit activity within selected M-pathway cells (von Grunau 1978; Baloch et al 1999). This raises the possibility that in the case of the jitter illusion, M-pathway activity arises as a result of the step-changes in luminance defined by the onset and offset of the dots of which Glass patterns are composed. Such an hypothesis is consistent not only with the properties of motion-sensitive M-pathway cells, but also with by the observation that illusory ‘jitter’ motion perceptions only arise at stimulus onset and offset. The general aim of the experiment reported in this chapter was therefore to determine whether step-changes in luminance defined by the onset and offset of stationary Glass patterns elicit the M-pathway activity on which the jitter illusion is based.

It has already been noted that cells located within the M-pathway are tuned to respond to abrupt changes in the luminance composition of the visual scene. In fact, there is evidence that they *selectively* respond to such changes; that they are not excited optimally by gradual changes in luminance (see Ohtani et al 1991; Baloch et al 1999). Perhaps surprisingly, reports generally do not include quantitative measures of the level of ‘abruptness’ required in order for M-pathway activity to arise. Maunsell and Gibson (1992) suggested simply that step-changes in luminance, when they are of sufficient magnitude, serve as an effective (and selective) stimulus for M-pathway cells. That is, they suggested that changes in luminance that describe a step- or *square-wave* function selectively stimulate at least some of the cells that make up the M-pathway.

Interestingly, the stimulus presentations that have so far been shown to elicit the jitter illusion are such that step-changes to the luminance composition of the visual scene arise at stimulus onset and offset. It has already been noted that the illusion arises in response to a sequence of images that includes a Glass pattern and uniform grey fields; motion perceptions arise when presentations of each Glass pattern are preceded and followed by presentations of the grey fields (see Figure 4.1(a)). It is also the case that the onset and offset of each Glass pattern is such that the dots making up the pattern are introduced and removed *in a single step* (see chapter 2). Importantly, this means that at stimulus onset the appearance of each dot is associated with a step-change in luminance, and similarly at stimulus offset the disappearance of each dot is associated with a step-change in luminance. Critically, because the grey fields presented prior to and following the Glass pattern stimulus are of the same luminance as the background of the Glass pattern, *these changes only arise at the spatial locations at which the dots are positioned* (see Figures 4.1(b) and 4.1(c)). More specifically, for the spatial locations at which each *decrement* dot is positioned the onset of the Glass pattern defines a step down in luminance, whilst the offset of the stimulus defines a step up. Conversely, for the locations at which each *increment* dot is positioned the onset of the stimulus defines a step up in luminance whilst its offset defines a step down.

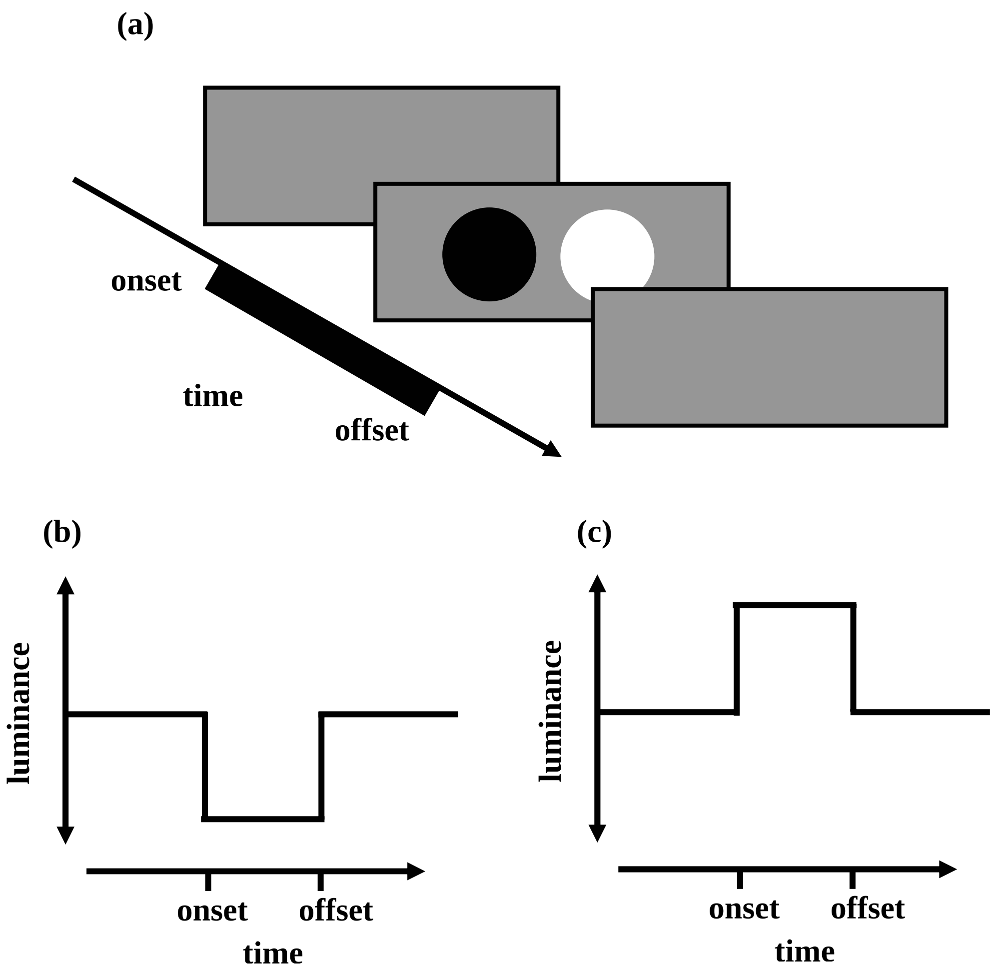


Figure 4.1: The sequence of frames that give rise to the jitter illusion (a) and the luminance profiles (over time) for the spatial locations at which a decrement dot (b) and an increment dot (c) are situated. At stimulus *onset*, the change from grey to black at the spatial location of the decrement dot is associated with a step down in luminance, and the change from grey to white at the location of the increment dot is associated with a step up in luminance. At stimulus *offset*, the change from black to grey at the location of the decrement dot is associated with a step up in luminance, and the change from white to grey at the location of the increment dot is associated with a step down.

The nature of the luminance changes defined by the onset and offset of each Glass pattern in the sequence referred to above raises the possibility that these changes serve to stimulate the M-pathway activity on which the jitter illusion is based. This hypothesis is consistent with both the known sensitivities of M-pathway cells (see above), and with the observation that motion perceptions arise only at the onset and offset of Glass pattern presentations (see chapter 3). The hypothesis also generates some testable predictions. One of these is that the jitter illusion should only arise in response to Glass pattern presentations in which *step*-changes in luminance are defined at stimulus onset and offset; it should not arise in response to presentations in which the changes in luminance at onset and offset manifest more slowly. So far, the data have been consistent with this prediction. That is, the illusion has only been demonstrated to arise in response to presentations in which *square-wave* stimulus onset and offset profiles were used (see chapter 3). However, the effects of using onset/offset profiles that define *gradual* changes to the luminance composition of the visual scene have not yet been tested. For this reason, the specific aim of the experiment reported in this chapter was to test whether the illusion also arises in response to stimulus presentations in which ramped onset/offset profiles are used. Based on the hypothesis, it was predicted that such presentations would *not* give rise to perceptions of illusory ‘jitter’ motion.

Methods.

Stimuli

All the stimuli used in this experiment were Glass patterns arranged according to a concentric function. Each pattern was composed of decrement- *and* increment-defined dot-pairs and was presented on a grey background with a luminance of 18cd/m^2. Blank fields presented prior to and following each stimulus presentation had a uniform luminance value of 18cd/m^2.

Two different conditions were tested in the experiment. Control patterns were presented using a square-wave stimulus onset/offset profile such that both stimulus onset and offset involved a one-step change in luminance at each dot’s spatial location (see Figure 4.2(a)). Pilot experiments indicated the illusion is reliably generated in response to patterns composed of decrement and increment dots with an assigned contrast value of 0.1. This value was adopted for use in the current experiment because it was easily matched to presentations in the test conditions. To yield a contrast with the background of 0.1, decrement dots were assigned a luminance value of 14.7cd/m^2 while increment dots were assigned a value of 22cd/m^2. Thus, with the exception of the luminance values assigned to the dots, the control stimuli were exactly equivalent to those stimuli in response to which the illusion was reliably elicited in the previous chapter. It was therefore predicted that presentations of these stimuli would yield high proportions of affirmative ‘motion’ responses.

Test presentations were equivalent to control presentations in every respect except for their onset/offset profiles. For these presentations a pseudo-ramped stimulus onset and offset profile was used. The ramping effect was achieved by increasing contrast across a set of the smallest practicable steps at stimulus onset, and by decreasing contrast in the same steps at stimulus onset (see Figure 4.2(b)). The perceptual effect of this was that patterns appeared to gradually increase to full contrast and then fade away. Control experiments (described in detail in chapter 8) showed that patterns defined by dots with a contrast of 0.05 are visible but do not give rise to the jitter illusion, so this value was used as the first step in contrast for each ‘ramped’ presentation. In order to generate a mean stimulus contrast of 0.1 (equivalent to the control stimuli) five contrast steps were used in each presentation: 0.05, 0.075, 0.10, 0.125 and 0.15. In order to generate these contrast values, decrement dots were assigned luminance values (in order of increasing contrast) of 16.2cd/m^2, 15.48 cd/m^2, 14.7cd/m^2, 14 cd/m^2, and 13.3cd/m^2. The luminance values assigned to increment dots (again in order of increasing contrast) were 19.89 cd/m^2, 20.91 cd/m^2, 22cd/m^2, 23.14 cd/m^2, and 24.3cd/m^2.

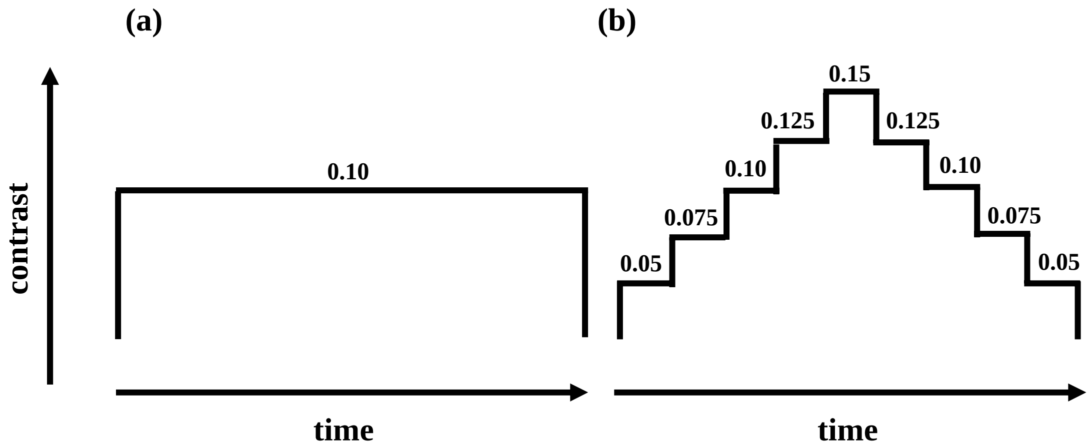


Figure 4.2: Representation of the techniques used to present stimuli in the control **(a)** and test **(b)** conditions. Stimuli were presented using square-wave and ramped onset and offset profiles in each condition respectively. In the square-wave condition, stimuli were stepped on and off in a single step. In the ramped condition, stimuli were introduced and removed in five small steps of equal duration. The average contrast in each condition was 0.10, and stimuli were visible for equal durations.

Subjects

Subjects consisted of two experienced psychophysical observers (AB and vdZ) and one trained observer (RB) who was naïve to the aims of the experiment.

Procedure

Both the test and control conditions consisted of 10 Glass pattern stimuli. These were presented in a single block consisting of 20 stimuli in total. The block was presented 3 times to each subject, so mean responses are based on 30 trials in total. In accordance with the procedures described in chapter 2, the order in which the stimuli were presented was randomised within each block.

The length or duration of each presentation was held constant. Software limitations dictated the duration of each step of the ramped (test) presentations – each of the (nine) contrast steps was presented for 40 milliseconds. This meant that the total duration of each presentation was 360 milliseconds. Based on the high proportions of affirmative 'motion' responses recorded for presentations lasting between 50 and 800 milliseconds (see previous chapter), it was anticipated that presentations lasting between 300 and 400 milliseconds would reliably elicit the illusion.

Consistent with the procedure described in chapter 2, the task of the subjects was to indicate whether or not patterns appeared to undergo coherent global motion.

Results.

The data are arranged as per the description provided in chapter 2. Results for the control and test conditions are represented in Figure 4.3. In that graph the mean proportions of affirmative 'motion' responses for individual subjects are represented as a function of the onset/offset profile of stimulus presentations (square-wave or ramped). As expected, the data clearly indicate that high proportions of affirmative 'motion' responses were elicited in the control or square-wave condition. In fact, the lowest mean proportion of 0.9 ± 0.055 (recorded by subject RB) suggests that *every* subject recorded an affirmative response to these presentations on almost *every* trial. By contrast, the test data clearly indicate that presentations involving the use of a ramped stimulus onset/offset profile elicited very few affirmative 'motion' responses. The data show that this was the case for each of the subjects tested: the *highest* average proportion of affirmative responses recorded in this condition was just 0.13 ± 0.062 (again by subject RB). These results clearly indicate that perceptions of illusory 'jitter' motion were *not* reliably elicited by stimulus presentations in which *ramped* profiles were used.

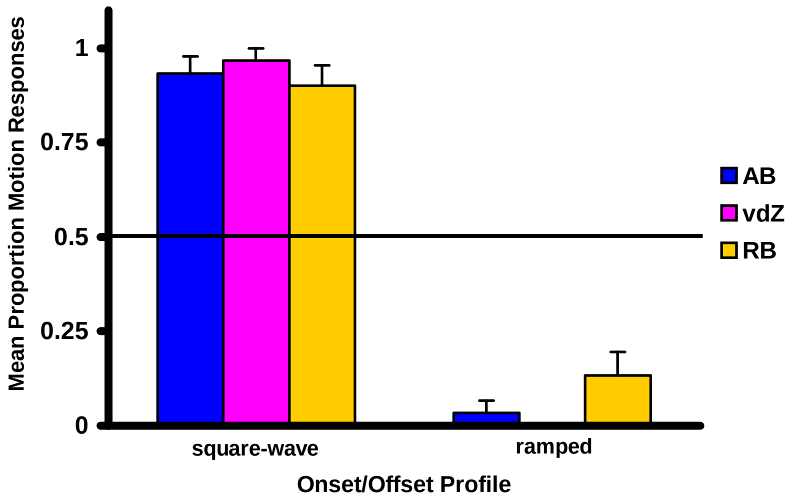


Figure 4.3: The mean proportion of affirmative 'motion' responses for patterns presented using square-wave and ramped onset/offset profiles. The data indicate that, in contrast to presentations in which a square-wave onset/offset profile was used, affirmative 'motion' responses were not reliably elicited by presentations in which a ramped onset/offset profile was used. Error bars represent one standard error.

Discussion.

The data presented here constitute firm evidence that the nature of the stimulus onset/offset profile used in presenting Glass patterns is critical in determining whether or not the jitter illusion arises. They confirm that *square-wave* stimulus onset/offset profiles reliably elicit perceptions of illusory 'jitter' motion, and in combination with data from the previous chapter serve as evidence that this is the case across a range of stimulus contrast values. In addition, the data clearly indicate that presentations in which *ramped* onset/offset profiles are used do not (at least under the conditions tested here) reliably elicit the illusion. It is therefore the case that the data provide support for the prediction that was made earlier - that the illusion would only reliably arise in response to presentations in which both the onset and offset of the Glass pattern stimuli constitute an abrupt or *step*-change to the luminance composition of the visual scene. In so doing, the data suggest that the M-pathway activity on which the jitter illusion is based is elicited by the step-changes in luminance arising at the onset and offset of Glass pattern presentations in which square-wave profiles are used.

Of course, the observation that the current findings reflect the perceptual consequences of presenting just one type of ramped (or pseudo-ramped) stimulus onset/offset profile must be taken into account. It is possible that a different pattern of results would be observed in the event that ramped onset/offset profiles with different parameters were used. However, this would only pose a problem for the current hypothesis if it could be demonstrated that perceptions of illusory 'jitter' motion arose in response to presentations in which the luminance changes arising at stimulus onset and offset were *more gradual* than those used in the current experiment (it would of course be expected that *less gradual* changes would at some point be sufficiently abrupt to elicit M-pathway activity, thereby giving rise to the illusion). If this were found to be the case, then of course the suggestion that the luminance changes arising at stimulus onset and offset elicit the M-pathway activity on which the illusion is based would have to be revised.

In addition to the empirical evidence, the suggestion that luminance changes introduced at stimulus onset and offset serve to mediate the perceptions of illusory 'jitter' motion is supported by observations regarding the nature of the motion perceptions that arise. If as suggested the step-changes in luminance stimulate the neural activity on which perceptions of illusory 'jitter' motion are based, then it would be expected that these perceptions would be *temporally* associated with the events at which the changes manifest. That is, it would be expected that perceptions of the illusion would arise *specifically* at the onset and offset of each Glass pattern. And indeed, there is evidence that this is the case – it was reported in chapter 3 that for longer presentation durations it becomes perceptually apparent that perceptions of illusory 'jitter' motion only arise (briefly) at stimulus onset and offset. The consistency of this observation with the prediction referred to above lends further support to the proposal that step-changes in luminance elicit the M-pathway activity on which the jitter illusion is based.

In summary, the finding arising on the basis of the data reported here is that the abrupt or step-changes in luminance associated with square-wave stimulus onset and offset profiles elicit M-pathway responses to stationary Glass pattern presentations. This finding is supported both by the data presented above, and by the observation that the illusion only arises at the onset and offset of Glass pattern presentations. It is the case, however, that while this finding provides an account of how M-pathway activity is stimulated in the first place, the mechanisms by which this activity is converted into perceptions of coherent global motion remain unclear. Determining the nature and identity of those mechanisms is the second condition that any M-pathway-based model of the jitter illusion must satisfy (see chapter 1). To that end, evidence indicating that the illusion only arises in response to presentations of Glass patterns that are composed of decrement- and increment-defined dot-pairs is significant. The implications of this for determining the neural correlates of the jitter illusion will be discussed in the following chapter.

CHAPTER 5
the role of M-pathway off- and on-channel cells in generating the illusion

Evidence that motion perceptions only arise in response to Glass patterns that are composed of decrement- and increment-defined dot-pairs raises the possibility that particular patterns of M-pathway Off- and On-channel activity are required in order for the jitter illusion to arise. In the previous chapter it was noted that the onset of decrement and increment dots is associated with a step *down* and *up* in luminance respectively, whilst the offset of the same dots is associated with a step *up* and *down* in luminance respectively (see Figure 4.1). These changes are compatible with the tuning characteristics of the so-called Off- and On-channel cells of the M-pathway; there is physiological evidence that M-pathway Off-channel cells are excited by abrupt downwards steps in luminance, whilst M-pathway On-channel cells are excited by abrupt upwards steps in luminance (Schiller 1984; Schiller, Sandell & Maunsell 1986; Schiller & Logothetis 1990; Schiller, Logothetis & Charles 1990(a) & (b)). One consequence of this is that the onset and offset of a decrement- and increment-defined dot-pair gives rise to a *unique* pattern of Off- and On-channel activity. That is, of the signal compositions tested so far, only the decrement- and increment-defined dot-pairs stimulate excitatory activity within the cells of both the Off- and On-channels. This raises the possibility that perceptions of illusory ‘jitter’ motion are based on the specific patterns of Off- and On-channel activity elicited by the onset and offset of decrement- and increment-defined dot-pairs. The general aim of the experiments reported in this chapter was to test this hypothesis.

Within the visual system there exists more than one population of Off- and On-channel cells. All the populations are sensitive to luminance variations arising within the visual scene. This sensitivity is such that Off-channel cells are generally excited by luminance decrements and inhibited by luminance increments, whilst On-channel cells are generally excited by luminance increments and inhibited by luminance decrements (Schiller 1982; Schiller 1984; Schiller 1992). The unique feature of *M-pathway* Off- and On-channel cells is that these patterns of activity arise in response to luminance variations that take place over short periods of time (Schiller & Logothetis 1990; Schiller et al 1990(a) & (b)). That is, the cells of each channel respond to *abrupt* changes in the luminance composition of the visual scene (Maunsell & Gibson 1992 – see the previous chapter). Considering just the excitatory activity, this means that an abrupt downward step in luminance excites M-pathway Off-channel cells, whilst an abrupt upward step elicits excitatory responses in M-pathway On-channel cells.

The tuning of the M-pathway Off- and On-channel cells is such that they are sensitive to the (abrupt) luminance changes that arise at the onset and offset of Glass pattern presentations in which square-wave onset/offset profiles are used. In fact, based on the known sensitivities of the cells, it is possible to predict the patterns of Off- and On-channel activity that will arise in response to the onset and offset of each of the dots of which patterns that elicit the jitter illusion are composed. At the spatial location of each *decrement* dot the downward step in luminance at stimulus onset elicits excitation within cells of the Off-channel, whilst the upward step at stimulus offset elicits excitation in On-channel cells (see Figure 5.1(a)). At the spatial location of each *increment* dot the opposite is true; the upward step in luminance at stimulus onset elicits excitation in cells of the On-channel, whilst the downward step at stimulus offset elicits excitation in Off-channel cells (see Figure 5.1(b)).

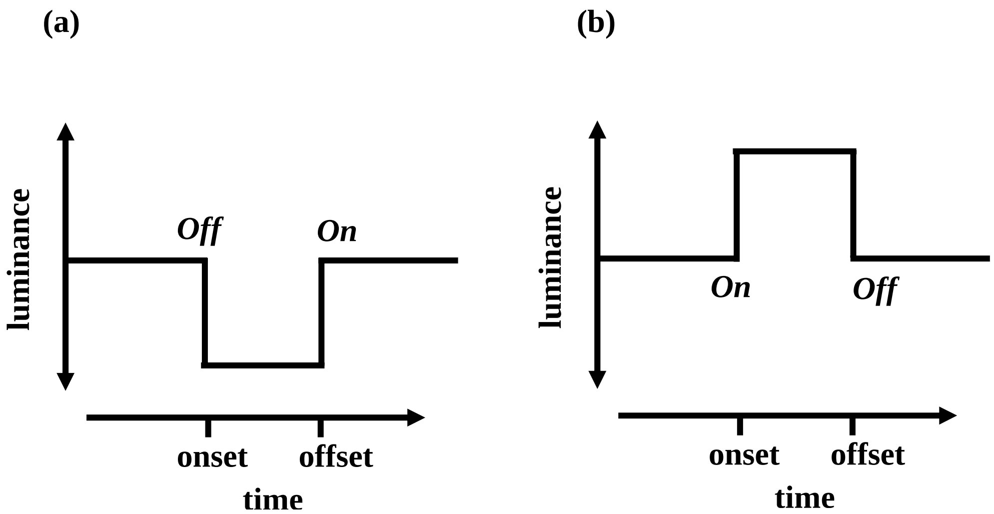


Figure 5.1: The pattern of Off- and On-channel excitation that arises in response to the luminance changes defined by the onset and offset of (a) a decrement and (b) an increment dot (refer also to Figure 4.1). The channel within which each change generates excitatory activity is marked in *italics*, so for example the onset of a decrement dot elicits an excitatory response in cells located within the *Off*-channel.

When viewed in combination with evidence that only Glass patterns composed of *decrement- and increment-defined* dot-pairs reliably elicit the jitter illusion, the tuning characteristics of M-pathway Off- and On-channel cells raise an interesting possibility. That is, they suggest that perceptions of the illusion only arise when the dot-pairs of which a Glass pattern is composed elicit excitatory activity within the cells of *both* the Off- and On-channels of the M-pathway at stimulus onset and offset. Such an hypothesis generates some testable predictions that have not been addressed by the data so far presented. One is that the illusion should *only* arise in response to patterns that are composed of decrement- and increment-defined (or 'opposite-polarity') dot-pairs – that it should not arise in response to patterns defined by same-polarity dot-pairs. Another is that the illusion should arise in response to *any* pattern composed of opposite-polarity dot-pairs. That is, it gives rise to the prediction that the illusion should be reliably elicited by presentations of Glass patterns that are composed of opposite-polarity dot-pairs *independent of the contrast of the composite dots*. The specific aim of the experiments reported in this chapter was to test each of these predictions.

Methods.

Stimuli

All stimuli were generated with an intra-pair Michelson contrast (the contrast between dots within a pair) of 0.4, and all Glass patterns were generated according to a concentric function. In every respect other than the ones described below, stimuli were constructed as per the description provided in chapter 2.

The first experiment was designed to test the first of the two predictions – that the jitter illusion would only arise in response to Glass patterns composed of opposite-polarity dot-pairs and not in response to patterns composed of same-polarity dot-pairs. Data reported in chapter 3 indicate that perceptions of the illusion were reliably elicited by patterns composed of decrement- and increment-defined dot-pairs but not by patterns composed of decrement-defined or increment-defined dot-pairs. However, in those experiments the decrement-defined and increment-defined dot-pairs were composed of equiluminant decrement and increment dots respectively. This raises the possibility that the critical feature of stimuli that elicit the illusion is not that they are composed of opposite-polarity dot-pairs, but rather that they are composed of *non-equiluminant* dot-pairs. In order to rule out this possibility, two sets of same-polarity but non-equiluminant stimuli were generated. As is the case with patterns composed of equiluminant same-polarity dot-pairs, these stimuli elicited strong perceptions of a concentric structure. The first set of stimuli was comprised of Glass patterns that were composed of dot-pairs in which each dot was darker than the background (condition dec/dec; see Figure 5.2(a)). In order to be consistent with the values used in earlier experiments, luminance values assigned to the dots making up each pair in this condition were 6 and 14 cd/m^2, rendering Michelson contrasts with the background of 0.5 and 0.12 respectively. The second set comprised patterns that were composed of dot-pairs in which each dot was lighter than the background (condition inc/inc; see Figure 5.2(b)). The luminance of the dots making up each pair in this condition was 54 and 23 cd/m^2. Again, these values were selected to be consistent with earlier experiments and to render Michelson contrasts with the background of 0.5 and 0.12 respectively. Based on the hypothesis that the illusion only arises in response to opposite-polarity dot-pairs, it was predicted that presentations of these patterns would not reliably elicit perceptions of illusory 'jitter' motion.

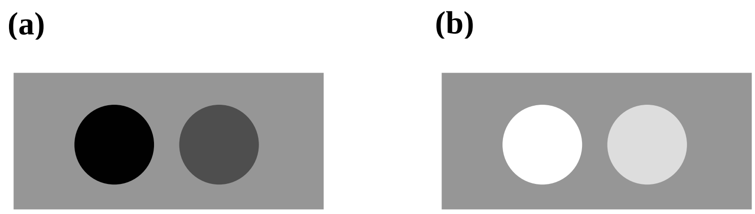


Figure 5.2: Same-polarity but non-equiluminant dot-pairs were composed of (a) decrement or (b) increment dots. These dot-pairs made up patterns in the dec/dec and inc/inc conditions respectively.

The second experiment was designed to test whether the illusion arises in response to *any* pattern that is composed of opposite-polarity dot-pairs. Data from chapter 3 indicate that the illusion arose in response to patterns composed of dot-pairs in which the dots were of opposite polarity and of equal contrast relative to the background. This raises the possibility that opposite-polarity dot-pairs must be composed of dots of equal contrast in order for the illusion to arise. In order to rule out this possibility, three sets of opposite-polarity stimuli were generated. As is the case for stimuli composed of equiluminant opposite-polarity dot-pairs, these stimuli did *not* give rise to strong perceptions of a concentric structure. The first set of stimuli (condition dec/incA; see Figure 5.3(a)) was composed of dot-pairs in which the luminance value assigned to each decrement and increment dot was 10 and 23 cd/m^2 respectively. These values yielded Michelson contrasts of 0.28 and 0.12 respectively. The second (condition dec/incB; see Figure 5.3(b)) was composed of dot-pairs in which the luminance value assigned to each decrement and increment dot was 14 and 33 cd/m^2 respectively, again yielding Michelson contrasts of 0.12 and ~0.28 respectively. The third set (condition dec/incC; see Figure 5.3(c)) was included as a control condition in which the decrement and increment dots were of equal contrast relative to the background. The luminance values assigned to decrement and increment dots were 12 and 27 cd/m^2 respectively, in each case yielding a Michelson contrast with the background of 0.2. Based on the hypothesis that the illusion arises in response to *any* Glass pattern that is composed of opposite-polarity dot-pairs, it was expected that the illusion would be reliably elicited by presentations of the stimuli in each of the conditions.

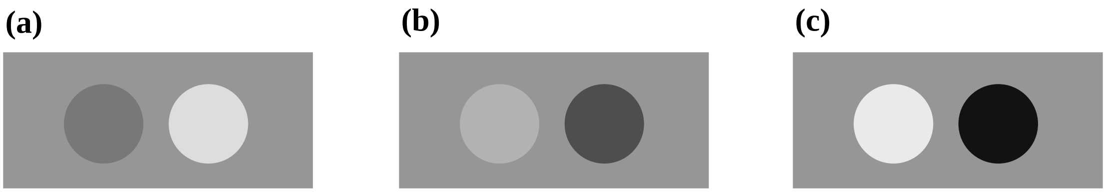


Figure 5.3: Three different sets of opposite-polarity stimuli were tested in (a) the dec/incA, (b) the dec/incB and (c) the dec/incC conditions. Patterns in the dec/incA and dec/incB conditions were composed of dots that were *not* of equal contrast relative to the background. Patterns in the dec/incC condition were composed of decrement and increment dots that were of equal contrast relative to the background.

For all Glass pattern stimuli, intra-pair contrast was held constant. This was done in order to rule out intra-pair contrast as a factor in the results. For both the first and second experiments control stimuli were equivalent to test stimuli in terms of their luminance profile. In fact, the only difference between the two groups was that control stimuli were composed of randomly positioned (unpaired) dots.

Subjects

Subjects consisted of two experienced psychophysical observers (AB and vdZ) and two trained observers (RB and US) who were naïve to the aims of the experiment.

Procedure

In both the first and second experiments each condition was represented by 10 stimuli. This means that in the first experiment a total of 40 patterns was tested (with 2 test and 2 control conditions), and in the second a total of 60 patterns was tested (with 3 test and 3 control conditions). As a result of the small number of total stimuli in each experiment, they were combined and tested in a single block. The block was presented 3 times, so mean responses for each condition are based on 30 trials.

Stimuli were presented for 100 milliseconds. Subjects were instructed to indicate whether each stimulus appeared to undergo coherent global motion or not. All other procedures were as per the description provided in chapter 2.

Results.

For each of the experiments reported here, the data are arranged as per the description provided in chapter 2. Data from the first experiment are represented in Table 5.4. In this case, group rather than individual data are reported because there was no variance between subjects. These data clearly indicate that the illusion did not arise in response to presentations of stimuli defined by same-polarity but non-equiluminant dot-pairs. That is, coherent motion perceptions were not reported by *any* of the subjects in response to *any* of the stimuli that were tested on *any* of the trials. These data rule out the possibility that the critical feature determining whether the illusion arises is that the Glass patterns presented are composed of *non-equiluminant* dot-pairs. In so doing, they provide support for the prediction that the illusion would *only* be reliably elicited by presentations of Glass patterns composed of opposite-polarity dot-pairs.

	condition dec/dec	**condition inc/inc**
test	0	0
control	0	0

Table 5.4: Group mean proportions of affirmative ‘motion’ responses to presentations of same-polarity but non-equiluminant Glass patterns. Data for both the test and control conditions are represented.

Data from the second experiment are represented in Figure 5.5. In this figure the data represent the mean proportions of affirmative 'motion' responses recorded by individual subjects. The data clearly indicate that the illusion was reliably elicited by presentations of patterns composed of opposite-polarity dot-pairs, independently of the contrast of each dot relative to the background. This is evidenced by the fact that the *lowest* mean proportion of affirmative responses recorded in any of the conditions was 0.87 ± 0.062 (by subject AB in condition dec/incA). In addition to this, the data confirm the findings of previous experiments: that opposite-polarity Glass pattern stimuli in which the dots are of equal contrast relative to the background reliably elicit perceptions of the illusion (see the data for condition dec/incC). Clearly, these data rule out the possibility that the illusion is only reliably elicited by presentations of Glass patterns that are composed of opposite-polarity dot-pairs in which the composite dots are of the same contrast relative to the background. In so doing, they provide support for the prediction that the illusion would be reliably elicited by presentations of *any* Glass pattern composed of opposite-polarity dot-pairs.

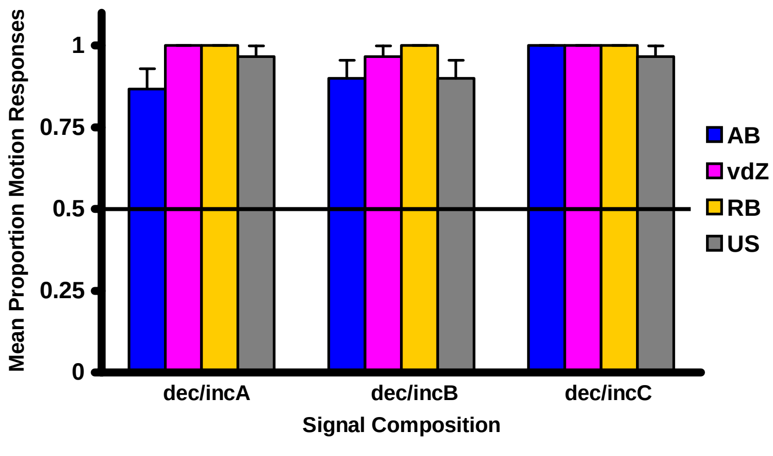


Figure 5.5: The mean proportions of affirmative 'motion' responses recorded by individual subjects across each of the conditions. The data indicate that the illusion was reliably elicited by presentations of opposite-polarity patterns that were composed of dots of both unequal (conditions dec/incA and dec/incB) and equal (condition dec/incC) contrast relative to the background.

Discussion.

The data presented in this chapter suggest that the jitter illusion is reliably elicited only when Glass pattern stimuli are composed of decrement- and increment-defined (or opposite-polarity) dot-pairs. Data from the first experiment indicate that perceptions of the illusion were *not* reliably elicited by presentations of Glass patterns that were composed of same-polarity dot-pairs, even when the dots making up each pair were of different contrasts relative to the background. This rules out the possibility that *non-equiluminance* is a sufficient condition for perceptions of the illusion to arise. Data from the second experiment indicate that the illusion *was* reliably elicited by presentations of Glass patterns that were composed of opposite-polarity dot-pairs regardless of whether the dots making up these pairs were of the same or different contrasts relative to the background. In combination, these results support predictions that the illusion would be reliably elicited *only* by presentations of Glass patterns composed of opposite-polarity dot-pairs, and that it would arise reliably for *any* Glass pattern defined in this way. In so doing, they also support the hypothesis that the jitter illusion arises on the basis of the unique patterns of neural activity elicited by the onset and offset of opposite-polarity dot-pairs. That is, the data suggest that perceptions of the illusion arise on the basis of excitatory *M-pathway Off- and On-channel responses* to each of the decrement- and increment-defined dot-pairs of which the Glass patterns are composed.

Of course, the results presented here reflect the perceptual consequences of presenting Glass pattern stimuli composed of dots of only a limited range of contrast values. This means that these data alone are not sufficient to draw categorical conclusions about the perceptual consequences of presenting patterns defined by all possible contrast combinations. It is possible, for instance, that the illusion arises in response to only a *small sample* of patterns composed of opposite-polarity dot-pairs and not to the entire range of such patterns. However, this possibility seems unlikely given the range of contrasts across which the illusion has so far been shown to arise. In fact, data from experiments reported in this chapter and in chapter 3 indicate that the illusion is reliably elicited by patterns composed of dot-pairs that range in contrast from 0.2 to 0.5. Assuming that the illusion is also elicited by patterns defined by dots of the intermediate contrast values, and allowing for the fact that the scope for *increasing* contrast is limited by the fact that the display background must fall at an intermediate luminance value, the range of contrasts over which the illusion has been shown to arise is large. The same argument applies in the case of patterns composed of same-polarity dot-pairs; the range of contrasts over which the illusion has been shown *not* to arise is large. Based on findings from several experiments, it is therefore likely that the illusion *only* arises in response to Glass patterns composed of opposite polarity dot-pairs, and that it arises in response to *any* pattern defined in this way.

The main finding to emerge from this chapter is therefore that perceptions of illusory 'jitter' motion are likely to arise on the basis of excitatory Off- and On-channel activity elicited by the onset and offset of the decrement- and increment-defined dot-pairs of which the Glass patterns are composed. Of course, this raises the question of *how* the Off- and On-channel activity thus generated gives rise to the perceptions of coherent global motion described by subjects. The characteristics of a population of M-pathway cells known as *local motion detectors* provide some clues as to how to address this question. That is, they suggest that perceptions of the illusion may arise (at least in part) on the basis of local motion detector-activity. This possibility will be addressed in the chapter that follows.

CHAPTER 6
the role of local motion detectors in generating the illusion

Features of M-pathway *local motion detectors* suggest the involvement of these cells in generating the jitter illusion. Psychophysical evidence indicates that local motion detectors (referred to henceforth as 'LMDs') arise at the earliest cortical level of the M-pathway hierarchy - in area V1 (Edwards & Badcock 1994). As their name suggests, LMDs are sensitive to *local* motion signals that arise within the visual scene. That is, they selectively encode shifts in luminance that describe linear trajectories over short spatial distances. In addition, there is psychophysical evidence that LMDs are stimulated by activity that arises within the Off- and On-channels of the M-pathway. That is, it has been reported that stimuli defined by decrement and increment elements can drive LMD activity such that (with additional processing at higher levels of the M-pathway) perceptions of coherent global motion arise (Edwards & Badcock 1994). When viewed in relation to the findings reported in previous chapters, these characteristics raise the possibility that LMDs are involved in generating perceptions of illusory 'jitter' motion. They suggest that the patterns of Off- and On-channel activity elicited by the onset and offset of each decrement- and increment-defined (Glass pattern) dot-pair stimulate LMDs such that the illusion arises. The general aim of the experiments reported in this chapter was to test whether this is the case.

The defining characteristic of the population of cells known as LMDs is that they are sensitive only to *local* motion energy. That is, the receptive fields of these cells are such that they only encode shifts in luminance that fall within two specific parameters. The first is that the shifts must describe a *linear* trajectory; cells tuned to complex motion trajectories do not arise until higher levels of the M-pathway (see Tanaka & Saito 1989; Morrone, Burr & Vaina 1995). The second is that the shifts in luminance must arise over *short* distances. In fact, evidence suggests that the maximum spatial range (the 'integration range') over which the cells are sensitive to these shifts is approximately 30 arc minutes of visual angle (Mikami, Newsome & Wurtz 1986; Smith, Singh, Williams & Greenlee 2001). This is a unique characteristic of LMD cells - evidence suggests that motion-sensitive cells located at higher levels of the M-pathway selectively encode only longer-range motion signals (Mikami et al 1986; Smith et al 2001).

While the *precise* relationship between LMDs and M-pathway Off- and On-channel cells will not be discussed until the following chapter, it is at this stage critical to make reference to evidence that activity arising within the Off- and On-channels can drive LMD activity. Electrophysiological evidence indicates that M-pathway Off- and On-channel cells first become distinguishable at the retinal level, and that they remain distinct from each other at least until the level of area V1 (Nelson, Famiglietti & Kolb 1978; Schiller 1982). Critically, psychophysical evidence suggests that within this area (the area at which LMDs arise – see Morrone et al 1995), Off- and On-channel responses to decrement- or increment-defined stimuli can drive LMD activity such that perceptions of coherent global motion arise (Edwards & Badcock 1994). That is, it has been proposed that output from Off- and On-channel cells effectively drives LMD activity, and that the combination of this activity and subsequent higher-order M-pathway activity forms the neural basis for perceptions of coherent global motion (Edwards & Badcock 1994; Morrone et al 1995).

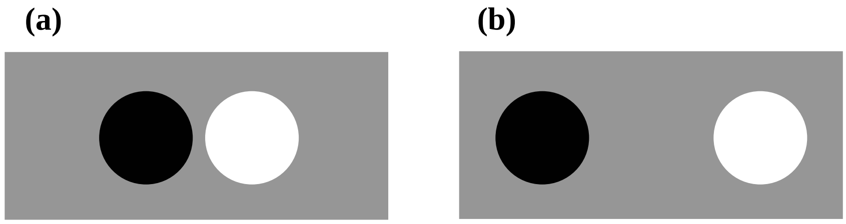
The characteristics of LMDs raise the possibility that the cells are involved in generating perceptions of illusory 'jitter' motion. That is, it is possible that the patterns of Off- and On-channel excitation elicited by the onset and offset of *each dot-pair* of which a Glass pattern is composed stimulates LMDs such that perceptions of coherent global motion arise. This hypothesis is strengthened by the compatibility of the receptive field characteristics of LMDs with the stimuli so far shown to reliably elicit the jitter illusion; consistent with the tuning of the cells for *trajectory* (see above) when considered individually each Glass pattern dot-pair describes a linear spatial relationship, and consistent with the maximum *integration range* of LMDs (≤ ~30 arc minutes visual angle; see above) the dots making up each Glass pattern dot-pair have so far fallen at a maximum distance of 21 arc minutes from each other (see chapter 2).

In order to test the hypothesis that Glass pattern dot-pairs stimulate LMDs such that the jitter illusion arises, it is possible to exploit the perceptual correlates of LMD characteristics. It has already been reported that the maximum integration range over which LMDs reliably integrate motion signals is approximately 30 arc minutes of visual angle (Mikami et al 1986). This means that global motion perceptions arising on the basis of LMD activity should only be reliably elicited when the local motion energy defined by the stimulus falls within this range (see Mikami et al 1986; Smith et al 2001). In the case of random dot kinematograms (RDKs), for instance, the finding that coherent global motion perceptions are only reliably elicited when the local motion signals describe a distance of ≤15 arc minutes of visual angle (Braddick 1974) has been used as evidence that the global perceptions arise on the basis of LMD activity (Eagle & Rogers 1996 & 1997). A similar test of LMD involvement in generating the jitter illusion can be devised. That is, in order to test whether perceptions of illusory 'jitter' motion do arise as a result of LMD activity elicited by the presentation of each Glass pattern dot-pair, the distance between dots within each pair (the 'intra-pair distance') can be manipulated. If the illusion *does* arise on the basis of LMD activity, then the maximum intra-pair distance at which it is observed should be consistent with the integration range of LMDs. That is, perceptions of the illusion should only arise in response to presentations of Glass patterns with a maximum intra-pair distance of approximately 30 arc minutes of visual angle. The specific aim of the experiments reported in this chapter was to test this prediction.

Methods.

Stimuli

All Glass pattern stimuli were generated according to a concentric function and were composed of decrement- and increment-defined dot-pairs. In each experiment intra-pair distance (the distance between the centre of the two dots of which each pair is composed) was manipulated. In total, 6 conditions were tested. Within these, the intra-pair distances tested increased from 15 to 45 arc minutes of visual angle in increments of 6 arc minutes. This range was selected in order to include distances within and beyond the maximum integration range of local motion detectors (~30 arc minutes of visual angle). Intra-pair distance was manipulated across, not within, Glass patterns (see Figure 6.1). Of course, changing the intra-pair distance did not introduce the confound of simultaneously changing the overall global 'form' perception elicited by these patterns – each was composed of decrement- and increment-defined dot-pairs and therefore did not elicit strong perceptions of a structure consistent with the function according to which they were generated anyway. In all other respects (with the exception of the features described below) stimuli were generated as per the description provided in chapter 2.



Figures 6.1: Intra-pair distance was manipulated such that it ranged from 15 to 45 arc minutes of visual angle (compare (a) and (b)). Intra-pair distance was held constant *within* each Glass pattern.

The first experiment was designed to test the range of intra-pair distances across which Glass patterns composed of decrement- and increment-defined dot-pairs reliably elicit the jitter illusion. In this experiment (and consistent with the stimuli used in earlier experiments), stimuli were composed of a total of 200 dots that were arranged in 100 dot-pairs. As noted, it was predicted that the illusion would only be reliably elicited by patterns with a maximum intra-pair distance of ~30 arc minutes of visual angle.

The second experiment served as a control experiment. One of the problems associated with manipulating the intra-pair distance of Glass patterns is that the signal-to-noise ratio is also effectively altered (see Dakin 1997). That is, as intra-pair distance is increased so too is the likelihood that the dots in each pair are no longer nearest neighbours, and that spurious matches (with dots from other pairs) will be made as a result. These ‘spuriously-matched’ dot-pairs will be randomly oriented and thus act like noise. In order to rule out the possibility that the data from the first experiment actually reflect the effects of changing the signal–to-noise ratio, patterns of a lower density (and thus decreased opportunity for making spurious matches) were tested in the second experiment. It was expected that the data generated in response to these patterns would be consistent with the data generated in the first experiment *only* if the paradigm was testing the effects of manipulating intra-pair distance and not signal-to-noise ratio. To that end, stimuli used in the second experiment were composed of 64 dots (or 32 dot-pairs). This density was selected on the basis of pilot data indicating that stimuli consisting of 32 dot-pairs are the lowest-density patterns to reliably elicit perceptions of the illusion (to review the data see chapter 11). In all other respects conditions in the second experiment were consistent with those in the first.

For both experiments reported here, control stimuli were equivalent to test stimuli in all respects except for the fact that the dots of which each *control* stimulus was composed were positioned randomly throughout the stimulus field.

Subjects

Subjects consisted of two experienced psychophysical observers (AB and vdZ) and two trained observers (ME and US) who were naïve to the aims of the experiment. However, in the second (control) experiment the data from only one of the naïve subjects (subject US) was recorded.

Procedure

In both the first and second experiments each condition was represented by 10 stimuli. Each experiment therefore consisted of a total of 120 stimuli (with 6 test and 6 control conditions). The stimuli from each experiment were tested in separate blocks. Each block was presented to subjects 3 times, so mean responses for each condition are based on 30 trials.

Stimuli were presented for 100 milliseconds, and subjects were instructed to indicate whether each stimulus appeared to undergo coherent global motion or not. All other procedures were as per the description provided in chapter 2.

Results.

For each of the experiments reported here, the data are arranged as per the description provided in chapter 2. It is also the case that for each of the experiments the maximum intra-pair distance at which the jitter illusion is reliably elicited was estimated (extrapolated) using a 50% threshold (this threshold is marked on each graph). This value was selected in order to be consistent with previous experiments. However, it must be noted that relative to the much higher thresholds used in similar studies (see Braddick 1974; Eagle & Rogers 1996), this threshold yields a *liberal* estimate of the maximum intra-pair distance at which perceptions of coherent global motion are reliably elicited (see the discussion section below).

Data from the first experiment are shown in Figure 6.2. This figure illustrates changes in the responses of individual subjects to test stimuli as a function of intra-pair distance. Perhaps the most obvious feature of these data is that they indicate that proportions of affirmative 'motion' responses declined as intra-pair distance increased. That is, as intra-pair distance increased motion perceptions declined from a point where they were recorded in response to almost every trial (with the *lowest* mean proportion of 0.83 ± 0.06 recorded by subject MS in the 15 arc min condition) to a point where they were recorded in response to only very few presentations (with the *highest* mean proportion of 0.1 ± 0.05 recorded by subject ME in the 45 arc min condition). This was generally the case for each of the subjects tested. In fact, the consistency of the data across subjects and conditions allows for it to be summarised as a single function (see Figure 6.3).

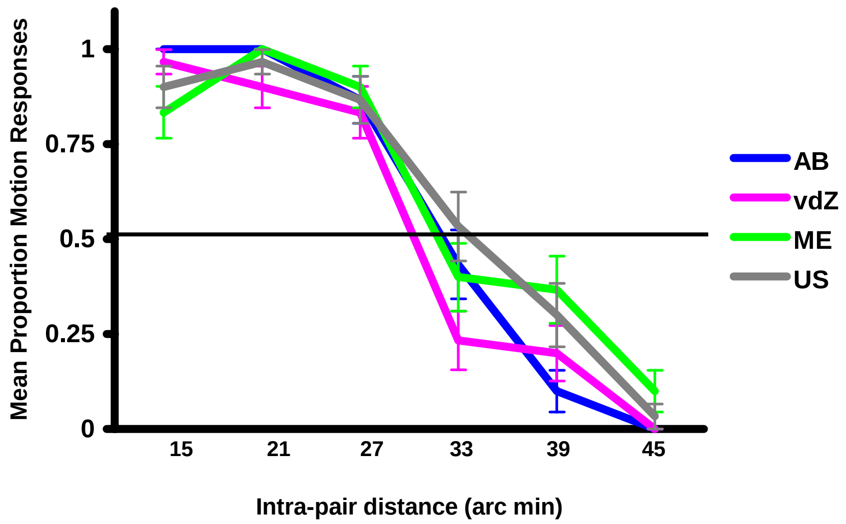


Figure 6.2: The mean proportions of affirmative 'motion' responses for individual subjects. The proportions are represented as a function of intra-pair distance. Error bars represent one standard error.

Figure 6.3 illustrates group responses to both test and control stimuli. Inspection of the proportions of affirmative responses to control stimuli confirms that motion perceptions were almost never elicited by those stimuli: while the proportion of affirmative responses to *test* stimuli decreased from a high level (0.93 ± 0.02) in the shortest intra-pair distance condition to a low level (0.03 ± 0.02) in the longest intra-pair distance condition, the control stimuli never reliably elicited motion perceptions. Critically in terms of the hypothesis, the data indicate that of the test stimuli that were presented, only those with intra-pair distances of 15, 21 and 27 arc minutes of visual angle reliably elicited the jitter illusion. They show that the illusion was *not* reliably elicited by Glass patterns with intra-pair distances of 33, 39 and 45 arc minutes of visual angle. In fact, using the 50% threshold described above, the data indicate that coherent global motion perceptions were reliably elicited by patterns with an estimated maximum of *31* arc minutes of visual angle. This value is remarkably consistent with the predicted maximum intra-pair distance at which perceptions of the illusion would arise. Data from this experiment therefore provide support for the notion that LMDs are involved in generating perceptions of illusory 'jitter' motion.

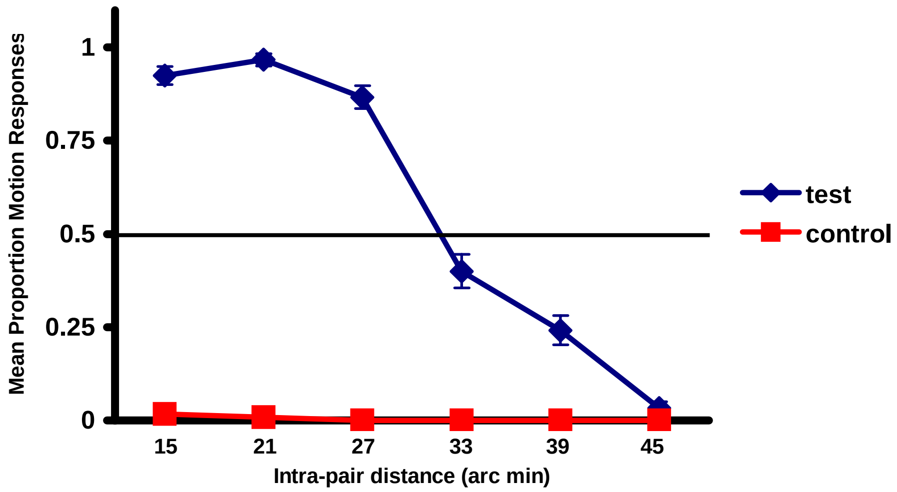


Figure 6.3: Group mean proportions of affirmative 'motion' responses. The data are presented as a function of intra-pair distance, and error bars represent one standard error. The data indicate that reliable motion perceptions were elicited by patterns with an estimated maximum intra-pair distance of 31 arc minutes of visual angle.

Data from the second experiment are represented as a function of intra-pair distance in Figure 6.4. The data generated in this experiment were again remarkably consistent across subjects, so only the group data are represented (to review individual data see chapter 11). Inspection of these data reveals that responses to control stimuli were consistent with those recorded in the first experiment; motion perceptions were almost never elicited by presentations of control stimuli. In the test conditions, proportions of affirmative responses are also similar to those recorded in the first experiment. That is, proportions of affirmative responses decreased from a high level (0.9 ± 0.03) in the shortest intra-pair distance condition to a low level (0.07 ± 0.03) in the longest intra-pair distance condition, and reflected a general downward trend in the intermediate conditions. In addition, the data indicate that the illusion was reliably elicited by stimuli with intra-pair distances of 15, 21 and 27 arc minutes of visual angle but not by stimuli with intra-pair distances greater than or equal to 33 arc minutes of visual angle. Based on these data the estimated maximum intra-pair distance at which lower-density Glass patterns reliably elicit the jitter illusion is ~29 arc minutes of visual angle. The similarity of this value and the one recorded in the first experiment (31 arc minutes of visual angle) is *inconsistent* with the suggestion that the results reflect the perceptual effects of manipulating the signal-to-noise ratio. Rather, they suggest that (as intended) the paradigm tested the perceptual consequences of manipulating intra-pair distance. Importantly, the data provide good support for the hypothesis that LMDs are involved in generating the jitter illusion.

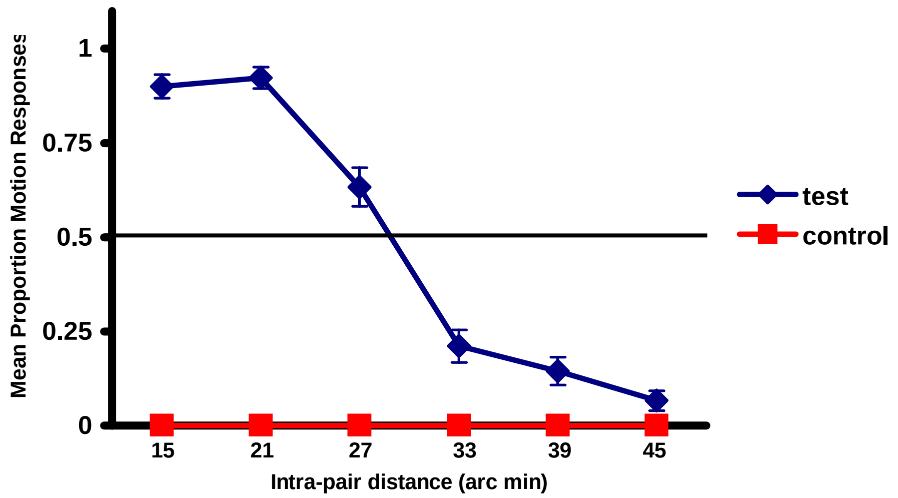


Figure 6.4: Group mean proportions of affirmative 'motion' responses for the low-density experiment. In this case, the data indicate that reliable motion perceptions were elicited by patterns with an estimated maximum intra-pair distance of 29 arc minutes of visual angle. Error bars represent one standard error.

Discussion.

The data presented in this chapter are consistent with the suggestion that LMDs are involved in generating the jitter illusion. On the basis of the supposed involvement of these cells it was predicted that the illusion would be reliably elicited only by Glass patterns with intra-pair distances of less than or equal to approximately

30 arc minutes of visual angle. This prediction was supported by the data in both the first and second experiments. In fact, the maximum intra-pair distances of 31 and 29 arc minutes recorded in each experiment respectively are remarkably similar to the maximum integration range of LMDs (Mikami et al 1986) – so much so that any discrepancies can easily be accounted for by variance arising either in the physiological measurement of the LMD integration range, or in the psychophysical measurements reported here. An additional and critical finding is that the results reflect the perceptual consequences of manipulating the intended IV; the similarity of the values recorded in each experiment suggests that these values reflect the effects of manipulating *intra-pair distance*. It is therefore the case that these data provide support for the hypothesis that the patterns of Off- and On-channel excitation elicited by the onset and offset of *each* Glass pattern dot-pair stimulates LMDs such that perceptions of illusory 'jitter' motion arise.

Of course, the maximum intra-pair distance at which the jitter illusion arises is considerably *larger* than the maximum spatial displacement over which evidence suggests LMDs integrate the local motion signals defined by other types of stimuli. In the case of RDKs for instance, it has been well documented that coherent motion perceptions only arise on a reliable basis when the maximum spatial displacement between related dots is *15 arc minutes* of visual angle (Braddick 1974). This raises the question of how to account for discrepancies between RDK-related data, and the jitter-related data that have been reported here. One possible answer to this question lies in the 'reliability' measures used in each case. That is, estimates of the maximum spatial displacements over which RDKs reliably elicit motion perceptions are often based on an 80% threshold (see Eagle & Rogers 1997). In the case of the jitter illusion however, the estimates were based on a threshold of *50*%. While the data suggest this procedural difference does not account for the entire discrepancy between the two data sets, the remainder may be accounted for by other procedural differences. For instance, more recent work using RDKs indicates that features such as element size and eccentricity influence the maximum spatial displacement at which coherent motion perceptions break down (see Eagle & Rogers 1996). On these bases, conflicting results generated in relation to RDK-related and jitter-related experiments need not pose a problem for the hypothesis that *in each case* motion perceptions arise on the basis of LMD activity.

In summary, the data presented in this chapter suggest that perceptions of illusory 'jitter' motion arise as a consequence of LMD activity that is elicited by each Glass pattern dot-pair. Critically, when viewed in combination with findings from previous chapters, the findings reported in this chapter make it possible to define some parameters for any model of the neural correlates of the jitter illusion: it appears that the patterns of Off- and On-channel activity elicited by the abrupt onset and offset of each decrement- and increment-defined (Glass pattern) dot-pair stimulates LMD activity, and that this activity (in combination with subsequent higher-order M-pathway activity) forms the neural basis for perceptions of illusory 'jitter' motion. Of course, this proposal raises the question of *how* the patterns of Off- and On-channel activity that arise in response to presentations of stationary dot-pairs effectively stimulate LMDs. One possibility is that the stimulation arises as a result of *asynchronous* Off- and On-channel responses to the presentation of the decrement and increment members of each dot-pair. This possibility is addressed in the chapter that follows.

CHAPTER 7
LMD activity: a model based on asynchronous off- and on-channel processing

Models of LMD activity raise the possibility that the jitter illusion arises as a result of asynchronous Off- and On-channel responses to the dots that make up each decrement- and increment-defined dot-pair. Reichardt (1959; 1961) proposed a model that, when applied to human visual processing, suggests the mechanisms that underlie the sensitivity of LMDs to local shifts in luminance (see Adelson & Bergen 1985). The model suggests that LMDs receive input from two cells with spatially disparate receptive fields. It proposes that the *asynchronous* activity elicited in these cells by a local shift in luminance is temporally calibrated by a ‘delay’ mechanism, such that under appropriate conditions excitatory signals from the cells are *simultaneously* transmitted to LMDs. According to the model the detectors are only stimulated when this is the case. Reichardt’s model represents a problem for suggestions that in the case of the jitter illusion, the onset and offset of decrement- and increment-defined dot-pairs stimulates LMD activity; each event respectively involves the simultaneous (synchronous) introduction and removal of the decrement and increment members of each dot-pair. One possible solution to this problem is that in the case of the jitter illusion, the origin of the asynchronous activity required for LMD stimulation arises not at a stimulus level but at a cellular one; that excitatory, asynchronous Off- and On-channel responses to the onset and offset of the decrement and increment members of each dot-pair serve as the catalyst for LMD activity. While such a model involves a number of problematic assumptions (see below), it cannot be ruled out on the basis of the findings so far presented in relation to the jitter illusion. The general aim of the experiments reported in this chapter was therefore to test the plausibility of the model.

It has already been noted that LMDs are sensitive to local shifts in luminance. A model of the means by which this sensitivity arises was proposed by Reichardt (1959 & 1961), and later adapted for human vision (see, for example, Adelson & Bergen 1985). Such a model is represented in its simplest form in Figure 7.1.

According to the model, LMDs receive input from two cells with spatially disparate but proximal receptive fields. When luminance signals from the visual scene fall on the two receptive fields sequentially (as is often the case when local shifts in luminance arise), a particular pattern of cellular activity results. That is, the responses of the cells to which the receptive fields belong arise asynchronously. In order for these asynchronous signals to be simultaneously transmitted to LMDs – the condition required for LMD activity to arise (Reichardt 1959; 1961) – the model proposes the existence of a so-called 'delay' mechanism. According to the model, under appropriate conditions this mechanism temporally calibrates the excitatory cellular responses elicited by a stimulus. The mechanism also partially determines the 'direction-tuning' of the LMD with which it is associated; its position within the 'local motion detection system' determines the order in which luminance signals must fall on the two receptive fields in order for LMD activity to arise. In the example represented in Figure 7.1, for instance, the position of the mechanism dictates that signals must first fall on the receptive field located on the left (a), and then on the receptive field (b) located on the right in order to stimulate the LMD. Consequently, this particular detector is tuned for motion in a *rightwards* direction. Reichardt's model (1959; 1961) therefore provides both a general account of how local shifts in luminance stimulate LMDs, and a more specific account of the tuning of these detectors for particular directions of motion.

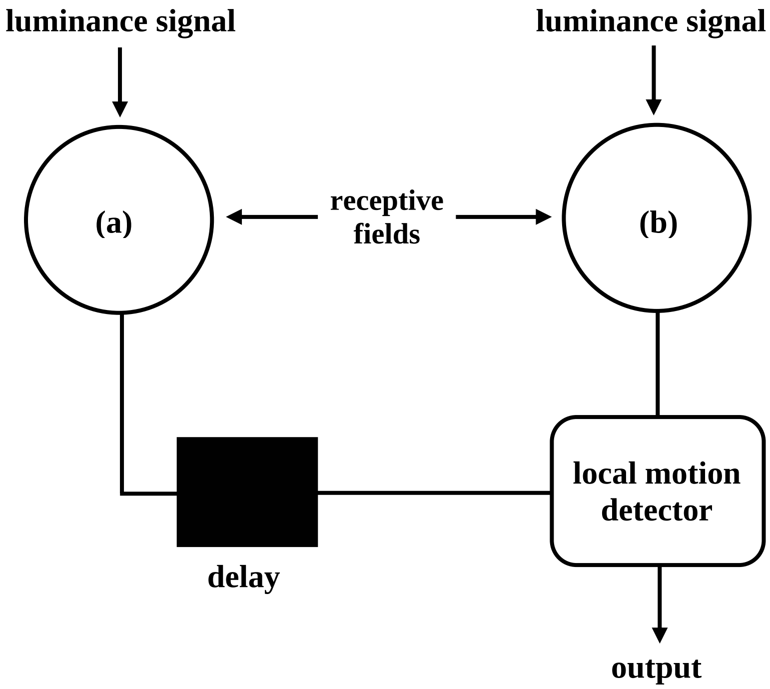


Figure 7.1: Reichardt's (1959; 1961) model of the means by which the sensitivity of LMDs to local shifts in luminance arises. Outputs from two cells (not shown) with spatially disparate but proximal receptive fields ((a) and (b)) are transmitted to LMDs. Transmission of the output is delayed in the case of *one* of these cells (in this case, the cell to which receptive field (a) belongs). LMD activity arises when transmissions from the two cells arrive simultaneously. The position of the delay mechanism within the system determines the tuning of the LMD for direction-of-motion within the (in this case) *horizontal* range determined by the spatial configuration of the two receptive fields. In this example, the mechanism is positioned such that simultaneous signals can only be transmitted when the signal falls first on receptive field (a) and then on receptive field (b). The LMD represented is therefore tuned for local motion in a *rightwards* direction.

Based on Reichardt's model, the onset and offset of the decrement and increment members of Glass pattern dot-pairs should *not* stimulate LMD activity. This is because even if it is assumed that the spatial position of each dot corresponds to the spatial position of one of the receptive fields associated with a LMD, the *simultaneous* changes in luminance arising at the onset and offset of the dot-pair should elicit synchronous (rather than asynchronous) cellular responses. This raises the possibility that in the case of the jitter illusion, the origin of the asynchronous activity required for LMD stimulation arises at a cellular level. While it is generally accepted that the cells of the Off- and On-channels have equivalent response latencies (Schiller 1982; 1992) a more recent study raises an alternative possibility. Kondo and Sieving (2001) presented ERG evidence of a frequency-dependent phase-lag between Off- and On-channel responses to flicker stimuli. This finding can (despite a lack of corroborating psychophysical evidence) be interpreted as evidence of an Off-/On-channel processing asynchrony. If it is assumed that this asynchrony or 'processing lag' exists (see also a discussion of the mechanisms by which the Pulfrich and Hess effects arise; Williams & Lit 1983), and that cross-channel input (from one Off- and one On-channel cell - see below for a discussion of the plausibility of this assumption) can drive LMD activity, then a model of the means by which the onset and offset of stationary decrement- and increment-defined dot-pairs stimulate LMDs can be constructed. That is, in the case of the system represented in Figure 7.1, if the asynchrony manifests as a lag in (say) Off-channel processing, and if the receptive field located to the left (a) belongs to an Off-channel cell while the receptive field located to the right (b) belongs to an On-channel cell, then the onset of a dot-pair in which the decrement dot falls on receptive field (a) and the increment dot falls on receptive field (b) *should* elicit activity in the (rightward motion-tuned) LMD.

One prediction arising on the basis of an 'Off-/On-channel processing asynchrony model' is that the spatial relationship between the decrement and increment dots making up each dot-pair should determine the direction in which entire Glass patterns appear to move. This prediction is based on the widely accepted notion that the direction of global motion perceptions is determined by the distribution of direction-tuned LMDs in which a stimulus elicits activity; if the Off-/On-channel asynchrony is consistent over time, then the only variable determining which LMDs are stimulated by a Glass pattern presentation - and therefore in which direction the pattern will appear to move - is the spatial configuration of the decrement and increment members of each dot-pair. Unfortunately, the findings reported by Kondo and Sieving (2001) do not provide a basis for suggesting the nature of the proposed Off-/On-channel asynchrony; whether it manifests as a lag in Off- or On-channel processing. It is therefore not possible to predict the specific direction (clockwise or counter-clockwise in the case of concentric patterns, up or down in the case of linear patterns, and so on) in which particular Glass patterns should appear to move at stimulus onset and offset. The model does, however, give rise to at least one testable prediction. That is, independent of the nature of the processing asynchrony it should be the case that Glass patterns arranged in 'opposing' spatial configurations (configurations in which the spatial positions of the decrement and increment members of the dot-pairs are reversed across patterns) will elicit perceptions of motion in *opposite* directions. This should be the case at both stimulus onset and stimulus offset. The specific aim of the experiments reported in this chapter was to test this prediction.

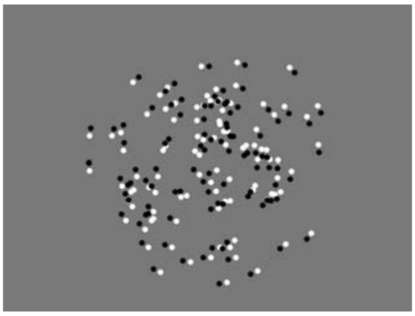
Methods.

Stimuli

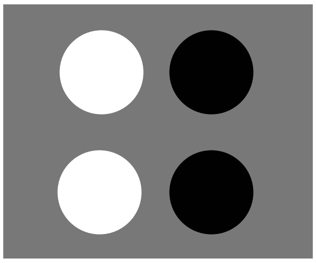
For the purposes of comparison with results from earlier experiments, all stimuli were generated according to a concentric function. All stimuli were composed of decrement- and increment-defined dot-pairs. For the sake of convenience, the spatial configuration of the decrement and increment dots making up each Glass pattern dot-pair will be described with reference to the *decrement* dot. For all features not described below, stimuli were as described in chapter 2.

Two experiments were conducted, the first to test whether patterns arranged according to ‘opposing’ spatial configurations give rise to perceptions of motion in opposite directions at stimulus *onset*, and the second to test whether this is the case at stimulus *offset*. Two sets of test stimuli were generated for use in each experiment: one consisted of stimuli composed of dot-pairs in which the decrement dots were positioned clockwise (CW) of the increment partner dots (condition decCW; see Figure 7.2), and the other consisted of stimuli composed of dot-pairs in which the decrement dots were positioned counter-clockwise (CCW) of the increment partner dots (condition decCCW; see Figure 7.3). Based on the model described above, it was predicted that stimuli from each of these groups would appear to move in *opposite directions*, and that this would be the case at stimulus onset and at stimulus offset.

Control stimuli consisted of concentric Glass patterns arranged such that the spatial configuration of the decrement and increment dots making up the dot-pairs was balanced across each pattern. That is, half the dot-pairs in each pattern were arranged such that the decrement dot was positioned CW of the increment partner dot, and the remaining half were arranged such that the decrement dot was positioned CCW of the increment partner dot (condition balanced; see Figure 7.4). These ‘balanced’ patterns were demonstrated in a pilot experiment to reliably elicit perceptions of illusory ‘jitter’ motion. In fact, subjects tested in the pilot experiment reported that the motion perceptions arising in response to balanced patterns were perceptually indistinguishable from the perceptions elicited by the traditional Glass pattern presentations.



Figures 7.2(i) & 7.2(ii): Patterns in condition *decCW* were configured such that for each dot-pair the decrement dot was positioned CW of the increment dot.



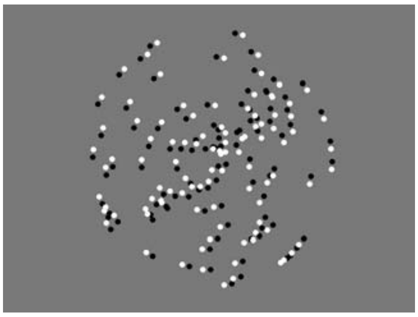
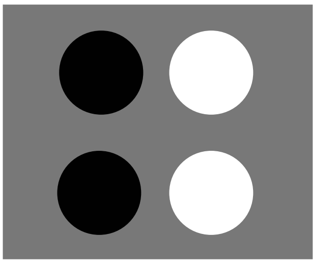


Figure 7.3(i) & 7.3(ii): Patterns in condition *decCCW* were configured such that for each dot-pair the decrement dot was positioned CCW of the increment dot.



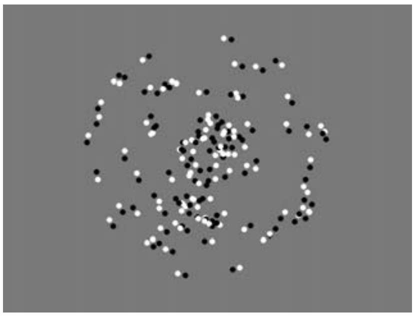
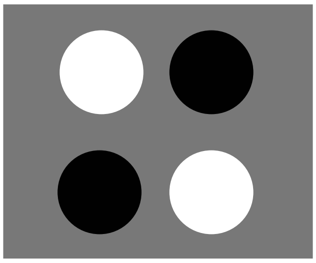


Figure 7.4(i) & 7.4(ii): Patterns in the *balanced* condition were configured such that for equal numbers of dot-pairs the decrement dot was positioned CW and CCW of the increment dot. These patterns made up the control condition.



Subjects

Subjects consisted of two experienced psychophysical observers (AB and vdZ) and two trained observers (RB and ME) who were naïve to the aims of the experiment.

Procedure

In both the first and second experiments each condition was represented by 10 stimuli. Each experiment therefore consisted of a total of 60 stimuli (with 3 test and 3 control conditions). The stimuli from each experiment were tested in separate blocks. Each block was presented to subjects 3 times, so mean responses for each condition are based on 30 trials.

Stimuli were presented for 1600 milliseconds. This duration was selected in order to allow subjects to easily distinguish between the directions in which stimuli appeared to move at stimulus onset and offset. Subjects were required to indicate by means of a key-press whether the stimulus appeared to move in a CW or CCW direction. Responses were registered by means of a key-press – depression of the ‘l’ key indicated the pattern appeared to move in a CW direction, while depression of the ‘a’ key indicated it appeared to move in a CCW direction. In the first experiment subjects were instructed to make this judgement on the basis of perceptions arising at stimulus *onset*. In the second they were instructed to make the judgement on the basis of perceptions arising at stimulus *offset*. All other procedures were as per the description provided in chapter 2.

Predicted pattern of results

Two patterns of results, each of which would support the predictions of the Off-/On-channel processing asynchrony model, are represented in Figure 7.5. These *hypothetical* data represent the mean proportions of CW responses expected to arise at stimulus onset if the particular asynchrony on which perceptions are based is a lag in Off-channel processing (red markers), or a lag in *On-channel* processing (blue markers). By interchanging the markers, the expected pattern of responses at stimulus offset can be observed. The critical feature of these results is that for both types of processing lag, responses in the test conditions are in an *inverse relationship relative to the responses recorded in the control condition*. That is, in comparison to responses in the control condition, those in one test condition indicate a higher proportion of CW responses, while those in the other indicate a lower proportion of CW responses. In interpreting the *actual* data reported below it is critical that proportions in the control condition be used as a baseline. This ensures that analyses of data in the test conditions take subject response biases into account. It should also be noted that a further prediction arising on the basis of the model is that the direction in which patterns in the decCW and decCCW conditions appear to move at stimulus onset should be the opposite to the one in which they appear to move at stimulus offset. However, this prediction need only be tested if either pattern of results represented in Figure 7.5 is first observed in the data recorded at stimulus onset and offset. For this reason, independent analyses of the onset and offset data are reported below.

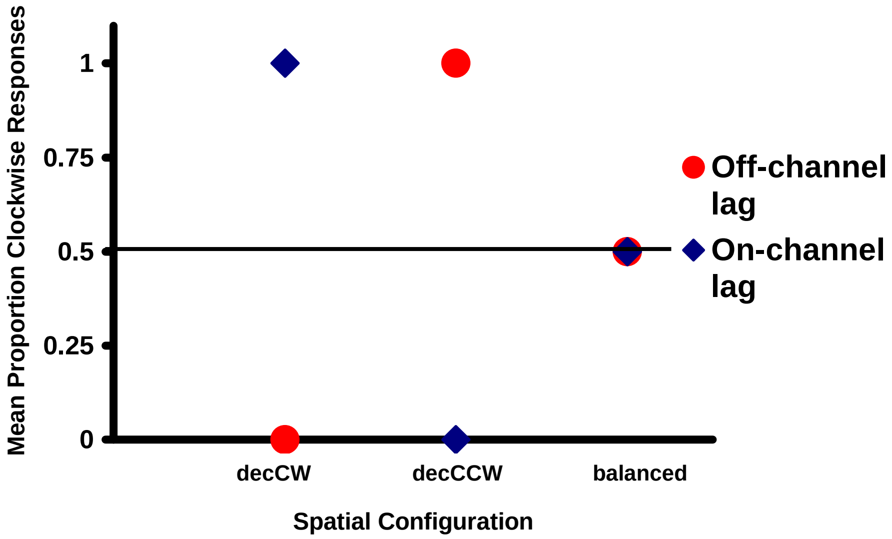


Figure 7.5: The pattern of results expected at stimulus onset if the illusion arises as a result of an Off-/On-channel processing asynchrony. The patterns expected in the event that this asynchrony manifests as a lag in either Off- or On-channel processing are represented. The data reflect the mean proportion of CW motion responses to patterns in test (decCW and decCCW) and control (balanced) conditions. As predicted, responses in the test conditions are in an inverse relationship relative to those recorded in the control condition. Interchanging the markers generates the pattern of results expected at stimulus offset.

Statistical Analyses

Data were analysed using the z-test for dependent proportions (McNamar 1947). Z-scores were generated in order to compare results in each of the test conditions to those in the control conditions for individual subjects. That is, for the reasons outlined above one set of z-scores compared results from the decCW condition to results from the balanced condition (the decCW/balanced comparison), while the other compared results from the decCCW condition to results from the balanced condition (the decCCW/balanced comparison). As already noted, the Off-/On-channel processing asynchrony model does not predict the actual direction in which patterns in the test conditions should appear to move. For that reason, a two-tailed test was used. The critical z-score was therefore $\pm 1.96_{(alpha\ =\ 0.05)}$. Positive z-scores indicate that the proportion of CW responses to test patterns *decreased* relative to those recorded in the control condition, whilst negative z-scores indicate that the proportion of CW responses *increased* relative to those recorded in the control condition.

Results.

Data from the first experiment (designed to test the direction in which patterns appear to move at stimulus *onset*) are represented in Figure 7.6. This figure represents the responses of individual subjects to test and control stimuli. Inspection of the figure suggests that the data from the two test conditions do *not* reflect the predicted inverse relationship. In fact, when considered in relation to the CCW response bias exhibited by each subject, only the data recorded by subject RB shows the expected pattern; relative to results in the control condition subject RB recorded fewer CW responses in the decCW condition, and more CW responses in the decCCW condition. In the case of the remaining subjects, proportions of CW responses either increased in each test condition relative to the control (subjects AB and vdZ) or decreased in each test condition relative to the control (subject ME).

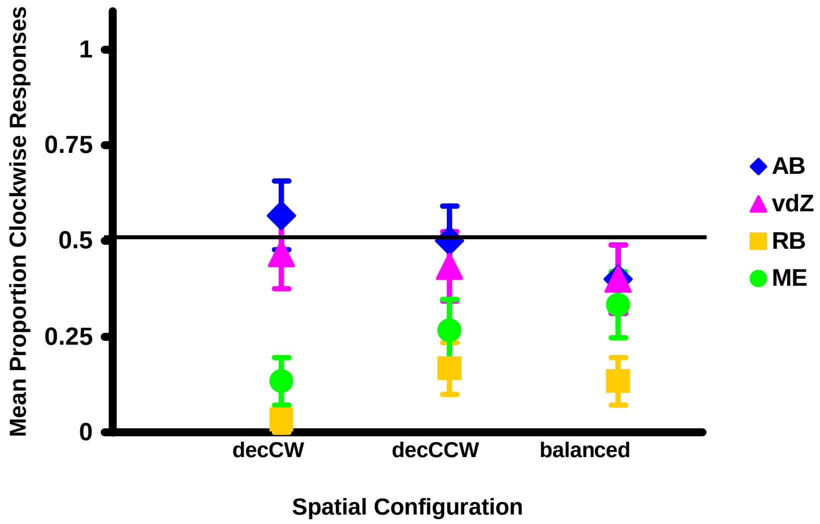


Figure 7.6: Mean proportions of CW responses for individual subjects at stimulus *onset*. Only data from subject RB showed the expected inverse response relationship. Error bars represent one standard error.

The z-values for these data are represented in Table 7.7. Of these values, only two (marked with an asterisk) indicate a significant difference between responses in the test and control conditions. For subjects AB and ME, results in the decCW (test) condition were significantly different to those recorded in response to patterns in the balanced (control) condition. However, as already noted neither of these subjects recorded the expected inverse response relationship. Importantly, data for subject RB (the only subject to record the expected inverse response relationship) did *not* yield a significant result in either comparison. While in the case of the decCW/balanced comparison this may in part have been due to a floor effect (low proportions of CW responses in the control condition left little scope for a *reduction* in proportions of CW responses), results from the decCCW/balanced comparison cannot be similarly accounted for. On this basis it must be concluded that data from the first experiment do *not* support the predictions arising from a model based on an Off-/On-channel processing asynchrony.

	AB	**vdZ**	**RB**	**ME**
decCW/balanced	-2.24*****	-1.41	1.73	2.45*****
decCCW/balanced	-1.73	-1	-1	1.41

Table 7.7: Z-values comparing results from the two test conditions (decCW and decCCW) to those recorded in the control (balanced) condition at stimulus *onset*. Cases in which responses recorded in the test conditions were significantly different to those recorded in the control condition are marked with an asterisk.

Data from the second experiment (designed to test the direction in which patterns appear to move at stimulus *offset*) are represented in Figure 7.8. Within this figure the responses of individual subjects to test and control stimuli are represented. The data indicate that for each subject there was very little difference between the responses recorded in the test and control conditions. In fact, data recorded by only one of the subjects – this time subject vdZ - indicated the expected inverse response relationship. In the case of the remaining subjects (subjects AB, RB and ME) mean proportions of CW responses in the decCW and decCCW conditions increased relative to proportions in the balanced condition.

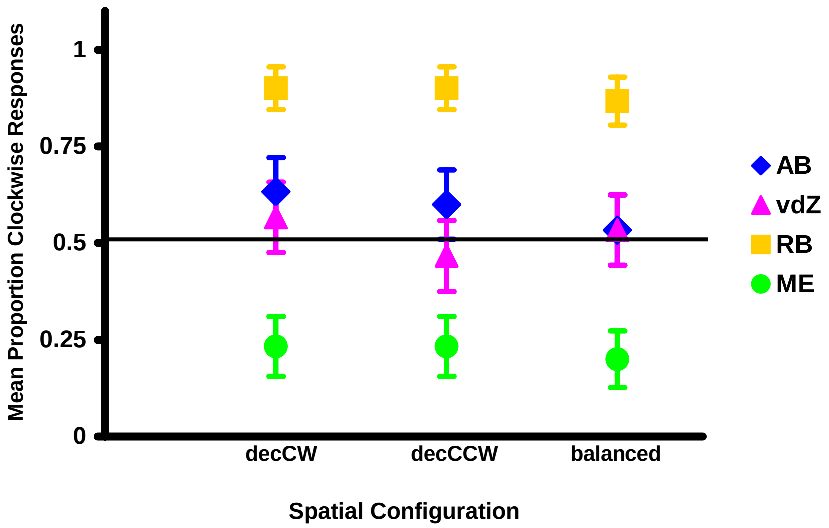


Figure 7.8: Mean proportions of CW responses at stimulus *offset* for individual subjects. Only data recorded by subject vdZ showed the expected inverse response relationship. Error bars represent one standard error.

The z-values that were generated in order to compare results from the two test conditions to results from the control condition at stimulus offset are represented in Table 7.9. None of these values indicates a significant difference between responses in the test and control conditions. This constitutes evidence that for each subject (including subject vdZ – the only subject to record the expected inverse response relationship), results in the test conditions can be accounted for by response biases. It is therefore the case that data from the second experiment do *not* support the predictions arising from an Off-/On-channel processing asynchrony model. Furthermore, the lack of support offered by data from the first and second experiments for the model render it unnecessary to compare results across the two experiments.

	AB	**vdZ**	**RB**	**ME**
decCW/balanced	-1.73	-1	-1	-1
decCCW/balanced	-1.41	1.41	-1	-1

Table 7.9: Z-values generated in order to compare results from the two test conditions (decCW and decCCW) to results from the control (balanced) condition at stimulus *offset*. The values reveal that for each subject, data generated in the test conditions were statistically equivalent to those generated in the control condition.

Discussion.

The results presented here are not consistent with the hypothesis that LMD activity arises as a result of asynchronous Off- and On-channel responses to the dots that make up each decrement- and increment-defined (Glass pattern) dot-pair. On the basis of the model that stemmed from this hypothesis, it was predicted that patterns in which the decrement and increment dots were arranged in ‘opposing’ spatial configurations would elicit perceptions of motion in opposite directions. Data from the first experiment indicate that this was not the case at stimulus onset. Within this experiment only one subject recorded a pattern of responses that was consistent with the predictions of the model. However, the effects were not statistically significant and can be accounted for on the basis of the subject’s response biases. Data from the second experiment, designed to test the direction in which patterns appeared to move at stimulus offset, similarly do not support the model. Again, only one (different) subject recorded a pattern of responses that was consistent with predictions arising on the basis of the model. Statistical analyses of those data indicated that they too can be accounted for on the basis of the subject’s response biases. Thus, the data from the two experiments suggest that Glass patterns arranged in opposing spatial configurations do *not* reliably give rise to perceptions of motion in opposite directions at either stimulus onset or offset. On this basis, it must be concluded that the LMD activity on which perceptions of illusory ‘jitter’ motion are based is unlikely to arise as a result of asynchronous Off- and On-channel processing.

Of course, these findings do not rule out the possibility that the LMD activity on which perceptions of the jitter illusion are based arises as a result of an asynchronous Off- and On-channel processing-relationship that *changes over time*. The predictions tested here were based on the assumption that any Off-/On-channel processing asynchrony would remain constant over time; that it would consistently manifest as a lag in either Off- or On-channel processing. If, however, the asynchronous relationship between Off- and On-channel activity is *temporally fluid* (such that the Off-channel sometimes responds more slowly than the On-channel and vice versa) then the prediction that patterns arranged in opposing spatial configurations should consistently elicit perceptions of motion in opposite directions would no longer hold. While a model based on this suggestion is consistent with the data reported here, the existence of a processing relationship of this type is unlikely. Evidence arising in relation to other vision pathways indicates that the relative speed at which different cell populations respond to visual stimuli is constant over time. For example, there is evidence that the P-pathway consistently responds more slowly than the M-pathway (Sestokas & Lemkuhle 1986; Maunsell & Gibson 1992) and the second-order system consistently responds more slowly than the first-order system (Yo & Wilson 1992; Derrington, Badcock & Henning 1993; Lin & Wilson 1996). On the basis of this evidence and in combination with the current results, it is therefore unlikely that the LMD activity on which the jitter illusion is based arises as a result of *any* type of Off-/On-channel processing asynchrony.

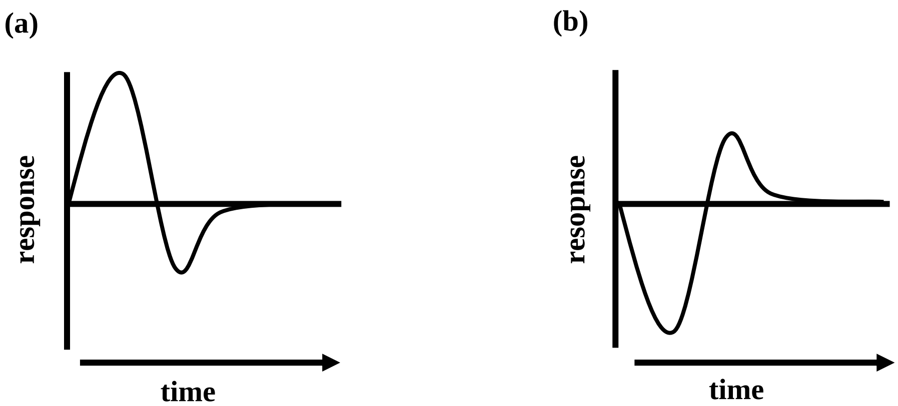
Evidence that LMDs are *not* stimulated by cross-channel (Off- *and* On-channel) input lends additional weight to the argument against the Off-/On-channel processing asynchrony model. One of the assumptions on which the model is based is that LMD activity arises when excitatory signals are transmitted from two cells - one *Off*-channel cell and one *On*-channel cell. However, there is strong psychophysical evidence to suggest that input from cells located in different channels does not effectively drive LMD activity. Edwards and Badcock (1994) reported evidence that local motion signals defined by dots that change luminance polarity across frames do not elicit perceptions of coherent global motion. They interpreted this as evidence that within the M-pathway, LMD stimulation does not arise when signals are transmitted from cells associated with different channels – that the detectors only receive effective input from two cells located within the *same* channel. On the basis of this finding, it therefore appears that the very neural architecture of the M-pathway is inconsistent with the Off-/On-channel processing asynchrony model of LMD stimulation.

The main finding to arise from this chapter is, therefore, that the LMD activity required in order for the jitter illusion to arise *cannot* be accounted for on the basis of asynchronous Off- and On-channel responses to decrement- and increment-defined dot-pairs. Of course, this finding leaves the question that was raised in the previous chapter unanswered. That is, it remains unclear *how* the patterns of Off- and On-channel activity elicited by the onset and offset of decrement- and increment-defined dot-pairs stimulate LMDs such that perceptions of illusory 'jitter' motion arise. One further and (as yet) untested possibility is that the LMD activity is a product of the unique temporal impulse-response functions characteristic of M-pathway Off- and On-channel cells. This possibility is addressed in the chapter that follows.

CHAPTER 8
LMD activity: a model based on diphasic temporal impulse-response functions

Models of the so-called ‘temporal impulse-response functions’ of M-pathway cells raise the possibility that these responses form the basis for the LMD activity on which perceptions of illusory ‘jitter’ motion are based. An impulse-response is the theoretical response of a cell to an infinitely brief stimulus (see Burr & Morrone 1993). Using psychophysical techniques, these ‘theoretical’ responses (patterns of cellular activity over time) can be modelled for different visual cortical cell populations. The resulting *temporal impulse-response functions* (or TIRFs) can then be used to predict the responses of these cells to actual stimulus presentations. In the case of the M-pathway, *diphasic* TIRFs have been attributed to the cell population (Marrocco 1976; Saito & Fukada 1986; Swanson, Ueno & Pokorny 1987; Burr & Morrone 1993). This means that for each M-pathway cell, a single visual event elicits *two* phases of activity, one of which is defined by an excitatory response and the other by an inhibitory response. Evidence that this is the case for all M-pathway cells, including those that make up the Off- and On-channels, has implications for the neural correlates of the jitter illusion. That is, by incorporating *diphasic* responses into a model of the Off- and On-channel activity that is elicited by the onset and offset of decrement- and increment-defined dot-pairs, it is possible to account for the LMD stimulation on which the jitter illusion is based. The general aim of the experiments reported in this chapter was to test the plausibility of such a model.

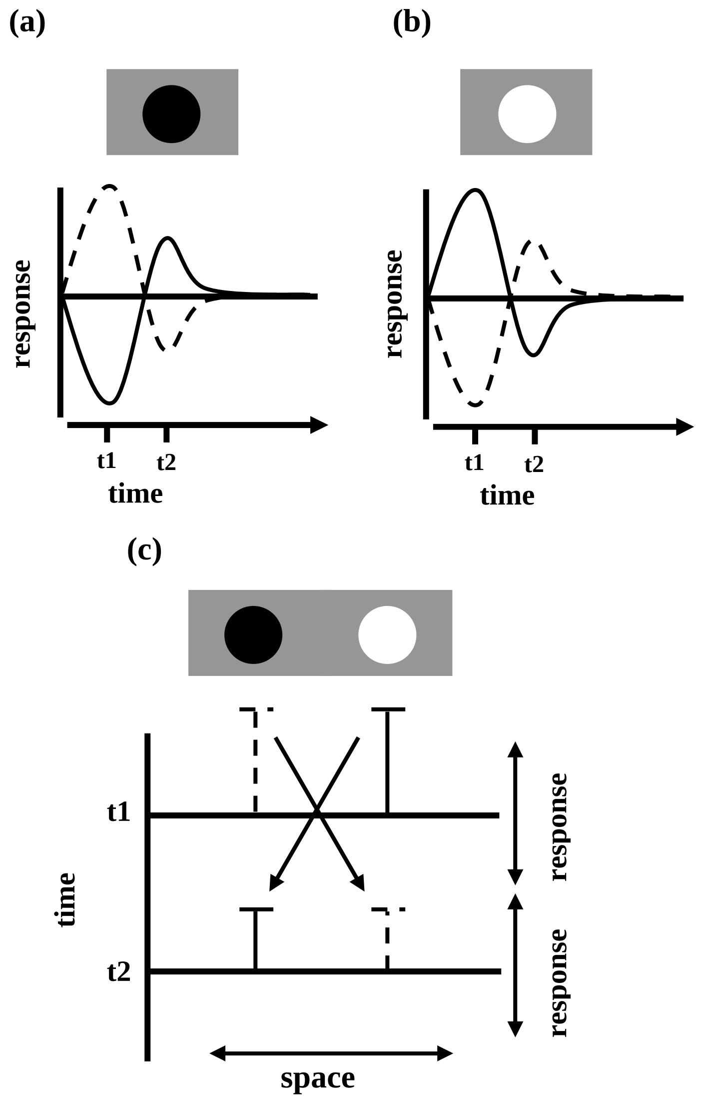
As noted above, psychophysical techniques make it possible to derive the TIRFs of cells that belong to different visual cortical cell populations. On the basis of evidence generated using these techniques, models attributing *diphasic* TIRFs to the cells that make up the M-pathway are now widely accepted (Marrocco 1976; Saito & Fukada 1986; Swanson et al 1987; Burr & Morrone 1993). These models predict that for M-pathway cells, individual visual events will elicit two, temporally sequential phases of cellular activity - phases are defined by antagonistic patterns of cellular activity. That is, one phase is defined by an *excitatory* cellular response, while the other is defined by an *inhibitory* cellular response. The models also predict that across these phases the pattern of cellular activity will describe a type of damped oscillation function – that responses in the first phase will be of greater magnitude than those in the second. Consistent with this, it has been reported that for M-pathway cells, a visual event that elicits a first-phase excitatory response also elicits a second-phase inhibitory response of lesser magnitude (Burr & Morrone 1993; see Figure 8.1(a)). From this the converse follows – that a visual event that elicits a first-phase inhibitory response will also elicit a second-phase excitatory response of lesser magnitude (see Figure 8.1(b)).



Figures 8.1(a) and 8.1(b): A pictorial representation of the TIRFs attributed to M-pathway cells. The (unmarked) horizontal line represents baseline activity. Individual visual events elicit either a first-phase excitatory response followed by a second-phase inhibitory response of lesser magnitude (a), or a first-phase inhibitory response followed by a second-phase excitatory response of lesser magnitude (b).

By incorporating diphasic responses into a model of the Off- and On-channel activity elicited by the onset and offset of decrement- and increment-defined dot-pairs, it is possible to account for the LMD activity on which the jitter illusion is based. It has already been reported that within the M-pathway, downward steps in luminance elicit excitatory responses in Off-channel cells and inhibitory responses in On-channel cells, whilst upward steps in luminance elicit inhibitory responses in Off-channel cells and excitatory responses in On-channel cells (see chapter 5). However, the temporal characteristics of M-pathway cellular activity suggest these are only the *first-phases* of each cell's response; that they are followed in time by antagonistic, second-phase responses. This means that in the case of the onset of, say, a *decrement* dot, the response pattern represented in Figure 8.2(a) would be elicited. Similarly, the onset of an *increment* dot would elicit the pattern represented in Figure 8.2(b). On the basis of these figures, it is clear that the onset of each type of dot elicits *two* peak excitatory responses over time – one in the cells of the Off-channel (broken lines) and the other in the cells of the On-channel (unbroken lines).

In Figures 8.2(a) and (b) the temporal ‘snapshots’ at which the peaks (and troughs) of cellular activity arise have been arbitrarily labelled t1 and t2. If the excitatory responses at these times are plotted *across space* for a decrement- and increment-defined dot-pair, the pattern of activity represented in Figure 8.2(c) is observed. Inspection of this figure indicates that the excitatory responses elicited within each channel effectively shift across space over time. That is, within the Off-channel excitatory responses shift from left to right over time, while within the On-channel excitatory responses shift from right to left over time (as indicated by the arrows in Figure 8.2(c)). This has important implications for models of the means by which LMD activity arises in response to such dot-pairs. In fact, based on the conditions under which LMD activity arises (see the previous chapter), the patterns of activity represented in this figure should stimulate at least two LMDs; output from Off-channel cells with receptive fields onto which the decrement and increment dots fall should stimulate at least one detector tuned for motion in a rightward direction, while output from On-channel cells with receptive fields onto which the dots fall should stimulate at least one detector tuned for motion in a leftward direction. It is therefore the case that a model based on the diphasic TIRFs of M-pathway cells - a ‘diphasic TIRF model’ – can account for the stimulation of LMDs at both the onset and offset of decrement- and increment-defined Glass pattern dot-pairs (to model the pattern of activity at stimulus offset simply interchange the broken and unbroken lines in each of the figures below).



Figures 8.2(a), 8.2(b) and 8.2(c): A representation of the 'diphasic TIRF model'. Unless otherwise marked, horizontal lines represent baseline activity. Off- and On-channel responses are represented using broken and unbroken lines respectively. Diphasic Off- and On-channel responses to the onset of a decrement (a) and increment (b) dot are represented. In each case two peak excitatory responses are elicited. The peaks arise at two temporal 'snapshots' (t1 and t2), and have been plotted across space for a decrement- and increment-defined dot-pair (c). This figure indicates that spatial shifts in Off- and On-channel responses are suitable for stimulating LMDs sensitive to motion in opposite directions.

In order to test the diphasic TIRF model, predictions about the effects of presenting Glass patterns defined by *low-contrast* decrement- and increment-defined dot-pairs can be exploited. There is physiological (Schiller, personal communication 2003) and psychophysical (Swanson et al 1987) evidence to suggest that the magnitude of a cellular response is causally related to the magnitude of the luminance variation or contrast contained within the visual scene. That is, stimuli defined by large luminance variations elicit cellular responses that are of greater magnitude than those defined by small luminance variations. Combined with the magnitude-relationship of first- and second-phase responses (see above), one consequence of this is that the activity profile of M-pathway cells begins to approximate a *monophasic* (rather than a diphasic) function as the contrast of a visual stimulus is reduced through a certain threshold. This means that at some (sufficiently low) contrast level, stimulus presentations elicit significant first- but *not* second-phase responses within cells of the M-pathway (see Swanson et al 1987). According to the diphasic TIRF model described above, perceptions of illusory 'jitter' motion are dependent upon the generation of diphasic M-pathway cellular responses – they should only arise when stimulus presentations elicit both first- *and* second-phase responses. Consequently, one prediction arising on the basis of the model is that perceptions of the illusion will break down at low contrast levels. The specific aim of the experiments reported in this chapter was to test this prediction.

Methods.

Stimuli

For the sake of consistency with the methodology of previous experiments, all Glass patterns were generated according to a concentric function. In addition, all were composed of decrement- and increment-defined dot-pairs. In the descriptions that follow, the term 'contrast' is used with reference to the Michelson contrast yielded by *all* the dots of which a pattern was composed relative to the background. This is possible because for all patterns, decrement and increment dots were of equivalent contrast (but of opposite luminance polarity). In all other respects (and with the exception of the features described below), stimuli were generated as per the description provided in chapter 2.

The first experiment was conducted in order to test the prediction that the reliability with which the jitter illusion arises would completely break down at some low level of contrast. To that end, five sets of test stimuli were generated. The contrast of these stimuli was determined on the basis of data from previous experiments suggesting that the illusion was likely to break down at contrasts of less than 0.15 (see chapter 4) - as a result, contrasts of between 0.15 and 0.05 were tested. Across this range contrast was reduced in steps of 0.025. The luminance values that yielded each contrast value are represented in Table 8.3.

	0.15	**0.125**	**0.1**	**0.075**	**0.05**
decrement dot	13.3	14	14.7	15.5	16.2
increment dot	24.3	23.1	22	20.9	19.8

Table 8.3: The luminance values assigned to the decrement and increment dots of which each set of stimuli were composed.

The second experiment was designed as a control experiment. One obvious problem with presenting low-contrast patterns is that at some point, the luminance changes arising at stimulus onset and offset may not even elicit an effective *first-phase* response in M-pathway cells. In order to ensure this was not the case (and that, as intended, any results could be attributed to the effective absence of only *second*-phase responses), the visibility of stimuli used in the lowest contrast condition (contrast = 0.05) of the first experiment was tested. For each presentation subjects were required to identify whether or not a stimulus was ‘structured’ (in the sense that it was composed of dot-pairs). Of course, information about stimulus ‘form’ may be extracted on the basis of P- (and not M-) pathway activity. However, the existence of physiological and psychophysical evidence indicating that cells of the M-pathway are *more sensitive* to luminance changes than those of the P-pathway (Schiller & Logothetis 1990; Schiller, Logothetis & Charles 1990) has already been reported (see chapter 1). From this it follows that any luminance changes that effectively stimulate P-pathway cells should also stimulate *at least* an effective first-phase response in M-pathway cells. On this basis, it was hypothesised that the ability of subjects to reliably distinguish between Glass patterns and random patterns at low contrast levels would constitute evidence that any effects observed in the first experiment could be attributed to the (effective) absence of second-phase responses alone.

For both the experiments reported here, control stimuli were equivalent to test stimuli in all respects except for the fact that the dots of which each *control* stimulus was composed were positioned randomly throughout the stimulus field.

Subjects

Subjects consisted of two experienced psychophysical observers (AB and vdZ) and one trained observer (RB) who was naïve to the aims of the experiment.

Procedure

In both the first and second experiments each condition was represented by 10 stimuli. This meant that the first experiment consisted of a total of 100 stimuli (with 5 test and 5 control conditions), and the second consisted of a total of 20 stimuli (with 1 test and 1 control condition). Stimuli from each experiment were tested in separate blocks. Each block was presented to subjects 3 times, so mean responses for each condition are based on 30 trials.

Stimuli were presented for 100 milliseconds in each of the experiments. Within each block the order of stimulus presentations was randomised. For the first experiment subjects were required to indicate (by the means outlined in chapter 2) whether or not each stimulus appeared to undergo coherent global motion. For the second experiment subjects were required to indicate whether or not each stimulus appeared to be ‘structured’ (in the sense that they were composed of dot-pairs). To that end, depression of the ‘l’ key indicated an affirmative response, while depression of the ‘a’ key indicated a negative response. All other procedures were as per the description provided in chapter 2.

Results.

Data from the first experiment are arranged as per the description provided in chapter 2 and are represented for individual subjects in Figure 8.4. Only data from the test conditions have been represented in this figure, as each subject recorded proportions of 0 in each of the control conditions (to review those data see chapter 11). Data from the test conditions indicate that the reliability with which the illusion arose *decreased* as contrast was reduced from a certain level. That is, for each of the subjects tested, proportions of affirmative ‘motion’ responses decreased as contrast fell below 0.1. Indeed, at contrasts of 0.05 the data indicate that motion was almost never observed. At this level, subject RB recorded the highest proportion of affirmative responses, reporting motion perceptions on just 10% of trials. The remaining two subjects did not report motion perceptions on any trials at this level. It is therefore the case that data from the first experiment are consistent with the prediction that the reliability with which the illusion arises would break down at sufficiently low contrast levels.

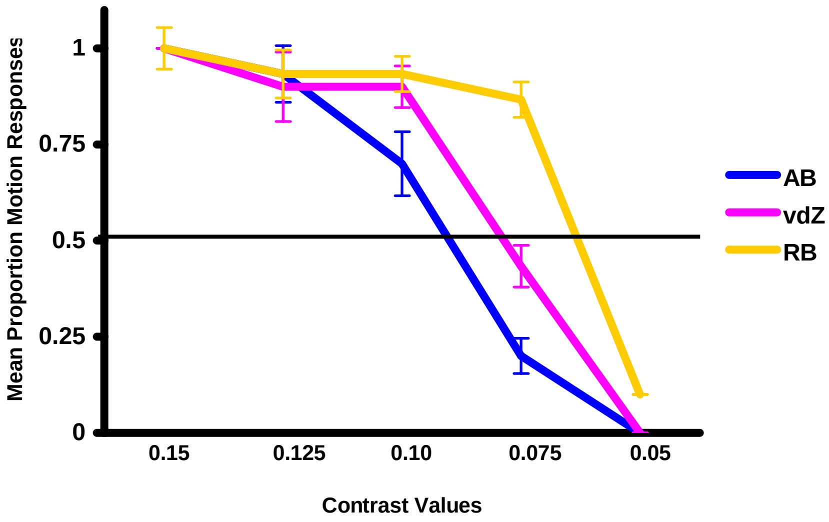


Figure 8.4: Mean proportions of affirmative 'motion' responses for individual subjects at each of the contrast values tested. Only data recorded in response to test stimuli are represented. The data clearly indicate that the illusion is not reliably elicited by presentations of stimuli that are composed of low-contrast (contrast = 0.05) decrement and increment dots. Error bars represent one standard error.

Data from the second experiment are represented in Figure 8.5. These data represent the mean proportion of affirmative 'structured' responses of individual subjects to the low-contrast stimuli. Within the figure, data from both the test and control conditions are represented. Inspection of these data indicates that high proportions of affirmative responses were recorded in the test condition. In fact, subjects could identify the 'structured' patterns on at least 90% of trials. Critically, inspection of Figure 8.5 also reveals that low proportions of affirmative responses were recorded by each of the subjects in the control condition. This indicates that subjects were neither guessing nor did they have a response bias. The large and systematic difference in these data constitute evidence that subjects were able to reliably distinguish 'structured' Glass patterns from patterns composed of randomly positioned dots. On this, it can therefore be concluded that even at contrasts of 0.05, the luminance changes arising at stimulus onset and offset *are* sufficient to elicit at least first-phase M-pathway cellular responses.

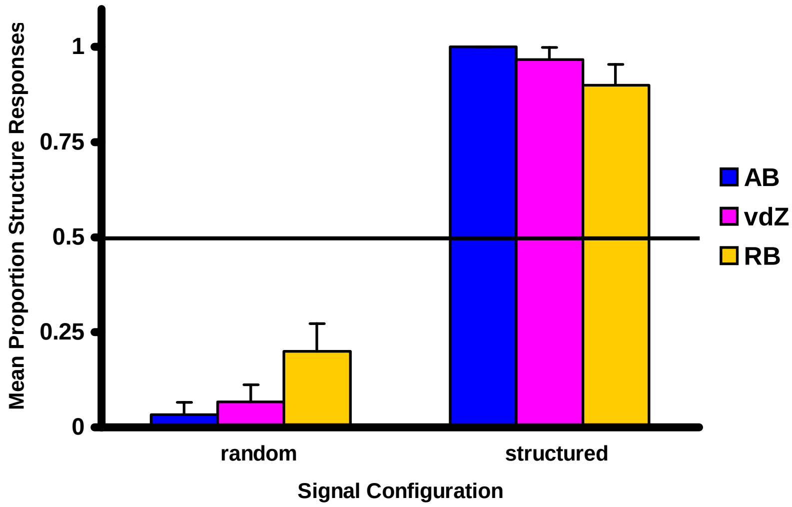


Figure 8.5: Mean proportions of affirmative 'structured' responses for individual subjects. Both test (structured) and control (random) stimuli were composed of dots with a contrast of 0.05. The figure indicates that each subject was able to reliably distinguish structured from random patterns at this low contrast level. Error bars represent one standard error.

Discussion.

The data presented in this chapter are consistent with the hypothesis that the diphasic responses of M-pathway cells serve as the basis for the LMD activity on which the jitter illusion is based. Using evidence that these M-pathway responses can, under some circumstances, become effectively monophasic, it was predicted that perceptions of the illusion would break down at low contrast levels. Results from the first and second experiments confirm this prediction. That is, data from the first experiment indicate that Glass patterns composed of decrement and increment dots with a Michelson contrast of 0.05 almost *never* elicited perceptions of coherent global motion – thereby supporting the predicted existence of a low level of contrast at which the illusion completely breaks down. Data from the second experiment indicate that Glass patterns of the same low contrast (0.05) could be distinguished reliably from random patterns of equivalent contrast – thereby supporting the notion that effects in the first experiment were the result of an effective absence of second-phase responses alone. In combination, therefore, the data from the two experiments provide support for the notion that perceptions of illusory 'jitter' motion are dependent upon the generation of significant first- *and* second-phase M-pathway cellular responses. On this basis, it must be concluded that the diphasic TIRF model represents a plausible account of the means by which the onset and offset of decrement- and increment-defined dot-pairs elicits LMD activity.

In addition to these results, one of the strengths of the diphasic TIRF model is its dependence upon, and therefore consistence with, the notion that LMDs are *not* stimulated by cross- (Off- and On-) channel input. In the previous chapter evidence that LMD activity only arises on the basis of Off-channel *or* On-channel input was reported (see Edwards & Badcock 1994). Consistent with this, the diphasic TIRF model proposes that the LMD activity on which the jitter illusion is based arises as a result of signals that are independently transmitted from Off- and On-channel cells. In fact, inspection of Figure 8.2 reveals that the model can *only* account for LMD stimulation if it is assumed that this is the case; only when they are considered independently do the patterns of excitatory Off- and On-channel activity elicited by each dot-pair describe the shifts across space over time required for LMD activity to arise (see Reichardt 1961; Edwards & Badcock 1994).

Of course, in spite of its strengths (and consistent with a point that was first raised in chapter 6) the diphasic TIRF model *does not* represent a comprehensive account of the neural activity on which perceptions of illusory 'jitter' motion arise. Evidence that these perceptions only arise in response to Glass patterns of a minimum density (see chapter 6) indicates that the neural activity elicited by each dot-pair must be *summated* at some additional stage of M-pathway processing. Similarly, the observation that LMDs only extract *linear* motion signals, and yet perceptions of motion can arise in *complex* trajectories, suggests the involvement of an additional processing stage. Indeed, evidence that coherent global perceptions *usually* arise on the basis of at least two major stages of processing – one 'lower-order' stage at which LMD activity arises, and an additional 'higher-order' or summation stage (see Morrone et al 1995) – also supports the proposed involvement of an additional stage of M-pathway processing in the case of the jitter illusion. While it is the case that the diphasic TIRF model offers a detailed account of only the lower-order stages of M-pathway activity, its characteristics suggest some of the mechanisms likely to be involved at higher stages of M-pathway processing. The nature of these mechanisms will (amongst other things) be discussed in the following chapter.

The main finding to arise from this chapter is, therefore, that a model based on the diphasic responses of M-pathway Off- and On-channel cells constitutes a physiologically and psychophysically plausible account of the means by which the onset and offset of decrement- and increment-defined dot-pairs elicits LMD activity. This finding is important because it represents a novel account of the means by which stationary visual presentations can, under some circumstances, elicit patterns of M-pathway activity that form the basis for perceptions of coherent global motion. Of course, the compatibility of the diphasic TIRF model with results from earlier experiments has not yet been reviewed. Nor have the higher-order stages of M-pathway processing involved in generating the coherent global motion perceptions yet been discussed in detail. Finally, the broader implications of the model have not yet been explored. Each of these issues will be addressed in the chapter that follows.

CHAPTER 9
general discussion

The aim of the work presented in each of the preceding chapters was to describe the previously unreported jitter illusion, and to identify its neural correlates. On the basis of all the psychophysical and physiological evidence reported in those chapters, the diphasic TIRF model of the illusion was constructed. Of course, many aspects of this model have already been discussed. However, a few important issues have yet to be addressed in detail. Firstly, it is the case that to this point, the model's compatibility with only the results reported in chapter 8 has been assessed. While of course the results reported in earlier chapters contributed to the development of the model and should therefore be broadly consistent with it, a detailed, retrospective analysis of those results in relation to the model is warranted. Secondly, in preceding chapters the suggestion was raised that the diphasic TIRF model represents an account of only the *lower-order* stages of M-pathway activity on which the jitter illusion is based. For that reason, the discussion that follows will also focus on the nature of some of the higher-order M-pathway processes likely to be involved in generating the illusion. Finally, it has already been suggested (see the previous chapter) that the diphasic TIRF model has implications that reach *beyond* its ability to account for the mechanisms on which the jitter illusion is based. Consequently and perhaps fittingly, the final topic of discussion will be the broader implications of the jitter illusion and its associated model.

Review of the findings

Based on evidence that eye-movements elicit the M-pathway activity on which other motion-from-form illusions are based, the aim of the experiments reported in chapter 3 was to determine whether the same is true in the case of the jitter illusion. On the basis of that hypothesis *and* evidence indicating that the minimum latency involved in initiating an eye-movement is 130 milliseconds (Robinson 1965; Leigh & Zee 1985), it was predicted that the jitter illusion would not arise in response to presentations lasting 50 and 100 milliseconds. However, the data emphatically indicated this was not the case – motion perceptions were reported on high percentages of trials that lasted 50 and 100 milliseconds. That was interpreted as evidence that eye-movements do not mediate the M-pathway activity on which the jitter illusion is based. In retrospect, the results reported in chapter 4 are entirely consistent with the diphasic TIRF model – the model does *not* attribute illusion-related M-pathway activity to the execution of eye-movements. Moreover, under the diphasic TIRF model the illusion would be *expected* to arise in response to presentations lasting 50 and 100 milliseconds. Indeed the model gives rise to the prediction that provided viewers are exposed to the step-changes in luminance arising at stimulus onset and offset, perceptions of illusory 'jitter' motion should arise in response to presentations lasting for *any* length of time.

Following on from this, and based on evidence that the cells of the M-pathway are tuned to respond to *abrupt* changes to the luminance composition of the visual scene (Ohtani et al 1991; Baloch et al 1999), the aim of the experiment reported in chapter 4 was to test whether step-changes in luminance arising at stimulus onset and offset elicit the M-pathway activity necessary for the jitter illusion to arise. Based on the hypothesis that this is the case, it was predicted that the illusion would only arise in response to presentations in which *square-wave* onset and offset profiles were used. The data were consistent with that prediction; they suggested that the square-wave onset and offset profiles used in Glass pattern presentations *do* mediate the M-pathway activity on which the illusion is based. The results from this experiment are, again not surprisingly, consistent with the diphasic TIRF model. Indeed, on the basis of the findings that were reported in chapter 4, the model attributes the generation of the M-pathway activity on which the jitter illusion is based to step-changes in luminance arising at the onset and offset of Glass pattern presentations. An additional noteworthy point is that the findings reported in chapter 4 are consistent with the working hypothesis that was laid out in the first chapter. That is, based on the relative sensitivities of M- and P-pathway cells (see chapter 1), the finding that the illusion *only* arises when changes in luminance manifest abruptly is consistent with the notion that the illusion is mediated by M- (and *not P-*) pathway activity.

In chapter 5, evidence was reported that downward steps in luminance elicit excitatory responses in the cells that make up the M-pathway Off-channel, whilst upward steps in luminance elicit excitatory responses in cells that make up the M-pathway On-channel (Schiller 1982, 1984 & 1992). On the basis of that evidence, combined with the observation that the jitter illusion only arises in response to Glass patterns that are composed of decrement- and increment-defined dot-pairs, it was hypothesised that the illusion arises as a product of excitatory cross- (Off- *and* On-) channel activity elicited by the onset and offset of each Glass pattern dot-pair. This hypothesis gave rise to the prediction that the illusion would *only* arise in response to Glass patterns composed of opposite polarity (decrement- and increment-defined) dot-pairs, and that it would arise in response to *any* pattern defined in this way. Data from each of the experiments reported in chapter 5 were consistent with those predictions. It was therefore suggested that the illusion arises as a result of cross-channel excitation elicited by the onset and offset of Glass pattern dot-pairs. An analysis of the findings reported in chapter 5 suggests they are consistent with the diphasic TIRF model. Indeed, according to the model, LMD activity (and thus perceptions of illusory 'jitter' motion) will not arise unless excitatory Off- *and* On-channel responses are elicited by the individual dot-pairs of which Glass patterns are composed.

In chapter 6, the possibility was raised that the pattern of Off- and On-channel responses to the onset and offset of each Glass pattern dot-pair is such that *LMDs* are stimulated, and that this stimulation forms the basis for perceptions of illusory 'jitter' motion. Based on that hypothesis, combined with evidence relating to the maximum integration range of LMDs (Mikami et al 1986; Smith et al 2001), it was predicted that the illusion would only arise in response to Glass patterns with a maximum intra-pair distance of approximately 30 arc minutes of visual angle. The data that were reported were in good agreement with that prediction. As a result, it was suggested that LMDs *are* involved in generating the jitter illusion – that LMD activity somehow arises as a product of the Off- and On-channel activity elicited by individual Glass pattern dot-pairs. An analysis of the data suggests they are in good agreement with the diphasic TIRF model. Indeed, on the basis of the findings reported in chapter 6, the whole purpose of constructing the diphasic TIRF model was to account for the LMD activity underlying perceptions of illusory 'jitter' motion. Consequently, *any* predictions arising on the basis of the model (including those related to the perceptual correlates of manipulating intra-pair distance) must by definition be constrained by the properties of LMDs.

Based on the properties referred to above, it was suggested in chapter 7 that LMD activity may arise as a consequence of *asynchronous* Off- and On-channel responses to the decrement and increment members of each Glass pattern dot-pair. On the strength of this hypothesis (and despite a number of highly problematic assumptions), it was predicted that Glass patterns arranged according to opposing spatial configurations (configurations in which the spatial positions of the decrement and increment members of dot-pairs are reversed across patterns) would appear to move in opposite directions at stimulus onset and offset. The data reported in chapter 7 were clearly inconsistent with that prediction. As a result, it was suggested that asynchronous Off- and On-channel processing, even if it does arise, does *not* mediate the LMD activity on which the jitter illusion is based. An analysis of the data reported in chapter 7 suggests they provide a good fit with the diphasic TIRF model. That is, according to the model the direction in which a pattern appears to move at onset and offset *should* be independent of the spatial configuration of the decrement and increment members of each dot-pair. Indeed, the model predicts that provided the pairs of which a Glass pattern is composed are made up of one decrement and one increment dot, the patterns should (according to the model) stimulate LMDs tuned for motion in opposite directions, and should consequently elicit perceptions of illusory 'jitter' motion. On this basis, the diphasic TIRF model is consistent not only with the observation that the direction in which patterns appear to move at stimulus onset and offset is not determined by the spatial configuration of decrement and increment member of each dot-pair, but also with the observation that 'balanced' patterns elicit the illusion.

Higher-order processing

While the retrospective analysis presented above highlights the strengths of the diphasic TIRF model as an account of the LMD activity on which the jitter illusion is based, there remain a number of observations that cannot be explained directly on the basis of the model. One of those observations was alluded to above, when it was suggested that even though the diphasic TIRF model suggests individual Glass pattern dot-pairs stimulate LMDs tuned for motion in *opposite* directions, coherent perceptions of motion *in one direction or the other* arise. On the basis of the model, the means by which these apparently conflicting local direction-of-motion signals give rise to coherent global perceptions are unclear. A second, related observation raised in the previous chapter was that while LMDs are only sensitive to *linear* motion signals, perceptions of motion can arise in *complex* trajectories. Again, the mechanisms by which this occurs are unclear on the basis of the diphasic TIRF model alone. The third and final observation was also touched upon in the previous chapter. That is, it was noted that the illusion only arises in response to Glass patterns of a minimum density – according to the diphasic TIRF model as it currently stands, even an individual dot-pair should stimulate LMDs and should therefore appear to move.

Thankfully, a possible explanation for each of these observations arises in the form of more a ‘two-stage’ model of the neural correlates of the jitter illusion. It has already been reported that other motion-processing models propose that coherent global perceptions are based on activity that arises in *at least two major stages* – one lower-order stage that is mediated by LMD activity, and one higher-order stage (see Morrone et al 1995). The diphasic TIRF model therefore represents an account of only the *lower-order* stage of motion processing. This raises the possibility that a model of the illusion that incorporates an additional, *higher-order* stage may shed some light on each of the observations referred to above. In the discussion that follows, the ability of such a model to account for each of the observations will be assessed.

The ability of a two-stage processing model to account for the observation that that the jitter illusion only arises in response to Glass patterns composed of *multiple* dot-pairs will be discussed first. Models of motion processing generally propose that at higher-order stages of M-pathway activity, the neural signals generated at the earlier stage are *summated* (Morrone et al 1995). They also suggest that on the basis of a stimulus-dependent threshold that is associated with activity at the higher-order stage (see Edwards & Badcock 1994), the ‘summated’ activity *may or may not* be sufficient to elicit perceptions of coherent global motion. This has implications for the jitter illusion. That is, if it is assumed that the same principles of higher-order activity apply in the case of the jitter illusion, then it follows that that the *minimum number of Glass pattern dot-pairs* required in order for the illusion to arise simply reflects the threshold associated with the higher-order stage of M-pathway processing - that at lower densities, the LMD activity elicited by each Glass pattern presentation is simply not sufficient for perceptions of the illusion to arise. On this basis, a model of the jitter illusion that incorporates both the diphasic TIRF model and a higher-order processing stage of this nature can successfully account for the observation that the jitter illusion only arises in response to Glass patterns composed of multiple dot-pairs.

Following on from this, the ability of a two-stage model to account for the observation that even though LMDs are only sensitive to *linear* motion signals, perceptions of motion can arise in *complex* trajectories will be addressed. Based on evidence that cells arising at lower levels of the M-pathway are sensitive to linear motion trajectories, while those arising at higher levels are sensitive to *complex* motion trajectories (see Mikami et al 1986; Smith et al 2001), some models of motion-processing propose that the local (linear) motion signals extracted by lower-order mechanisms are effectively 're-analysed' for complex trajectories at the higher-order stage (see Morrone et al 1995). Again, this has implications for the jitter illusion. That is, if it is assumed that the same principles apply in the case of the jitter illusion, then a model based on the diphasic TIRF model and higher-order activity of this nature can successfully account for the generation of perceptions of illusory motion in complex trajectories.

Finally, the ability of a two-stage model to account for the observation that coherent global motion perceptions arise on the basis of apparently conflicting local direction-of-motion signals will be addressed. In this instance, *two* possible models of higher-order activity can account for the observation. Each is based on evidence that *non-linearities* are in some cases introduced at higher-order stages of M-pathway processing (see Solomon & Sperling 1994; Edwards & Badcock 1995). Each is also based on the notion that these non-linearities manifest in the process of summating two different sets of LMD signals – the signals arising in LMDs that receive input from Off-channel cells ('Off-channel LMDs') and the signals arising in LMDs that receive input from On-channel cells ('On-channel LMDs'). In order to describe each of the models, it must be borne in mind that under the diphasic TIRF model, each Glass pattern presentation generates signals in Off-channel LMDs that are consistent with motion in one direction, and signals in On-channel LMDs that are consistent with motion in the opposite direction (see the arrows in Figure 8.2). With that in mind, each of the models will be described below.

The first model proposes that the nature of the non-linearity involved at the higher-order stage of processing is such that signals from one set of LMDs are *consistently* weighted more heavily than those from the other set of LMDs. This means that if a concentric Glass pattern presentation elicits activity in Off-channel LMDs that is consistent with motion in, say, a *clockwise* direction, and if the nature of the non-linearity is such that signals arising in Off-channel LMDs are always weighted more heavily than the signals arising in On-channel LMDs (that would, of course, be consistent with motion in a counter-clockwise direction) then perceptions of coherent motion in a *clockwise* direction would be expected to arise. While such a model accurately predicts the generation of coherent motion perceptions *in one direction or the other*, it faces one obvious problem: it also predicts that the direction in which a particular Glass pattern appears to move will be consistent across any number of presentations. The data reported in chapter 7 indicate that is not the case. On these grounds, such a model can be ruled out.

The second and more likely model suggests that the non-linearity manifests as a *temporary* suppression of the signals that arise in either the Off-channel or the On-channel LMDs. If, as has been suggested for other visual perceptions, suppression of cellular activity is determined by the initial state of the (higher-order) cells involved, and this state *fluctuates over time* (see van der Zwan & Wenderoth 1994), then in the example referred to above it would be accurately predicted that over a number of presentations the Glass pattern would appear to move in both clockwise and counter-clockwise directions. It is therefore the case that by combining such a model of higher-order activity with the diphasic TIRF model of lower-order activity, it is possible to explain not only why the direction in which Glass patterns appear to move changes across presentations, but also how coherent perceptions of illusory 'jitter' motion arise on the basis of apparently conflicting local direction-of-motion signals.

Broader implications of the diphasic TIRF model

Of course, the precise nature of the higher-order mechanisms involved in generating the jitter illusion is a matter for future research. However, on the basis of the preceding discussion it is it (hopefully) clear that the diphasic TIRF model at least provides a basis upon which to develop a comprehensive model of the neural correlates of the jitter illusion. Even as it currently stands, however, the model has some important implications. These will be discussed below.

The significance of the diphasic TIRF model is not limited to its ability to account simply for the neural correlates of the jitter illusion. When considering the broader significance of the model three critical points must be considered. The first follows from the observation (consistent with the conditions laid out in the first chapter) that the model proposes an account both of the means by which *stationary* Glass patterns stimulate M-pathway activity, and of the means by which the ensuing M-pathway activity gives rise to perceptions of coherent 'jitter' motion. On this basis, the first point to be considered is that the model represents a plausible account of the means by which activity arising *entirely within the M-pathway* gives rise to the jitter illusion. The second point to be considered is that the trajectory of illusory 'jitter' motion perceptions reflects the *physical structure* of the Glass patterns that are presented, even though those patterns are composed of decrement- and increment-defined dot-pairs; concentric patterns appear to move in concentric trajectories, radial patterns to move in radial trajectories, and so on. The third and final point to be considered is the observation that the physical structure of *equivalent* Glass patterns (patterns composed of decrement- and increment-defined dot-pairs) is not 'extracted' on the basis of P-pathway activity (Prazdny 1986; Wilson et al 1997; Wilson & Wilkinson 1998 – see chapter 1). When viewed in combination, these three points have an important and novel implication. That is, they suggest that under some circumstances, *M-pathway mechanisms 'extract' structural information from static visual images that P-pathway mechanisms cannot.* On this basis, the significance of the diphasic model lies not only in its ability to account for the means by which the jitter illusion arises, but also in the insight it provides into the relative processing capabilities of the M- and P-pathways of the visual system.

Conclusion

In concluding, it must be noted that the jitter illusion represents a new addition to the small number of visual illusions in which stationary presentations elicit perceptions of coherent global motion. It has already been mentioned that because illusions arise when the visual system's interpretation of the information contained within the visual scene is objectively inconsistent with that information, investigations into their neural correlates can reveal some novel aspects of the processing that takes place within the visual system. The jitter illusion poses no exception to this rule. In the process of identifying the neural mechanisms on which it is based, the illusion has offered some valuable insights into the properties and structure of some of the major processing streams of the human visual system. Of course, as with any perceptual phenomenon, there is scope for further investigation into the precise mechanisms on which the illusion is based. However, the findings reported here serve as clear evidence of the significance of the illusion and the diphasic TIRF model; they underscore the value of each in the important task of developing a comprehensive model of the means by which light-induced activity within the human visual system gives rise to coherent global perceptions.

CHAPTER 10
references

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CHAPTER 11
appendices

CHAPTER 3

Proportions of affirmative 'motion' responses for individuals and the group

IV = luminance (signal) composition of the Glass patterns

Trials per proportion for individual subject data = 40

50 millisecond presentations

Concentric stimuli						
	Control			**Test**		
	dec/dec	**dec/inc**	**inc/inc**	**dec/dec**	**dec/inc**	**inc/inc**
AB	0	0	0	0	1	0
vdZ	0	0	0	0	1	0
RB	0	0	0	0	1	0
US	0	0.025	0	0	1	0
Group Mean	**0**	**0.006**	**0**	**0**	**1**	**0**
Group Std Err	**0**	**0.006**	**0**	**0**	**0**	**0**

Radial stimuli						
	Control			**Test**		
	dec/dec	**dec/inc**	**inc/inc**	**dec/dec**	**dec/inc**	**inc/inc**
AB	0	0	0	0	1	0
vdZ	0	0	0	0	0.975	0
RB	0	0.025	0	0	1	0.075
US	0	0	0	0.025	1	0.075
Group Mean	**0**	**0.006**	**0**	**0.006**	**0.994**	**0.037**
Group Std Err	**0**	**0.006**	**0**	**0.006**	**0.006**	**0.015**

Linear stimuli						
	Control			**Test**		
	dec/dec	**dec/inc**	**inc/inc**	**dec/dec**	**dec/inc**	**inc/inc**
AB	0	0	0	0	1	0
vdZ	0	0	0	0	0.95	0
RB	0	0	0	0.025	1	0
US	0	0.025	0.025	0.025	1	0.025
Group Mean	**0**	**0.006**	**0.006**	**0.012**	**0.9875**	**0.006**
Group Std Err	**0**	**0.006**	**0.006**	**0.009**	**0.009**	**0.006**

100 millisecond presentations

Concentric stimuli						
	Control			**Test**		
	dec/dec	**dec/inc**	**inc/inc**	**dec/dec**	**dec/inc**	**inc/inc**
AB	0	0	0	0	0.975	0
vdZ	0	0	0	0	1	0
RB	0	0	0	0	1	0.025
US	0	0	0.025	0	1	0.025
Group Mean	**0**	**0**	**0.006**	**0**	**0.994**	**0.012**
Group Std Err	**0**	**0**	**0.006**	**0**	**0.006**	**0.009**

Radial stimuli						
	Control			**Test**		
	dec/dec	**dec/inc**	**inc/inc**	**dec/dec**	**dec/inc**	**inc/inc**
AB	0	0	0	0	0.975	0.025
vdZ	0	0	0	0	1	0
RB	0	0	0.05	0.075	1	0.125
US	0	0	0	0	1	0.025
Group Mean	**0**	**0**	**0.012**	**0.019**	**0.993**	**0.043**
Group Std Err	**0**	**0**	**0.009**	**0.011**	**0.006**	**0.016**

Linear stimuli						
	Control			**Test**		
	dec/dec	**dec/inc**	**inc/inc**	**dec/dec**	**dec/inc**	**inc/inc**
AB	0	0	0	0	0.9	0
vdZ	0	0	0	0	0.9	0
RB	0	0	0	0	1	0
US	0	0	0	0	0.95	0
Group Mean	**0**	**0**	**0**	**0**	**0.937**	**0**
Group Std Err	**0**	**0**	**0**	**0**	**0.019**	**0**

800 millisecond presentations

Concentric stimuli						
	Control			**Test**		
	dec/dec	**dec/inc**	**inc/inc**	**dec/dec**	**dec/inc**	**inc/inc**
AB	0	0	0	0	0.95	0
vdZ	0	0	0	0	0.675	0
RB	0	0	0	0	0.9	0
US	0	0	0	0	0.8	0
Group Mean	**0**	**0**	**0**	**0**	**0.831**	**0**
Group Std Err	**0**	**0**	**0**	**0**	**0.029**	**0**

Radial stimuli						
	Control			**Test**		
	dec/dec	**dec/inc**	**inc/inc**	**dec/dec**	**dec/inc**	**inc/inc**
AB	0	0	0	0	0.825	0
vdZ	0	0	0	0	0.85	0
RB	0	0.025	0	0	0.9	0
US	0	0	0	0.15	0.975	0.025
Group Mean	**0**	**0.006**	**0**	**0.037**	**0.887**	**0.006**
Group Std Err	**0**	**0.006**	**0**	**0.015**	**0.025**	**0.006**

Linear stimuli						
	Control			**Test**		
	dec/dec	**dec/inc**	**inc/inc**	**dec/dec**	**dec/inc**	**inc/inc**
AB	0	0	0	0	0.875	0
vdZ	0	0	0	0	0.975	0
RB	0	0	0	0	0.95	0
US	0	0	0	0	0.9	0
Group Mean	**0**	**0**	**0**	**0**	**0.925**	**0**
Group Std Err	**0**	**0**	**0**	**0**	**0.021**	**0**

Additional experiment

'Dot-pair' control stimuli used

Presentation duration = 100 msecs

All other aspects were as described above

Concentric stimuli						
	Dot-pair Control			**Test**		
	dec/dec	**dec/inc**	**inc/inc**	**dec/dec**	**dec/inc**	**inc/inc**
AB	0	0	0	0	0.97	0
vdZ	0	0.02	0	0	1	0
RB	0	0	0	0	1	0
US	0	0	0	0	1	0
Group Mean	**0**	**0.01**	**0**	**0**	**0.99**	**0**
Group Std Err	**0**	**0.01**	**0**	**0**	**0.01**	**0**

CHAPTER 4

Proportions of affirmative 'motion' responses for individuals and the group

IV = onset/offset profile of jitter presentations

Trials per proportion for individual subject data = 30

	Square-wave	**Ramped**
AB	0.933	0.033
vdZ	0.967	0
RB	0.9	0.133
Group Mean	**0.933**	**0.055**
Group Std Err	**0.026**	**0.024**

CHAPTER 5

Proportions of affirmative 'motion' responses for individuals and the group

IV = luminance (signal) composition of the stimulus

Trials per proportion for individual subject data = 30

First experiment				
	Control		**Test**	
	dec/dec	**inc/inc**	**dec/dec**	**inc/inc**
AB	0	0	0	0
vdZ	0	0	0	0
RB	0	0	0	0
US	0	0	0	0
Group Mean	**0**	**0**	**0**	**0**
Group Std Err	**0**	**0**	**0**	**0**

Second experiment						
	Control			**Test**		
	dec/incA	**dec/incB**	**dec/incC**	**dec/incA**	**dec/incB**	**dec/incC**
AB	0	0	0	0.87	0.9	1
vdZ	0	0	0	1	0.97	1
RB	0	0.03	0	1	1	1
US	0	0	0	0.97	0.9	0.97
Group Mean	**0**	**0.01**	**0**	**0.96**	**0.94**	**0.99**
Group Std Err	**0**	**0.01**	**0**	**0.02**	**0.02**	**0.01**

CHAPTER 6

Proportions of affirmative ‘motion’ responses for individuals and the group

IV = intra-pair distance (arc minutes of visual angle)

Trials per proportion for individual subject data = 30

First experiment												
	Control						**Test**					
	15	**21**	**27**	**33**	**39**	**45**	**15**	**21**	**27**	**33**	**39**	**45**
AB	0	0	0	0	0	0	1	1	0.87	0.43	0.1	0
vdZ	0	0	0	0	0	0	0.97	0.9	0.83	0.23	0.2	0
RB	0.67	0.03	0	0	0	0	0.83	1	0.9	0.4	0.367	0.1
US	0	0	0	0	0	0	0.9	0.97	0.87	0.53	0.3	0.03
Group Mean	**0.17**	**0.01**	**0**	**0**	**0**	**0**	**0.93**	**0.97**	**0.87**	**0.4**	**0.24**	**0.03**
Group Std Err	**0.01**	**0.01**	**0**	**0**	**0**	**0**	**0.02**	**0.02**	**0.03**	**0.04**	**0.04**	**0.02**

Second (control) experiment												
	Control						**Test**					
	15	**21**	**27**	**33**	**39**	**45**	**15**	**21**	**27**	**33**	**39**	**45**
AB	0	0	0	0	0	0	1	1	0.67	0.1	0.03	0
vdZ	0	0	0	0	0	0	0.97	0.87	0.63	0.13	0.07	0.1
US	0	0	0	0	0	0	0.73	0.9	0.6	0.4	0.33	0.1
Group Mean	**0**	**0**	**0**	**0**	**0**	**0**	**0.9**	**0.92**	**0.63**	**0.21**	**0.14**	**0.07**
Group Std Err	**0**	**0**	**0**	**0**	**0**	**0**	**0.03**	**0.03**	**0.05**	**0.04**	**0.04**	**0.03**

Pilot experiment:

Proportions of affirmative 'motion' responses for individuals and the group

IV = density of Glass patterns; number of dot-pairs of which each was composed

Trials per proportion for individual subject data = 30

	Control						**Test**					
	1pr	**2pr**	**4pr**	**8pr**	**16pr**	**32pr**	**1pr**	**2pr**	**4pr**	**8pr**	**16pr**	**32pr**
AB	0	0	0	0	0	0	0.17	0.1	0.1	0.57	0.77	0.93
vdZ	0	0	0	0	0	0	0	0	0.07	0.43	0.87	0.97
RB	0	0	0	0	0	0	0	0	0.03	0.3	0.93	1
CC	0.1	0.07	0.03	0.07	0.1	0	0.07	0.07	0.23	0.4	0.67	0.87
Group Mean	**0.03**	**0.02**	**0.01**	**0.02**	**0.02**	**0**	**0.06**	**0.04**	**0.11**	**0.43**	**0.81**	**0.94**
Group Std Err	**0.01**	**0.01**	**0.01**	**0.01**	**0.01**	**0**	**0.02**	**0.02**	**0.03**	**0.05**	**0.04**	**0.02**

CHAPTER 7

Proportions of 'clockwise' responses for individuals and the group

IV = signal configuration of the stimulus

Trials per proportion for individual subject data = 30

Stimulus onset			
	decCW	**decCCW**	**balanced**
AB	0.57	0.5	0.4
vdZ	0.47	0.43	0.4
RB	0.03	0.17	0.13
ME	0.13	0.27	0.33
Group Mean	**0.3**	**0.34**	**0.32**
Group Std Err	**0.04**	**0.04**	**0.04**

Stimulus offset			
	decCW	**decCCW**	**balanced**
AB	0.63	0.6	0.53
vdZ	0.57	0.47	0.53
RB	0.9	0.9	0.87
ME	0.23	0.23	0.2
Group Mean	**0.58**	**0.55**	**0.53**
Group Std Err	**0.04**	**0.04**	**0.04**

Pilot experiment:

Proportions of affirmative ‘motion’ responses for individuals and the group

IV = spatial configuration of the decrement and increment dots of which each Glass pattern was composed.

Trials per proportion for individual subject data = 30

	random	**balanced**
AB	0	0.93
vdZ	0	0.9
RB	0	0.93
ME	0	0.83
Group Mean	**0**	**0.9**
Group Std Err	**0**	**0.02**

CHAPTER 8

Proportions of affirmative 'motion' responses for individuals and the group

IV = contrast of the component dots

Trials per proportion for individual subject data = 30

First experiment										
	Control					**Test**				
	0.05	**0.075**	**0.10**	**0.125**	**0.15**	**0.05**	**0.075**	**0.10**	**0.125**	**0.15**
AB	0	0	0	0	0	0	0.2	0.7	0.93	1
vdZ	0	0	0	0	0	0	0.43	0.9	0.9	1
RB	0	0	0	0	0	0.1	0.87	0.93	0.93	1
Group Mean	**0**	**0**	**0**	**0**	**0**	**0.03**	**0.5**	**0.84**	**0.92**	**1**
Group Std Err	**0**	**0**	**0**	**0**	**0**	**0.02**	**0.05**	**0.04**	**0.03**	**0**

Second (control) experiment		
	Random	**Structured**
AB	0.03	1
vdZ	0.07	0.97
RB	0.2	0.9
Group Mean	**0.1**	**0.95**
Group Std Err	**0.03**	**0.02**

ADDITIONAL DATA

Proportions of motion responses for individual subjects and the group

IV = Signals defining the elements of each dot-pair

Trials per proportion for individual subjects = 30

Configurations to test a model based on negative half-wave rectification

	condition a	condition b	condition c	condition d
AB	0	0	0	1
vdZ	0	0	0	0.933
RB	0	0	0	1
Group Mean	**0**	**0**	**0**	**0.978**
Group Std Err	**0**	**0**	**0**	**0.015**

Configurations to test a model based on positive half-wave rectification

	condition a	condition b	condition c	condition d
AB	0	0	0.933	0
vdZ	0	0	0.933	0
RB	0	0	0.933	0
Group Mean	**0**	**0**	**0.933**	**0**
Group Std Err	**0**	**0**	**0**	**0**

Appendices

Appendix A

Concentric patterns:

Proportions of ‘motion’ responses for individual subjects and the group

IV = luminance composition of the Glass patterns

Trials per proportion for individual subject data = 40

50 msecs

	Control			**Experimental**		
	dec/dec	**dec/inc**	**inc/inc**	**dec/dec**	**dec/inc**	**inc/inc**
AB	0	0	0	0	1	0
vdZ	0	0	0	0	1	0
RB	0	0	0	0	1	0
US	0	0.025	0	0	1	0
Group Mean	**0**	**0.006**	**0**	**0**	**1**	**0**
Group Std Err	**0**	**0.006**	**0**	**0**	**0**	**0**

100 msecs

	Control			**Experimental**		
	dec/dec	**dec/inc**	**inc/inc**	**dec/dec**	**dec/inc**	**inc/inc**
AB	0	0	0	0	0.975	0
vdZ	0	0	0	0	1	0
RB	0	0	0	0	1	0.025
US	0	0	0.025	0	1	0.025
Group Mean	**0**	**0**	**0.006**	**0**	**0.994**	**0.012**
Group Std Err	**0**	**0**	**0.006**	**0**	**0.006**	**0.009**

800 msecs

	Control			Experimental		
	dec/dec	**dec/inc**	**inc/inc**	**dec/dec**	**dec/inc**	**inc/inc**
AB	0	0	0	0	0.95	0
vdZ	0	0	0	0	0.675	0
RB	0	0	0	0	0.9	0
US	0	0	0	0	0.8	0
Group Mean	**0**	**0**	**0**	**0**	**0.831**	**0**
Group Std Err	**0**	**0**	**0**	**0**	**0.029**	**0**

Radial patterns:

Proportions of ‘motion’ responses for individual subjects and the group

IV = luminance composition of the Glass patterns

Trials per proportion for individual subject data = 40

50 msecs

	Control			Experimental		
	dec/dec	**dec/inc**	**inc/inc**	**dec/dec**	**dec/inc**	**inc/inc**
AB	0	0	0	0	1	0
vdZ	0	0	0	0	0.975	0
RB	0	0.025	0	0	1	0.075
US	0	0	0	0.025	1	0.075
Group Mean	**0**	**0.006**	**0**	**0.006**	**0.994**	**0.037**
Group Std Err	**0**	**0.006**	**0**	**0.006**	**0.006**	**0.015**

appendices

100 msecs

	Control			Experimental		
	dec/dec	**dec/inc**	**inc/inc**	**dec/dec**	**dec/inc**	**inc/inc**
AB	0	0	0	0	0.975	0.025
vdZ	0	0	0	0	1	0
RB	0	0	0.05	0.075	1	0.125
US	0	0	0	0	1	0.025
Group Mean	**0**	**0**	**0.012**	**0.019**	**0.993**	**0.043**
Group Std Err	**0**	**0**	**0.009**	**0.011**	**0.006**	**0.016**

800 msecs

	Control			Experimental		
	dec/dec	**dec/inc**	**inc/inc**	**dec/dec**	**dec/inc**	**inc/inc**
AB	0	0	0	0	0.825	0
vdZ	0	0	0	0	0.85	0
RB	0	0.025	0	0	0.9	0
US	0	0	0	0.15	0.975	0.025
Group Mean	**0**	**0.006**	**0**	**0.037**	**0.887**	**0.006**
Group Std Err	**0**	**0.006**	**0**	**0.015**	**0.025**	**0.006**

appendices

Linear patterns:

Proportions of ‘motion’ responses for individual subjects and the group

IV = luminance composition of the Glass patterns

Trials per proportion for individual subject data = 40

50 msecs

	Control			**Experimental**		
	dec/dec	**dec/inc**	**inc/inc**	**dec/dec**	**dec/inc**	**inc/inc**
AB	0	0	0	0	1	0
vdZ	0	0	0	0	0.95	0
RB	0	0	0	0.025	1	0
US	0	0.025	0.025	0.025	1	0.025
Group Mean	**0**	**0.006**	**0.006**	**0.012**	**0.9875**	**0.006**
Group Std Err	**0**	**0.006**	**0.006**	**0.009**	**0.009**	**0.006**

100 msecs

	Control			**Experimental**		
	dec/dec	**dec/inc**	**inc/inc**	**dec/dec**	**dec/inc**	**inc/inc**
AB	0	0	0	0	0.9	0
vdZ	0	0	0	0	0.9	0
RB	0	0	0	0	1	0
US	0	0	0	0	0.95	0
Group Mean	**0**	**0**	**0**	**0**	**0.937**	**0**
Group Std Err	**0**	**0**	**0**	**0**	**0.019**	**0**

800 msecs

	Control			Experimental		
	dec/dec	**dec/inc**	**inc/inc**	**dec/dec**	**dec/inc**	**inc/inc**
AB	0	0	0	0	0.875	0
vdZ	0	0	0	0	0.975	0
RB	0	0	0	0	0.95	0
US	0	0	0	0	0.9	0
Group Mean	**0**	**0**	**0**	**0**	**0.925**	**0**
Group Std Err	**0**	**0**	**0**	**0**	**0.021**	**0**

Appendix B

Density:

Proportions of ‘motion’ responses for individual subjects and the group

IV = number of dot-pairs of which a pattern was composed

Trials per proportion for individual subject data = 30

Control condition (randomly arranged patterns)

	1pr	**2pr**	**4pr**	**8pr**	**16pr**	**32pr**
AB	0	0	0	0	0	0
vdZ	0	0	0	0	0	0
RB	0	0	0	0	0	0
CC	0.1	0.667	0.033	0.667	0.1	0
Group Mean	**0.025**	**0.016**	**0.008**	**0.016**	**0.025**	**0**
Group Std Err	**0.014**	**0.011**	**0.008**	**0.011**	**0.014**	**0**

Experimental condition

	1pr	**2pr**	**4pr**	**8pr**	**16pr**	**32pr**
AB	0.167	0.1	0.1	0.567	0.767	0.933
vdZ	0	0	0.067	0.433	0.867	0.966
RB	0	0	0.033	0.3	0.933	1
CC	0.067	0.067	0.233	0.4	0.667	0.866
Group Mean	**0.058**	**0.042**	**0.108**	**0.425**	**0.808**	**0.942**
Group Std Err	**0.021**	**0.018**	**0.028**	**0.045**	**0.036**	**0.021**

Intra-pair distance: normal density

Proportion of ‘motion’ responses for individual subjects and the group

IV = the distance between elements in dot-pairs (in arc minutes)

Trials per proportion for individual subject data = 30

Control condition (randomly arranged patterns)

	15	**21**	**27**	**33**	**39**	**45**
AB	0	0	0	0	0	0
vdZ	0	0	0	0	0	0
ME	0.667	0.033	0	0	0	0
US	0	0	0	0	0	0
Group Mean	**0.017**	**0.008**	**0**	**0**	**0**	**0**
Group Std Err	**0.012**	**0.008**	**0**	**0**	**0**	**0**

Experimental condition

	15	**21**	**27**	**33**	**39**	**45**
AB	1	1	0.867	0.433	0.1	0
vdZ	0.967	0.9	0.833	0.233	0.2	0
ME	0.833	1	0.9	0.4	0.367	0.1
US	0.9	0.967	0.867	0.533	0.3	0.033
Group Mean	**0.925**	**0.967**	**0.867**	**0.4**	**0.242**	**0.033**
Group Std Err	**0.024**	**0.016**	**0.031**	**0.045**	**0.039**	**0.016**

Intra-pair distance: low density

Proportion of ‘motion’ responses for individual subjects and the group

IV = the distance between elements in dot-pairs (in arc minutes)

Trials per proportion for individual subject data = 30

Control condition (randomly arranged patterns)

	15	**21**	**27**	**33**	**39**	**45**
AB	0	0	0	0	0	0
VdZ	0	0	0	0	0	0
US	0	0	0	0	0	0
Group Mean	**0**	**0**	**0**	**0**	**0**	**0**
Group Std Err	**0**	**0**	**0**	**0**	**0**	**0**

Experimental condition

	15	**21**	**27**	**33**	**39**	**45**
AB	1	1	0.667	0.1	0.033	0
vdZ	0.967	0.867	0.633	0.133	0.067	0.1
US	0.733	0.9	0.6	0.4	0.33	0.1
Group Mean	**0.9**	**0.922**	**0.633**	**0.211**	**0.144**	**0.067**
Group Std Err	**0.055**	**0.049**	**0.088**	**0.074**	**0.064**	**0.045**

Appendix C

Contrast relationships:

Proportions of ‘motion’ responses for individual subjects and the group

IV = luminance composition of the Glass patterns

Trials per proportion for individual subjects = 30

Control condition (randomly arranged patterns)

	dec/dec	**inc/inc**	**dec/incA**	**dec/incB**	**dec/incC**
AB	0	0	0	0	0
vdZ	0	0	0	0	0
RB	0	0	0	0.033	0
US	0	0	0	0	0
Group Mean	**0**	**0**	**0**	**0.008**	**0**
Group Std Err	**0**	**0**	**0**	**0.008**	**0**

Experimental condition

	dec/dec	**inc/inc**	**dec/incA**	**dec/incB**	**dec/incC**
AB	0	0	0.867	0.9	1
vdZ	0	0	1	0.967	1
RB	0	0	1	1	1
US	0	0	0.967	0.9	0.967
Group Mean	**0**	**0**	**0.958**	**0.942**	**0.992**
Group Std Err	**0**	**0**	**0.018**	**0.021**	**0.008**

Appendix D

First-/second-order configurations:

Proportions of motion responses for individual subjects and the group

IV = Signals defining the elements of each dot-pair (see Chapter 6)

Trials per proportion for individual subjects = 30

Configurations to test a model based on negative half-wave rectification

	condition a	**condition b**	**condition c**	**condition d**
AB	0	0	0	1
vdZ	0	0	0	0.933
RB	0	0	0	1
Group Mean	**0**	**0**	**0**	**0.978**
Group Std Err	**0**	**0**	**0**	**0.015**

Configurations to test a model based on positive half-wave rectification

	condition a	**condition b**	**condition c**	**condition d**
AB	0	0	0.933	0
vdZ	0	0	0.933	0
RB	0	0	0.933	0
Group Mean	**0**	**0**	**0.933**	**0**
Group Std Err	**0**	**0**	**0**	**0**

Appendix D

Direction-of-motion:

Proportion of ‘clockwise motion’ responses for individual subjects and the group

IV = configuration of decrement and increment elements in each pair

Trials per proportion for individual subjects = 30

Data for stimulus onset

	Balanced	**decCW**	**decCCW**
AB	0.4	0.567	0.5
vdZ	0.4	0.567	0.433
RB	0.133	0.033	0.167
ME	0.333	0.133	0.267
Group Mean	**0.317**	**0.3**	**0.342**
Group Std Err	**0.042**	**0.042**	**0.043**

Data for stimulus offset

	Balanced	**decCW**	**decCCW**
AB	0.533	0.633	0.6
vdZ	0.533	0.567	0.467
RB	0.867	0.9	0.9
ME	0.2	0.233	0.233
Group Mean	**0.533**	**0.583**	**0.55**
Group Std Err	**0.045**	**0.045**	**0.045**

Need to do stuff to let them work out the z-scores