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Neuropsychological evidence for three distinct motion mechanisms

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Abstract

We describe psychophysical performance of two stroke patients with lesions in distinct cortical regions in the left hemisphere. Both patients were selectively impaired on direction discrimination in several local and global second-order but not first-order motion tasks. However, only patient FD was impaired on a specific bi-stable motion task where the direction of motion is biased by object similarity. We suggest that this bi-stable motion task may be mediated by a high-level attention or position based mechanism indicating a separate neurological substrate for a high-level attention or position-based mechanism. Therefore, these results provide evidence for the existence of at least three motion mechanisms in the human visual system: a low-level first-and second-order motion mechanism and a high-level attention or position-based mechanism.

Keywords

first-and second-order motion; stroke patients; anatomical localization; MT+; VP

Introduction

Motion can be defined by first-or second-order stimulus attributes. First-order motion consists of moving items defined by luminance. Second-order motion consists of moving items whose mean luminance is the same as the background but differ from the background in other features such as contrast, texture or temporal frequency [7, 8]. Psychophysical, electrophysiological, neurological, and brain imaging evidence suggests that first-and second-order motion stimuli are processed, at least initially, by distinct visual pathways and different mechanisms [3, 19].

Relatively low-level (e.g. filter-rectify-filter) [8] and high-level (attention-and/or position-based feature-tracking) [11, 23] mechanisms have been proposed to mediate the perception of second-order motion. The latter kind of motion mechanism tracks the position of image features over time, with properties similar to the “long-range motion” process proposed by Braddick [6]. These low and high-level second-order mechanisms are not necessarily mutually exclusive and, hence, high-level mechanisms have also been proposed as a separate parallel “third(-order) mechanism”, in addition to low-level second-order mechanisms [4, 17, 18, 25, 27].

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In this study we describe two stroke patients (JV and FD) with lesions in distinct regions in the left hemisphere. A detailed study of FD's motion perception was previously published [29]. The focus of this paper is the dissociation of deficits on second-order motion tasks between patient FD and a new patient, JV. Both patients are selectively impaired on direction discrimination in local and global second-order motion tasks, but only patient FD is impaired in a bi-stable motion task where the direction of motion is biased by object similarity [16]. These results support the hypothesis of at least three motion mechanisms in the human visual system [4, 17–19, 25, 27].

Methods

Patients

Patient JV was a 60 years old right-handed college-educated woman who suffered an infarct in the left occipital lobe. Neuropsychological evaluation was remarkable only for poor short-term memory, number manipulation, spelling errors and two-dimensional discrimination. These functions recovered within 5 months after the stroke. Initially, Humphrey and Goldmann perimetry visual field testing showed a well-defined upper right quadrantopsia, however, full vision was restored within 6 months when the data reported here were obtained. Patient FD was a 41 years old, right-handed college-educated social worker, who suffered a left hemisphere infarct encroaching the lateral occipital and the posterior temporal and parietal regions. Neuropsychological and neuro-ophthalmological examinations, including visual fields, were normal. Informed consent was obtained from the patients and the healthy control subjects according to the requirements of Boston University Human Subjects' Committee.

The anatomical locations of the lesions are shown on an average unfolded brain (Fig. 1). The lesion locations of patients JV and FD are illustrated in panels A and B, respectively. JV's lesion affects a local region of the ventral occipital lobe. FD's lesion involves both the superior and inferior lateral occipital cortex, and extends anteriorly involving portions of the angular gyrus and middle temporo-occipital cortex and terminates in the inferior portion of the posterior supramarginal gyrus [30].

In order to compare the lesion sites with the cortical areas identified by brain imaging studies of visual motion tasks, the average borders of areas V1 to V3/VP and the average 50% iso-probability lines of hMT+ are drawn [13, 14]. These probabilistic functional localizations suggest that JV's lesion encompasses cortical areas V2v/VP and that FD's lesion is located dorsally to hMT+ [29, 30].

For more than a year both patients participated on a regular basis in psychophysical testing of their visual perception, including contrast sensitivity, and a large psychophysical test battery of first-order motion discrimination tasks (e.g. direction, speed, 2-D form from motion, radial motion) and several static 2 D detection and discrimination tasks. At the time of the data presented here, JV and FD's performance was normal on these tasks. Here we will discuss four specific second-order motion conditions.

Apparatus and procedures

The apparatus and procedures are briefly summarized here. Details are provided in Vaina et al [29, 31]. The displays were generated and the responses collected using a Power Macintosh computer and presented on the Apple Triniton monitor. Luminance calibration was done before each presentation to assure linearity. The difficulty of the tests (except the bi-stable motion task) was titrated by an adaptive staircase procedure (for details see Vaina et al [32]) that was used to determine each subject's threshold, computed as the arithmetic

mean of at least six reversals. In the bi-stable motion test, proportion correct was determined based on the method of constant stimuli.

Prior to the tests, the subjects received practice trials of varying difficulty, which ensured that they understood the task. Feedback was provided during the practice trials only. Between trials subjects viewed a uniform blank screen, except for a fixation mark. Throughout the trial and testing periods, the subjects fixated on a fixation mark placed to the left or right of the stimulus such that the stimulus was presented at a 2 deg eccentricity in the left or right visual field (except for the bi-stable motion test which had central fixation). Subjects' responses were verbal and the examiner entered them on the computer keyboard. The healthy controls were psychophysical naive men and women age-matched to the patients (40–60 years old), without any known history of neurological or ophthalmologic diseases. All subjects were right handed and had normal or corrected-to-normal visual acuity.

Stimuli

Flickering bar—Discrimination of direction in second-order motion was measured using a stimulus adapted from Albright [1] (Fig. 2A). The display, 10×10 deg., consisted of a static dot pattern (50% white, 50% black) over which an imaginary square-wave grating of spatial frequency 0.5 cyc/deg moving at 4 deg/sec was displaced. The square wave was composed of flickering dots, created by inverting the contrast of a given percentage of dots in each frame. The stimulus was presented for 0.5 sec on each trial. The percentage of dots that flickered was varied from trial to trial. The subjects' indicated the direction of motion: upward or downward.

D-max in first-and second-order motion—The D-max test, adapted from Braddick [6], estimates the upper displacement limit for detecting the stimulus' direction of motion. The display subtended 10×10 deg, and was divided into a notional grid of 38×38 blocks, each consisting of a dense random dark-light flickering dot microtexture (Fig. 2C, E). 42% of the blocks, called token blocks, moved left or right while the remaining 58% constituted the background. The motion display consisted of two successive 42 ms frames with zero interframe interval. The step size of the displacement was varied from trial to trial. The mean luminance of first order motion token blocks was 12.3 cd/m^2 and contrast within the block was 0.2 (Fig. 2C), while the mean luminance of second order blocks was 9.5 cd/m^2 and internal contrast was 0.6 (Fig. 2E). The mean luminance of the background was in both cases 9.5 cd/m^2 with internal contrast of 0.2. The subjects indicated the direction of motion, left or right. Prior to performing the test, the patients were tested with static version of these stimuli where they had to detect the presence of the image features comprising the motion signal in the motion tasks. They were able to detect both the first-order or second-order tokens.

Direction discrimination in first-and second-order global motion—This task is conceptually similar to the classical motion coherence test (e.g. [21]). The luminance and contrast values of the displays (Fig. 2G and I) were identical to those used in the previous stimulus, but here the strength of the motion signal was systematically varied by changing the proportion of token blocks that moved coherently in the same direction while the remaining token blocks appeared at random locations on alternate frames. The token-block density remained constant at 42%. The stimulus frames were presented for twelve 42ms frames with zero interframe interval and the speed of the coherently moving tokens was 3 deg/sec. The subjects indicated the direction of motion, left or right.

Bi-stable motion task—The bi-stable motion task was adapted from Green [16]. The stimulus consisted of four consecutive frames, displayed twice in succession to give a total of eight frames in one trial (Fig. 3A). The Gabors of each pair have the same spatial frequency and during a ”rotation” only the position of the Gabors changes, not their orientation. The spatial frequency of one pair of Gabors was held constant at 5 cycles/deg, whereas the others were systematically varied: 1, 1.7, 3, 5 and 10 cycles/deg. The separation between each pair of Gabors was 3.6 deg and at consecutive frames each Gabors traveled 1.4 deg. The eight frames, each visible for 75ms with 45ms interframe intervals, were displayed in one of two sequences, corresponding to clockwise (order 1,2,3,4) or counterclockwise rotation (order 1,4,3,2). The subjects indicated whether the Gabor patches, which are otherwise univarying, “appear” to rotate clockwise or counter-clockwise [31]. Prior to performing the test, all subjects (including the patients) matched the Gabor patterns in their apparent contrast. To control for the possibility that the patients cannot detect the difference in spatial frequency, a static task was used in which three Gabors had the same spatial frequency and the fourth is different. Observers were asked to pick the odd one out. The spatial frequencies used were the same as in the motion task. Both patients were unimpaired for these control conditions.

Results

Flickering bar

In their contralesional visual field (right visual field), both patients required roughly three times more flickering elements to perceive the direction of second-order motion than in the ipsilesional visual field (left visual field) or than the normal controls (Fig 2B). Both patients performed significantly worse in the contralesional ($p<0.001$, two-sample two-tailed t-test) but not in the ipsilesional ($p>0.54$) visual field.

D-max in first-and second-order motion

For the first-order motion stimulus, both JV and FD’s performance was normal for stimuli presented in both left and right visual field (Fig 2D). For the second-order motion condition (Fig 2F), however, both patients were impaired for stimuli presented in the contralesional visual field ($p \ll 0.001$, two samples two-tailed t-test), but had normal performance in the ipsilesional field ($p > 0.1$).

Direction discrimination in first-and second-order global motion

Both FD and JV were not impaired on the first-order motion condition (Fig 2H), but Fig 2J shows that the thresholds were increased for the contralesional visual field in the second-order motion condition ($p \ll 0.001$, two-samples, two-tailed t-test). FD’s performance on the second order motion for the stimulus presented in the ipsilesional visual field was significantly better than the performance of controls and JV. This may be accounted in part by his high motivation and by 22 months after the lesion he was quite trained on motion psychophysical tasks.

Bi-stable motion task

On the bi-stable motion test, FD was impaired, as tested three different times across 22 months (Fig 3C). FD’s performance differed significantly from control subjects for the first three pairs of frequencies (1:5, 1.7:5 and 3:5 cyc/deg, chi-square test, 8.57, $p<0.003$; 11.4, $p<0.0007$; 8.25, $p<0.004$, respectively), There was no significant difference in FD’s performance on the three times he took the test ($p > 0.4$). JV’s performance was normal on this task (Fig. 3B). Typically, the bi-stable motion test is performed using central fixation. But Patient JV had a quadrantic visual field deficit and FD’s deficit may be due to a failure

to integrate information between the right and left visual field. To rule out this alternative explanation, the bi-stable motion stimulus was also tested within the visual field quadrants using eccentric fixation in both patients. Supplement 1 shows that at the eccentricities tested, the apparent spatial frequencies of the two physically identical Gabor patches, were also perceptually not significantly different one from the other. JV was tested in the upper and lower visual field ipsilateral and contralateral to the lesion, and FD was tested in each quadrant. Their performance was very similar in both presentations (not statistically significant). Therefore, we only report data from the basic experimental condition. Patient FD performance at the bi-stable motion task did not differ significantly from control subjects at one particular pair of frequencies (5:10 cyc/deg). This was the case for all three times he took the test. At this condition the Gabor patches are defined at the highest spatial frequencies. If patient FD's perception of the highest spatial frequency was impaired (10 cyc/deg), only one Gabor pair would dominate perceptually, and could drive the performance, i.e. the task would not be ambiguous anymore. But patient FD perception in static versions was normal in control experiments. However, Green suggested that low spatial frequencies are major determinants of correspondence [16]. We speculate that when one Gabor pair is at higher spatial frequencies beyond the sensitivity range of the correspondence mechanism, the task ceases to be bi-stable and is driven only by the low spatial frequency Gabors. This would be the case for both controls and patients and could explain why this particular condition remains relatively unimpaired when the performance of the correspondence mechanisms degrade.

Although with similar impairments on direction discrimination in the flickering bar and the local and global second-order tasks, JV had exactly the opposite pattern of performance compared to FD on the bi-stable motion task. Thus JV and FD's psychophysical results support the idea that several types of second-order motion mechanisms may co-exist with different neuronal substrates, one of which may be mediated by a high-level attention or position based mechanism.

Discussion

We describe two patients with lesions in the left hemisphere. One patient has a lesion in medial ventral occipital lobe around V2v/VP (JV), whereas the other (FD) had a lesion in superior temporal sulcus. These lesion locations are known to be able to disrupt motion perception [10]. Both FD and JV were impaired on the flickering bar test, and the second-order versions, but not first-order, of the local (D-max) and global motion tasks for stimuli presented in their contralesional visual field. Surprisingly, only FD was impaired on the bi-stable motion task.

Performance in the bi-stable motion task depends on the difference in Gabor spatial frequency, which is consistent with the operations of a second-order long-range mechanism [33]. Consistent with this idea, the distance and time between two successive frames are beyond the upper displacement limit for short-range motion [5, 6]. This kind of motion perception could be mediated by a high-order position or attention-based mechanism [11, 23]. We suggest that FD's impairment in the bi-stable motion task reflects a deficit in a high-level but not a low-level second-order mechanism. Therefore, these results suggest two mechanisms underlying the perception of second-order motion. Another alternative explanation may be that the bi-stable motion task contained less noise than the other second-order motion tasks, which contained dynamic noise carriers. This, however, cannot explain the results since JV and FD were not impaired on first-order tasks with the same dynamic noise carriers. Lastly, because FD's lesion was at higher level in the visual system than that of JV, we propose that different types of second-order mechanisms have different neuroanatomical substrates. Thus, in agreement with previous psychophysical results [4, 17–

19, 27], our data support the existence of a total of at least three motion mechanisms with different neuronal substrates.

The results are complimentary with brain imaging studies investigating a cortical specialization for first-and second-order motion. All of these studies implicate similar regions in processing either kind of motion [2, 12, 15, 22, 24, 26, 28]. The brain imaging studies that do report location differences in responses to these kinds of motion are consistent with the neuropsychological results reported here: both lesion sites are beyond the earliest visual areas proposed to be more involved in processing first-order motion [12], and overlap with regions implicated in a stronger processing of second-order motion [9, 12, 22, 26]. In addition, Claeys et al [9], revealed activations for a similar apparent motion task to our bi-stable motion task in a site in rough proximity of FD's lesion site and implicated this site in high-level saliency-based motion perception. Our results expand these brain imaging studies by providing evidence that a more anterior lesion can also affect a high-level mechanism, which suggests at least three motion mechanisms. That is, a low-level first and second-order mechanism, and a high-level (third-order) mechanism.

In conclusion, this study provides evidence from neurological patients for two mechanisms underlying the perception of second-order motion, giving a total of at least three mechanisms with different neuronal substrates mediating the human motion perception.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

Acknowledgments

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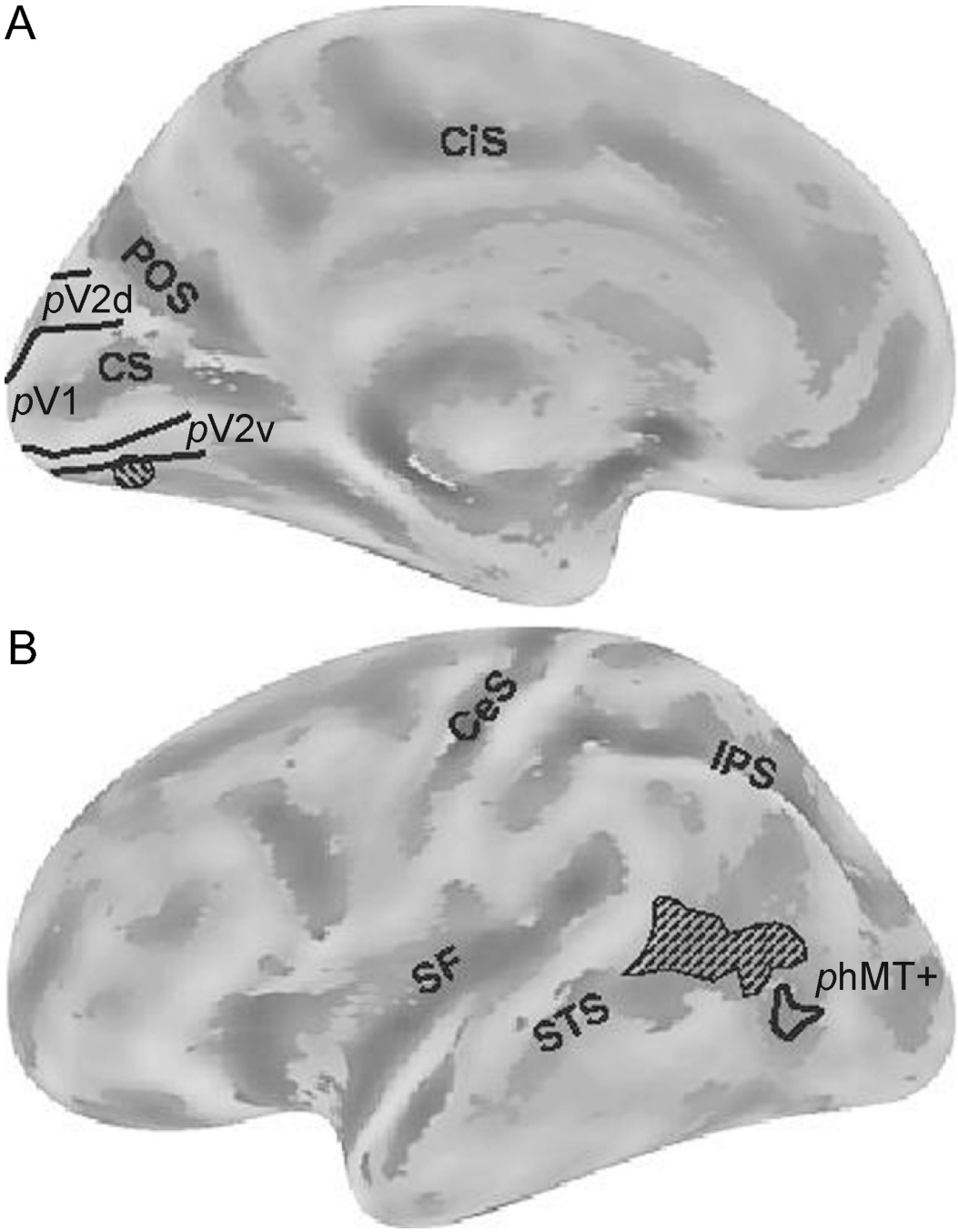

Figure 1.

The lesions are indicated on an average unfolded cortical surface of the left hemisphere [20]. (A) On a medial view the lesion of subject JV is shown (oblique striped region). (B) On a lateral view the lesion of subject FD is shown (oblique striped region) [29]. In order to facilitate orientation on the surfaces, several anatomical structures have been identified, including the Calcarine (CS), parietal-occipital (POS), and cingulate sulcus (CIS) on the medial view (A). On the lateral view (B) the cental sulcus (CeS), Sylvian fissure (SF), intra-parietal (IPS) and superior temporal sulcus (STS) has been identified. The average locations of functional areas have been indicated as well (solid black lines). On the medial view (A),

the average border of V1/V2/V3/VP have been drawn [14]. On the lateral view (B) the 50% iso-probability contour of hMT+ is indicated [13].

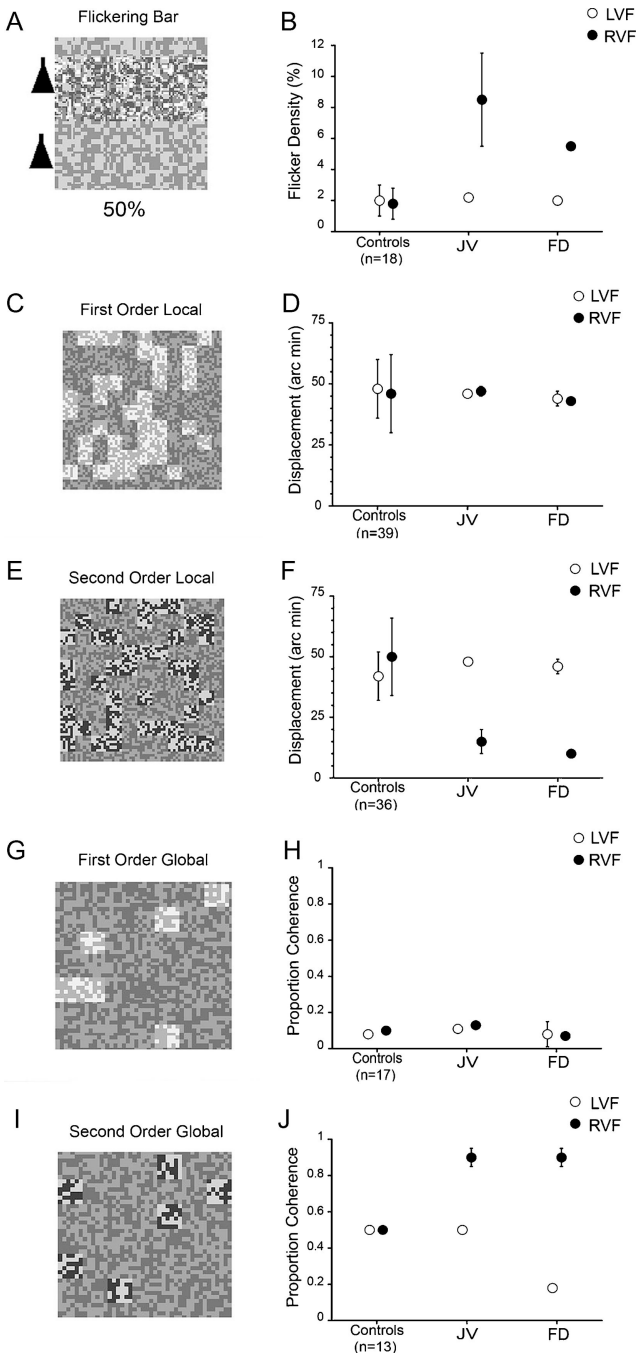

Figure 2.

Direction discrimination in first-and second-order motion stimuli for healthy control subjects and patients JV and FD. On the left of each pair of boxes are the schematic views of the visual stimuli, on the right the results for each test are shown. (A) flickering bar stimulus, the arrow heads indicate the direction of motion. (B) Results, indicating that both patients were impaired in their contralesional visual field only. (C & E) Single frames of the displays that were used to measure D-max for first-and second-order motion, respectively. (D & F) The results reveal an impaired performance of the contralesional visual field for both subjects for the second-order (F) but not the first order version (D). (G & I) Single frames of the displays that were used to measure first (G) and second-order (I) global

motion. (H & J) The results show an impaired performance for the second-order (J) but not the first order condition (H) in the contralesional visual field. Error bars reflect standard deviation.

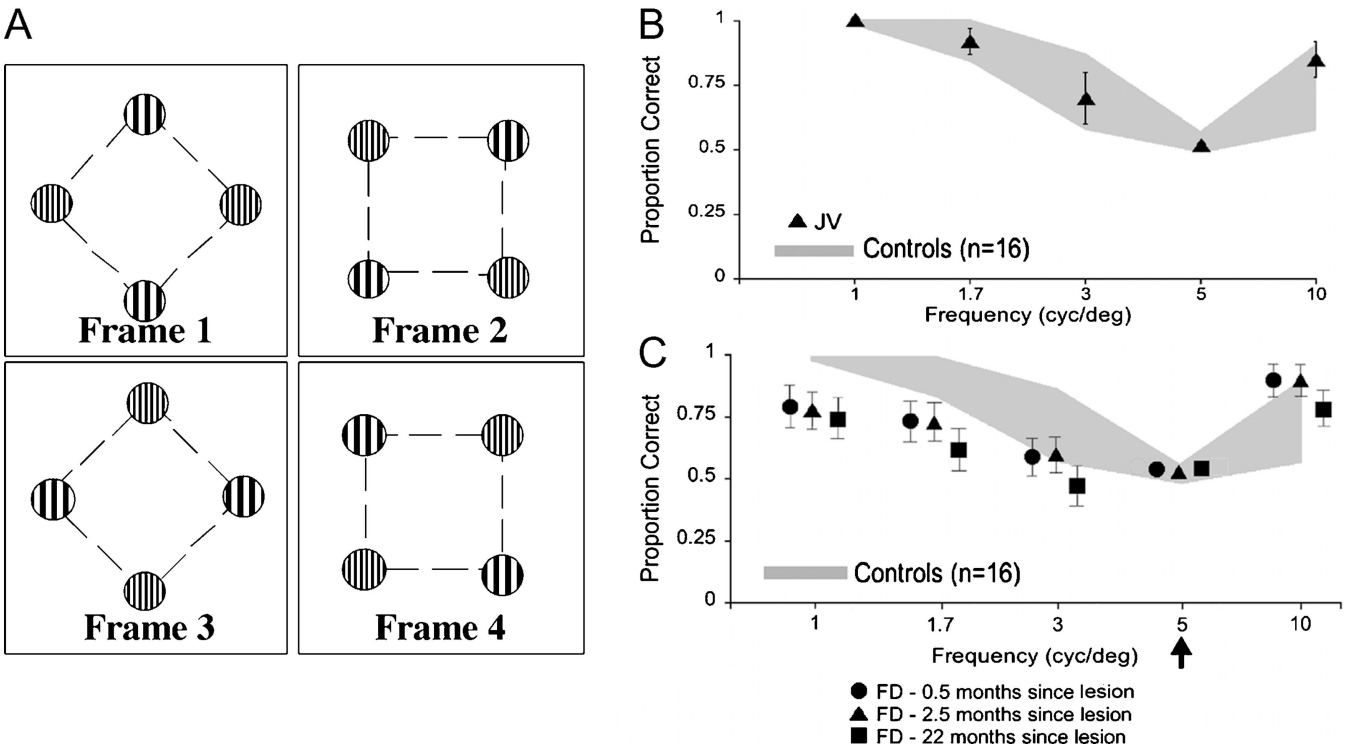

Figure 3.

(A) Schematic diagram for the bi-stable second-order motion using Gabor patches adapted from Green [16]. (B &C) Percent correct as a function of the spatial frequency values of the test Gabor pairs. The data from 16 normal controls are presented as a shaded area representing the mean +/−1 s.d. The results indicate a normal performance for patient JV (B) that contrasts with the impaired performance of patient FD (C) as measured on three distinct experimental sessions.