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Tapered dipoles in briefly flashed Glass-pattern sequences disambiguate perceived motion direction

Bareena Johnson, Peter Wenderoth
Department of Psychology, Macquarie University, North Ryde, Sydney, NSW 2109, Australia;
e-mail: Bareena.Johnson@gmail.com
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Abstract. In order to investigate the relationship between 'neural speedlines', form (shape), and fast motion-direction decisions, Glass patterns were constructed with dipoles assuming a tapered shape. The results of a 2-alternative forced-choice direction-discrimination task, for both concentric and translational Glass-pattern sequences, suggest that with short stimulus presentations (<1 s) form can influence direction decisions. This result implies that neural speedlines may be analogous to tapered lines and further supports Geisler's (1999, *Nature* **400** 65 – 69) model of form/motion interaction.

1 Introduction

The aim of ongoing research into motion perception is to understand how speed and direction are encoded, how local signals are integrated to produce global motion perception, and to determine the neural substrates that underlie these mechanisms (Zanker and Zeil 2001). In line with these goals, Geisler (1999) introduced the notion of neural 'speedlines'—lines similar to those drawn by cartoonists to imply motion. He reasoned that, when a fast moving object crosses the visual field, it should leave behind a 'streak' or 'speedline' due to the time required for the visual system to integrate information (approximately 100 ms). Geisler proposed a model to explain how narrowly tuned orientation-selective cells and broadly tuned motion-selective cells, found in the primary visual cortex (V1), might interact to create a single unit. This unit is thought to aid the visual system in direction discrimination by extracting information from the neural speedlines. Evidence supporting this model has emerged from neuroimaging (Alais et al 2010; Krekelberg et al 2003), single-unit neurophysiology (Geisler et al 2001), and psychophysical studies (Apthorp et al 2009, 2010; Edwards and Crane 2007). Importantly, Geisler's model, unlike earlier theories (see Ungerleider and Mishkin 1982), suggests that form (shape) and motion interact at an early stage of visual processing.

In an example of form and motion interaction, Ross et al (2000) used a sequence of static Glass patterns (Glass 1969) to demonstrate that the orientation of randomly positioned dot pairs (dipoles) can yield a strong global percept of structure (see figure 1) and motion. For example, when dot dipoles are aligned tangentially, circular structure and rotational motion are perceived. Note, that, for each pattern in the sequence, dipoles are randomly repositioned, resulting in no coherent velocity signals (Ross et al 2000), yet the form of the patterns produces coherent global motion perceptions. Altering the spatial relationship between the dots that comprise each dipole can change the global structural percept to spiral, radial, or translational, provided that the Glass shift (intradot distance) remains within the range of 6 – 15 min (Ross et al 2000). However, while motion is perceived, the direction of motion is bistable, switching from left to right (for translational patterns) or clockwise to anticlockwise (for concentric patterns) at random.

There is much evidence to suggest that the dipoles composing Glass patterns are encoded at an early stage of visual processing, the probable site being V1 (Burr 2000; Krekelberg et al 2005; Ross et al 2000; Smith et al 2007). If a dipole falls within the receptive field of a V1 cell, then the alignment of the dots within the dipole will dictate

Figure 1. Example of a concentric Glass pattern created by random placement of dipoles with all dots aligned tangentially. Global circular structure is apparent and, when uncorrelated sequences of such patterns are displayed, circular motion is perceived.

the orientation-selective cells that respond. In the above example the dots are aligned tangentially; therefore orientation-selective cells that respond to curved contours (Hubel and Livingstone 1987) should fire (Burr 2000). In keeping with Geisler's model (1999), the motion detectors working in conjunction with the excited cells should also be activated and produce a percept of rotational motion. However, a motion detector without coherent motion information could not relay specifics about direction; hence the perceived direction of Glass patterns should be, and is, ambiguous. With the above reasoning it is conceivable that the dipoles in a Glass pattern are comparable to Geisler's neural speedlines (Ross 2004). Furthermore, Burr (2000) states that the dipoles "approximate small line segments" (page R442) that are analogous to streaks and, while streaks themselves may not induce a perception of motion, they may imply it. Therefore, it is possible that manipulations of Glass patterns might allow inferences to be made about the characteristics of neural speedlines.

A photograph with an exposure time similar to that required for the temporal integration of motion signals in early visual cortex should depict the residual motion that hypothetically exists in V1 (see figure 2a). Notice that the object, in this case a cyclist, appears to be elongated from the direction in which he is moving. When viewing this

(a) (b)

Figure 2. (a) A photograph taken with an exposure time similar to that required for temporal integration demonstrates the motion blur that may be utilised by the visual system to assist in fast motion direction discrimination. Photograph reproduced from http://www.photoanswers.co.uk. (b) Example of a drawn cartoon with speedlines that imply fast motion.

photograph, the implied motion and direction are instantly recognised in a manner similar to that of cartoons with drawn speedlines (see figure 2b).

If we are to accept that Glass-pattern sequences produce neural signals that are analogous to neural speedlines, and if neural speedlines are representative of visual motion scenes that have become blurred due to a time lapse for temporal integration, then the speedlines drawn by cartoonists may imply motion by activating similar mechanisms in the visual-motion system. Importantly, all three imply motion from form and the only notable difference is that Glass patterns are directionally bistable. This may be due in part to the form (shape) of the speedline produced by each dipole. As the dots are identical in size and contrast, the resulting speedline lacks directional information, unlike the speedlines in figure 2. Notice that the photographed and drawn speedlines taper away from the direction of motion and in so doing convey a sense of direction. It could therefore be possible to give direction to Glass-pattern sequences by altering the dot sizes so that dipoles consist of one large and one small dot, thereby creating speedlines that appear tapered. Hence, we set out to empirically test whether increasing the degree of form at a local level can provide enough information for the human visual system to make global judgments of direction. It is expected that motion direction will be perceived in the direction of the larger dot from the smaller dot.

2 Experiment 1

2.1 *Method*

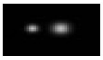
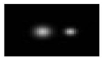
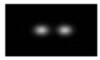
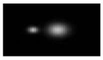
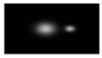
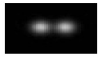
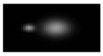
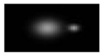
2.1.1 *Participants.* Seven males and four females who were emmetropic or had corrected-to-normal vision participated in this experiment. All were experienced psychophysical observers and all, with the exception of two, were naive to the purpose of this study.

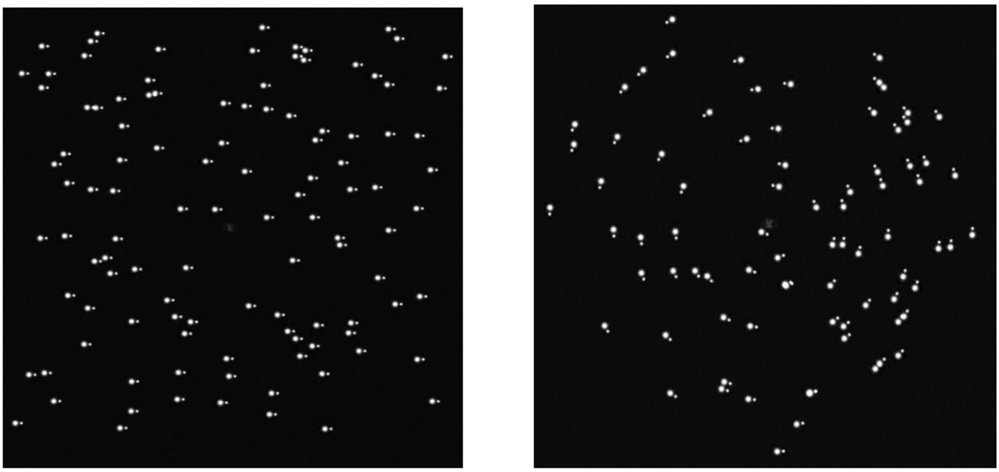
2.1.2 *Apparatus and stimuli.* Psykinematix software v1.0.0 (1000) (KyberVision, Montreal, Canada, psykinematix.com) was used to generate and present all stimuli as well as record responses. A G5 Macintosh Dual 2 GHz Power PC running the Mac OS X version 10.4.11 ran the software while stimuli were presented on a Sony Trinitron Multiscan G520 monitor. The monitor had a frame refresh rate of 75 Hz, a pixel resolution of 1152×870, and was viewed binocularly through a circular viewing tube (diameter 33 cm). A standard head-rest held the viewing distance constant at 57 cm and prevented head movements.

Glass patterns were constructed by using 100 pairs (dipoles) of randomly positioned white dots on a dark-grey background. The Glass shift was 13.8 min measured from the inner edges of the dots. One dot in the dipole remained a constant size, 2.4 min (0.04 deg), while its partner measured 3.6 min (0.06 deg), 4.8 min (0.08 deg), or 6 min (0.10 deg), for a given display. The position of the larger dot was then manipulated to be either left or right of the smaller dot, thus creating six different conditions. In addition, three traditional Glass patterns with dipoles constructed of same-size dots measuring either 3.6 min (0.06 deg), 4.8 min (0.08 deg), or 6 min (0.10 deg) formed the control conditions, giving nine conditions in total (see table 1). All parameters were chosen in accordance with previous studies (Burr and Ross 2002; Ostwald et al 2008; Wilson and Wilkinson 1998) and pilot work confirmed that the dot-pair size combinations (henceforth referred to as size combinations) produced Glass patterns yielding a strong percept of motion.

Two different stimulus patterns were used: translational and concentric (see figure 3). Each pattern was created by positioning the second dot of each dipole according to a geometric rule. For translational patterns, all dots were aligned horizontally (90°) giving a percept of leftward or rightward motion. The square stimulus display measured $21 \text{ deg} \times 21 \text{ deg}$ at a viewing distance of 57 cm. For concentric patterns, dots were oriented tangentially, creating clockwise or anticlockwise perceived motion. The stimulus display was circular and subtended a visual angle of 21.11 deg at the same viewing distance. All displays were centred on an 18-pixel red fixation cross.

Table 1. Dot size combinations and positions.

Dot size and position	Large dot right	Large dot left	Same-size dots
	perceived right (clockwise)	perceived left (anticlockwise)	ambiguous
Small: 0.04 deg and 0.06 deg			
Medium: 0.04 deg and 0.08 deg			
Large: 0.04 deg and 0.10 deg			



(a) (b)

Figure 3. Example of translational (a) and concentric (b) patterns used in experiment 1. In these examples, the larger dot position is expected to produce perceived motion in a leftward and clockwise direction, respectively.

Trials were composed of a sequence of twelve Glass patterns with a lifetime of 83 ms creating a 1 s display. A new array of randomly assigned dipoles was presented in each Glass pattern ensuring that there was no spatial relationship between successive dipoles and therefore no coherent velocity signals.

2.1.3 *Procedure.* The experimental trials were blocked according to pattern type, and presentations of the translational and concentric blocks were alternated between participants. Within each block there were 90 randomly presented trials (10 for each of the 9 conditions). A 2-alternative forced-choice paradigm was used where participants were asked to judge the direction of motion: left or right for translational patterns, clockwise or anticlockwise for concentric patterns. Responses were recorded with the left arrow key indicating left (anticlockwise) perceived motion and the right arrow key indicating right (clockwise) perceived motion.

2.2 *Results*

Data collected represent the number of hits (perceived direction indicated as hypothesised) or misses. Initially, results were obtained by performing a one-way repeated-measures analysis of variance (ANOVA) comparing each size combination within a position [eg small, medium, and large, expected to create rightward (clockwise) perceived motion].

Analysis showed no significant difference between any of the size combinations for a given position or for the traditional Glass patterns with α set at 0.05. Given this result, the data for all size combinations were pooled to compare the three directional conditions: left (anticlockwise), right (clockwise), and ambiguous (left or right) for both pattern types. The results can be seen in figure 4. Clearly left/right and anticlockwise/clockwise motion directions were perceived as hypothesised. For translational pattern sequences the eleven participants indicated, on average, the expected leftward and rightward directions on 27 of the 30 trials ($p < 0.0001$). The average for concentric pattern sequences was 25 out of 30 [$p < 0.0001$ (anticlockwise)] and 24 from 30 [$p = 0.0007$ (clockwise)]. A linear trend was also significant for the clockwise condition ($F_{1,10} = 5.000$, $p = 0.049$), suggesting that, as the size of the larger dot increased, so did the strength of perceived direction, but this was not apparent for the other conditions. All directional motion conditions were significantly different from the ambiguous conditions for both translational ($F_{1,10} = 50.449$, $p < 0.0001$) and concentric ($F_{1,10} = 27.534$, $p < 0.0001$) patterns. The analysis concerning traditional Glass-pattern sequences provides quantitative evidence that they are equally likely to be perceived in either direction. On inspection of figure 4, a slight bias towards the left and anticlockwise directions is evident but responses did not significantly differ from chance ($p > 0.05$).

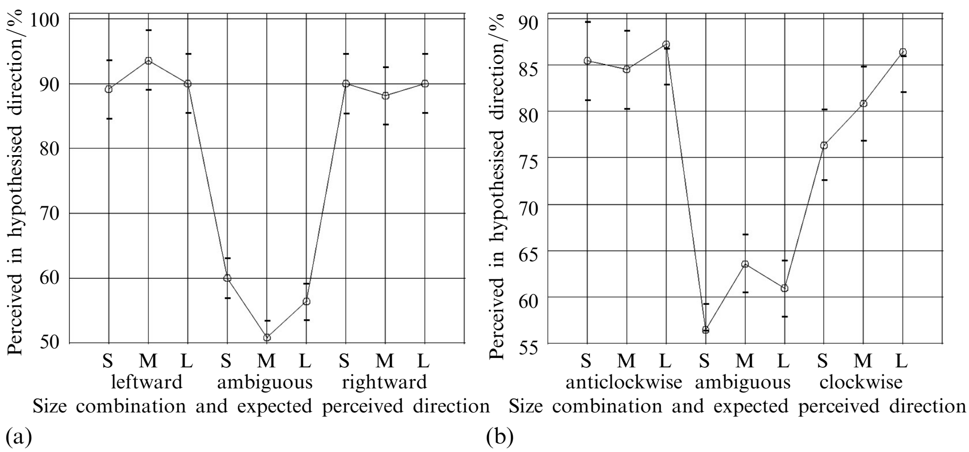


Figure 4. Plots indicate the percentage of responses in the hypothesised direction for each size combination: (a) translational Glass patterns; (b) concentric Glass patterns. Responses for ambiguous conditions were recorded for left (anticlockwise) motion. A slight yet non-significant left (anticlockwise) bias is apparent. Error bars represent ± 1 SEM. Note: S = small, M = medium, L = large.

2.3 *Discussion*

Results supported the hypothesis that increasing the degree of form at a local level can provide enough information for the human visual system to make global judgments of direction. The graphs in figure 4 appear to demonstrate this conclusively. However, two methodological problems may have confounded these results. First, as the participants were requested to fixate on a cross in the centre of the computer monitor and as the stimuli (dipoles) covered the entire area of the display, directional cues may have been extracted from the dipoles appearing close to the fixation point. Therefore, the local features of the dipoles, not the perceived global motion, may have prompted observer's responses. Second, eye movements have the potential to alter the perceived direction of traditional Glass patterns. As the length of each trial was 1 s, the possibility of participants unintentionally shifting their gaze in order to gain insight into the motion direction should not be overlooked. Given the experience of the participants in this experiment and the results for the ambiguous conditions [no statistical difference between left (anticlockwise) and right (clockwise) judgments], this confound is unlikely. Nevertheless, we decided to rerun this experiment with the addition of a blank inner annulus, effectively removing the dipoles from an area directly around the fixation point and decreasing the presentation time to reduce the possibility of eye movements.

3 Experiment 2

3.1 *Method*

3.1.1 *Participants.* Participants were ten volunteers all of whom were naive to the purpose of the study. The five males and five females had a mean age of 22.9 years (SD = 12.91 years) and were emmetropic or had corrected-to-normal vision.

3.1.2 *Stimuli.* All stimuli were identical to those in experiment 1 with the exception of the following:
(i) Both the translational and concentric patterns were viewed within a circular annulus with outer and inner radius measurements ($r_{\max}$ and $r_{\min}$) of 13 deg and 3.5 deg, respectively, as per Del Viva and Gori (2008).
(ii) The duration of the stimulus display was reduced to 150 ms, that is three Glass patterns each with a lifetime of 50 ms.
(iii) The number of randomly positioned dipoles in each display was increased to 120.

3.2 *Results*

Once again, results comparing each size combination within a position were obtained. While there was no significant difference found between the size combinations for perceived rightward motion ($F_{2,18} = 0.364$, $p > 0.05$), or ambiguous motion ($F_{2,18} = 1.108$, $p > 0.05$), in translational patterns a significant difference was apparent for perceived leftward motion ($F_{1.181,\,10.635} = 10.459$, $p = 0.001$) (F statistic reflects a Greenhouse–Geisser correction due to a significant departure from the assumption of sphericity). Contrasts, with a Bonferroni correction, revealed that the smallest size combination (0.04 deg and 0.06 deg) did not elicit the same degree of illusory direction than the two larger combinations did ($F_{1,9} = 12.570$, $p = 0.006$). A similar pattern of results was found for concentric patterns with no significant difference for anticlockwise perceived motion ($F_{2,18} = 1.622$, $p > 0.05$), while the size combinations did reach a significant level for the clockwise ($F_{2,18} = 5.718$, $p = 0.012$) and ambiguous ($F_{2,18} = 5.813$, $p = 0.011$) conditions. Contrasts revealed that this was due to the smallest ($F_{1,9} = 8.617$, $p = 0.017$) and the largest (0.04 deg and 0.10 deg) ($F_{1,9} = 7.338$, $p = 0.024$) size combinations, respectively, although the latter result is only marginal after correcting the α level for multiple contrasts ($\alpha = 0.025$). Further analysis comparing the smallest size combinations with the ambiguous conditions showed that, even though their ability to create unambiguous direction was reduced, they were still well above chance levels with an adjusted α of 0.016 ($F_{1,9} = 119.911$, $p < 0.0001$) (leftward) and ($F_{1,9} = 13.282$, $p = 0.005$) (clockwise). Similarly, while responses for the largest size pair in the ambiguous condition appeared biased in a clockwise direction, it remains significantly different from the expected clockwise motion conditions ($F_{1,9} = 32.129$, $p < 0.0001$). Emulating experiment 1, a linear trend was evident for clockwise ($F_{1,19} = 8.103$, $p = 0.019$) and additionally leftward perceived motion ($F_{1,9} = 7.364$, $p = 0.024$). All results can be seen in figure 5.

Data for all size combinations were pooled to compare the three directional conditions [left (anticlockwise), right (clockwise), and ambiguous (left or right)] for both pattern types. On average, the ten participants indicated perceived motion in both the expected leftward and rightward direction 29 times from a possible 30 ($p < 0.0001$). For concentric patterns, both clockwise and anticlockwise motions were perceived 25 times from 30 trials ($p = 0.0003$). As expected, both directional conditions were significantly different from the ambiguous conditions for translational ($F_{1.185,\,10.664} = 107.527$, $p < 0.0001$) (Greenhouse–Geisser correction) and concentric ($F_{2,18} = 21.515$, $p < 0.0001$) patterns.

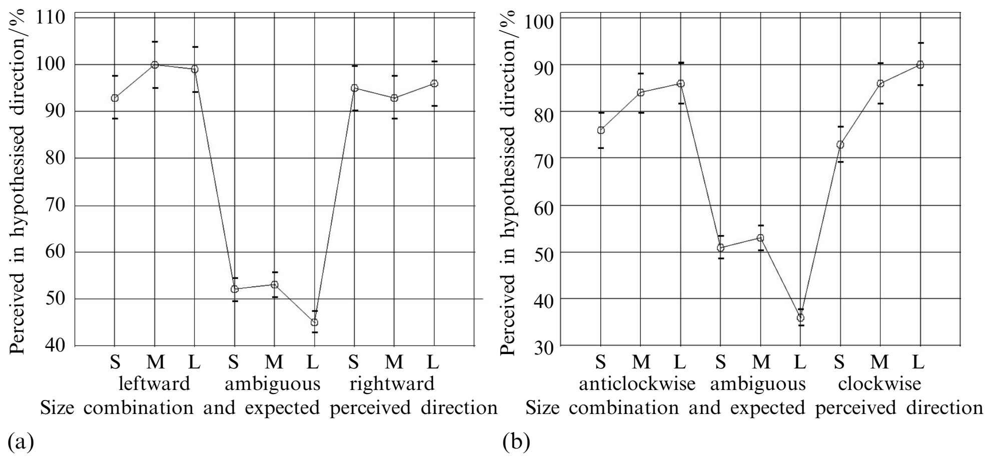


Figure 5. As in figure 4, all nine conditions are plotted for both translational (a) and concentric (b) patterns. Plots indicate the percentage of responses in the hypothesised direction for each size combination. Responses for ambiguous conditions were recorded for left (anticlockwise) motion. Error bars represent ± 1 SEM. Note: S = small, M = medium, L = large.

Once again, empirical evidence confirms the directionally ambiguous nature of traditional Glass patterns with averaged responses for translational patterns showing exactly 50% while the perceived direction of clockwise and anticlockwise motion was 54% and 46%, respectively.

3.3 *Discussion*

Overall it appears that altering the stimulus display and reducing the presentation times had little effect on the perceived direction of motion. However, in some conditions, leftward and clockwise perceived motion, the degree of direction illusion was reduced for the smallest size combination but remained significantly different from the ambiguous conditions. Also, trend analysis showed a linear relationship for the size combinations in these conditions suggesting that the dot-size difference in the small combination was difficult for the visual system to detect with the increased difficulty of the task owing to the parametric changes. In other words, the small combination represents the lower boundary of size difference (0.02 deg), where tapering is occasionally perceived but more often misperceived as same-size dots. Inspection of figure 5 suggests that the task was slightly more difficult when using concentric patterns, which may reflect their complex nature exhibiting multi-modal vectors in comparison to translational patterns where the motion vector is mono-modal (ie direction of movement restricted to left/right).

The clockwise bias found for the largest dot pair (0.10 deg) in the ambiguous condition is difficult to understand especially given the equal left/right and anticlockwise/clockwise responses for the other size combinations. However, the difference between this size and the smaller pairs was marginal and would likely be non-significant in a larger sample. Also, while a slight clockwise bias was evident, responses remained well below that of the size combinations hypothesised to create clockwise motion.

4 General discussion

The overall aim of this paper was to investigate the characteristics of neural speedlines and in so doing further explore the relationship between form and motion in the human visual system. The results indicate that decisions relating to the direction of fast motion may be heavily influenced by form, in turn suggesting that neural speedlines may be analogous to tapered lines. The importance of this finding is twofold: first, care should be taken when designing test stimuli, particularly if stimuli are in fast motion as any form (shape), visually noticeable or not, may have a directional effect. Second, the current results concur with Geisler's model suggesting that form and motion interact at an early visual processing stage, possibly V1.

4.1 *Future considerations and limitations*

As the latter assertion is in opposition to parallel processing theories of form and motion and as those theories were based on the notion of two isolated streams comprised of cells with fundamentally different characteristics (Leventhal et al 1981) eg magno (motion sensitive) and parvo (form and pattern sensitive) cells, a logical next step would be to experiment with an adaptation paradigm. In such a design, adapting to a moving stimulus should reduce the response of magno cells thereby teasing apart the magno versus parvo cell input and therefore the degree of implied versus apparent motion in the perception of tapered Glass patterns. This result may clarify one of the limitations of this study: the role of top–down processing.

Thus far we have assumed that all visual information is processed in a bottom–up manner. In contrast, top–down processing, where experience and knowledge are thought to shape the way particular information is processed (Sobel et al 2007), may explain the directional responses recorded. Here, participants were asked to indicate the direction of motion; directions are often associated with arrows and arrows mimic a tapered shape. When the test stimulus was presented, the most salient cue may have been what the visual system interpreted as an arrow pointing in the direction of motion, thereby prompting directional decisions.

It could also be argued that the speedlines evident in figure 2a result from decreasing contrast or brightness that give the appearance of tapering. This suggests that as the luminance flux (luminance times area of a single component—Kim and Mollon 2002) was far greater for the larger dot than the smaller dot, our results may have arisen from perceived brightness. However, when dots differing in size but of equal luminance are presented for 1 s or less (equivalent to the dipoles in this study), the smaller dot is perceived as brighter than the larger dot (Berman and Stewart 1979). This phenomenon is known as the spatial Broca–Sulzer effect (Higgins and Rinalducci 1975) and predicts that there should be no directional effect in this study due to luminous flux. Dipoles comprised of dots differing in contrast is an area that might be further explored.

It should be noted that this paper focused on immediate responses to fast motion direction and it should not be assumed that prolonged viewing of tapered Glass-pattern sequences will have the same directional effect. Only future testing with longer test presentations will elucidate the effect of tapering on the bistable nature of these patterns.

4.2 *Conclusion*

Evidence suggests that tapered Glass patterns, hypothesised to produce perceptions analogous to those produced by neural speedlines, can provide motion direction information, at least for short stimulus presentations up to 1 s. This result supports Geisler's notion of form/motion interaction at a processing level thought to integrate local visual features, namely V1.

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