

Attention modulates neuronal correlates of interhemispheric integration and global motion perception

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In early retinotopic areas of the human visual system, information from the left and right visual hemifields (VHFs) is processed contralaterally in two hemispheres. Despite this segregation, we have the perceptual experience of a unified, coherent, and uninterrupted single visual field. How exactly the visual system integrates information from the two VHFs and achieves this perceptual experience still remains largely unknown. In this study using fMRI, we explored candidate areas that are involved in interhemispheric integration and the perceptual experience of a unified, global motion across VHFs. Stimuli were two-dimensional, computer-generated objects with parts in both VHFs. The retinal image in the left VHF always remained stationary, but in the experimental condition, it appeared to have local

motion because of the perceived global motion of the object. This perceptual effect could be weakened by directing the attention away from the global motion through a demanding fixation task. Results show that lateral occipital areas, including the medial temporal complex, play an important role in the process of perceptual experience of a unified global motion across VHFs. In early areas, including the lateral geniculate nucleus and V1, we observed correlates of this perceptual experience only when attention is not directed away from the object. These findings reveal effects of attention on interhemispheric integration in motion perception and imply that both the bilateral activity of higher-tier visual areas and feedback mechanisms leading to bilateral activity of early areas

Citation: Akin, B., Ozdem, C., Eroglu, S., Keskin, D. T., Fang, F., Doerschner, K., Kersten, D., & Boyaci, H. (2014). Attention modulates neuronal correlates of interhemispheric integration and global motion perception. *Journal of Vision*, 14(12):30, 1–13, <http://www.journalofvision.org/content/14/12/30>, doi:10.1167/14.12.30.

play roles in the perceptual experience of a unified visual field.

Introduction

Early visual areas in the primate brain receive direct input largely from the contralateral visual field, which implies a discontinuity at the midline (Gazzaniga, 2000; Tootell, Switkes, Silverman, & Hamilton, 1988). Yet we have the perceptual experience of a unified world without any disruption in the midline. How this experience emerges still remains an open question. One possibility is that we consciously perceive a unified visual field as a result of activity in higher visual areas that respond bilaterally. Presumably, neurons in these areas have larger receptive fields that extend into the ipsilateral visual hemifield (VHF) (A. T. Smith, Williams, & Singh, 2004; Tootell, Mendola, Hadjikhani, Liu, & Dale, 1998; but see Lavidor & Walsh, 2004). However, it is not clear whether this kind of bilateral response is necessary and sufficient for perceptual experience of a unified visual field. Indeed results of studies with patients having lesion in V1 and those with healthy humans using backward masking paradigms and transcranial magnetic stimulation suggest that activity of early areas is critical for a conscious visual experience (Lamme & Roelfsema, 2000; Zeki & Ffytche, 1998). Therefore, it could be argued that early areas should be involved in the process for the perceptual experience of a unified visual field, either through feedback provided by the higher-tier areas with larger receptive fields in the same hemisphere or alternatively by callosal interactions (Clarke & Millosky, 1990).

Despite its obvious fundamental importance, little is known about the mechanisms underlying the perceptual experience of a unified visual field. Liu, Zhang, Chen, and He (2009), using fMRI and EEG combined, recorded responses while observers viewed flickering checkerboard patterns. They found evidence supporting that bilateral integration took place in the primary visual area (V1) as well as areas in the lateral occipitotemporal (LOT) regions, which includes MT+. Interestingly, the bilateral MT+ activity preceded the bilateral V1 activity. This suggests that interhemispheric integration first occurs in MT+ and other LOT areas, and then feedback is provided to earlier areas, such as V1. Vanni et al. (2004) studied bilateral responses in visual cortex using EEG and fMRI combined as well. Their results indicated that LOT areas, possibly including MT+, were among the first extrastriate areas to respond bilaterally. Both studies argue that these areas must be critical for unified perception across the midline. However, the stimuli

used were simple wedges and squares texture-mapped with flickering black and white checkers. When placed in both VHFs, the shapes were disjointed. Therefore, it is not obvious how to generalize the results of Liu et al. and Vanni et al. to explain the perceptual experience of a unified visual field.

Ban et al. (2006) conducted an fMRI experiment to address the critical question of the role of early areas in perceptual experience of a unified visual field. They measured the activity in early visual areas, V1, dorsal V2, and dorsal V3, to an arc placed in the lower left quadrant of the visual field. They found that the activity in the retinotopically defined regions was larger when the arc was part of a complete annulus than that of a single arc or multiple arcs that did not form a whole annulus even though in all conditions the stimulus was identical within the retinotopically defined region. Their results showed that activity in early retinotopic areas, V1, V2d, and V3d, depended not only on what is present in the contralateral visual field, but also on what is being presented on the ipsilateral visual field. Ban et al. argues that this result suggests that activity of early visual areas plays a role in perceptual experience of a unified visual field and is influenced by global perception, contextual cues, and perceptual grouping. However, the stimuli used in the Ban et al. study emphasized only shape perception, and visual areas other than V1, V2d, and V3d were not investigated.

Another important but little explored factor in the perceptual experience of a unified visual field is attention. Attention has been shown to strongly affect neuronal activity measured with fMRI in visual areas (Gandhi, Heeger, & Boynton, 1999), including motion-sensitive areas such as MT+ (Burr, Baldassi, Morrone, & Verghese, 2009; Crespi et al., 2011; Saenz, Buracas, & Boynton, 2002; also see Hansen, Kay, & Gallant, 2007; Womelsdorf, Anton-Erxleben, Pieper, & Treue, 2006). Feedback signals can also be modulated with attention, and feedback to early areas is believed to be a key factor in perceptual awareness (Lamme & Roelfsema, 2000). Therefore, understanding how attention modulates the neuronal correlates of perceptual experience of a unified visual field could be instrumental to understanding the details of the underlying information processing mechanisms, e.g., the roles of feedforward and feedback processes.

To explore the correlates of neuronal activity in visual areas that potentially perform interhemispheric integration and play a critical role in the perceptual experience of global object motion unified across VHFs and how attention affects the activity, we conducted an fMRI experiment. In the first condition, we measured the cortical responses to an oscillating “Pac-man” while participants were fixating at the center of the figure (Figure 1, left panel). The oscillations of the Pac-man

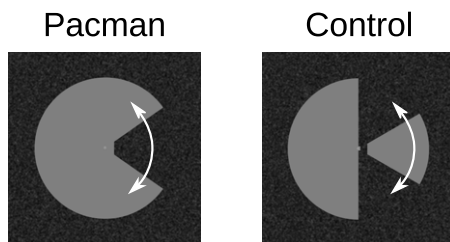


Figure 1. Stimuli used in fMRI experiments. When the Pac-man figure oscillates about the axis going through its center, the whole figure seems to oscillate even though the motion signals are only around its “mouth.” Importantly, when the oscillations are such that the local signals are confined to the right visual field, the part of the figure in the left visual field is still perceived as oscillating. In the control stimulus, in which a wedge on the right visual field oscillates, the left part of the figure appears static. Note that the local motion-dependent energy signals are approximately the same across the two conditions.

were such that the physical localized motion was restricted to the right visual field. Nevertheless, the whole Pac-man appeared as oscillating. In the second condition, we measured responses to a control stimulus, in which the localized motion signals were approximately identical in the right visual field, but unlike in the Pac-man condition, the left portion of the control figure appeared static (Figure 1, right panel). Because the stimulus is unified in the Pac-man but not in the control condition, we hypothesized that areas that integrate information across hemispheres and play a critical role in perceptual experience of global motion unified across two VHF should be differentially more active in the Pac-man condition compared to the control condition. We repeated the measurements under two attentional conditions. In the “fixation task” condition, participants were required to perform a demanding fixation task to direct attention away from the figure (see Methods section for details). In the “passive view” condition, the participants simply fixated the dynamic fixation mark without performing the fixation task. This resulted in four conditions overall (two stimulus conditions \times two attention conditions).

Methods

Participants

Bilkent University undergraduate students, including the authors DTK, SE, and CO, participated in the experiments. Informed written consents were obtained before the experiments in accordance with the proce-

dures and protocols approved by the Human Ethics Committee of Bilkent University. Participants were compensated for their participation with payment. All participants had normal or corrected-to-normal vision and had no known visual or neurological disorders. Eight participants participated in the “fixation task” condition, and seven participated in the “passive view” condition, including the authors DTK, SE, and CO. A different group of 20 naive observers participated in the behavioral experiments, and six observers participated in the eye-tracking experiments, including the authors HB and KD.

MR data acquisition

Magnetic resonance imaging was performed on a 3 Tesla scanner (Magnetom Trio, Siemens AG, Erlangen Germany) with a 12-channel phase-array head coil. A high-resolution T1-weighted three-dimensional anatomical-volume scan was acquired for each participant in the same session before the functional scans (single-shot turbo flash; voxel size = $1 \times 1 \times 1 \text{ mm}^3$; repetition time [TR] = 2600 ms; echo time [TE] = 3.02 ms; flip angle = 8° ; field of view [FOV] = $256 \times 224 \text{ mm}^2$; slice orientation: sagittal; phase encode direction: anterior–posterior; number of slices: 176; acceleration factor [GRAPPA]: 2). Functional MR signals were measured with an echo-planar imaging sequence (TE: 40 ms; TR: 2000 ms; FOV: $192 \times 192 \text{ mm}^2$; matrix size: 64×64 ; in-plane resolution: $3 \times 3 \text{ mm}^2$; flip angle: 71° ; slice thickness: 3 mm; no gap between slices; number of slices: 26; slice orientation: parallel to calcarine sulcus). Each participant participated in a retinotopic mapping session and two experimental sessions (one for the “fixation task” condition, one for the “passive view” condition) except for one subject who participated in only one experimental session (subject AA participated in the “fixation task” condition only). The experimental sessions included a structural scan; two region of interest (ROI) localization scans, one for early retinotopic areas, one for area MT+; and eight scans for the measurement of cortical responses to the experimental stimuli.

MR display system

The stimuli were back-projected onto a translucent screen placed inside the scanner bore using a video projector (NEC NP125, resolution: 1024×768 , refresh rate: 60 Hz) fitted with a long-throw lens (NuView 489MCZ900, Navitar, Rochester, NY, USA). Participants viewed the stimuli presented on the screen by an angled first surface reflectance mirror attached to the head-coil above their eyes. Total eye–screen distance was 72.5 cm, and the visible display subtended about

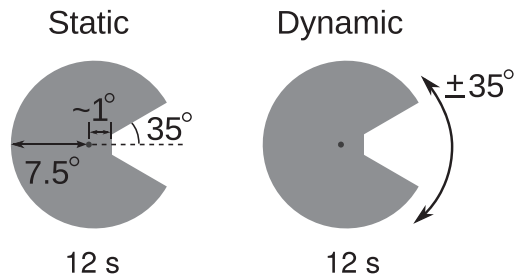


Figure 2. Experimental protocol and stimulus details. Responses to dynamic Pac-man and control stimuli were measured using a block design protocol. In each experimental run, a 12-s presentation of static stimulus was followed by 12 s of a dynamic block in which the figure oscillated about its center. This sequence was repeated 10 times in a run. In order to control for the effects of attention, observers were required to perform a demanding fixation task. In another condition, they passively viewed the stimulus while maintaining fixation at the central mark.

$30^\circ \times 22^\circ$ of visual angle. The maximum luminance achievable on the translucent screen was 1832 cd/m^2 with a CIE chromaticity of $x = 0.357$, $y = 0.351$.

Stimuli

All experimental software was written by us in the Java programming platform (<http://www.bilkent.edu.tr/~hboyaci/PsychWithJava/index.html>). All visual stimuli were computer-generated. The visual stimuli was composed of a random noise background that covered the whole display except the figures in the foreground (the luminance of each pixel was drawn from a Gaussian distribution with minimum luminance of zero and maximum luminance of 377.25 cd/m^2 , and then the resulting image was convolved with a 6×6 uniform filtering kernel, see Figure 1). In the foreground at the center of the display a “Pac-man” or “control” figure was presented. Both figures had a luminance value of 503 cd/m^2 . The left parts of the Pac-man and control figures were identical. But the figures differed on their right side. In the control condition, the right side of the figure was composed of a wedge, approximately as large as the “mouth” of the Pac-man. The dimensions are shown in Figure 2. A fixation mark was placed at the center of the display. The figures were presented either statically or dynamically. During the dynamic period, the figures oscillated sinusoidally with a half period of 480 ms. For both figures, the sinusoidal oscillations were about the axis going through the central fixation mark and perpendicular to the plane of the stimulus. The amplitude of oscillations were such that the local motion was always confined to the right side of the figures. In the case of the Pac-man figure, the

whole figure seemed to oscillate about the fixation mark even though there was no local physical motion on the left side. Whereas, in the control figure, the left portion seemed to be static; only the wedge on the right side appeared to oscillate (Figure 1).

Experimental procedure and fixation task

Correlates of neuronal activity were measured with fMRI using a block design experimental protocol. Each run started with a static presentation for 12 s, followed by a dynamic presentation for another 12 s. This sequence was repeated 10 times in each scanning run (Figure 2). Each run lasted 250 s, including a final blank period of 10 s. In order to examine the effects of attention, we employed two attentional conditions. In the “fixation task” condition, participants were required to perform a demanding fixation task. The fixation mark briefly changed its brightness for 200 ms at random intervals ranging between 1750 and 2250 ms, turning either darker or brighter (common luminance: 665 cd/m^2 ; brighter: 747 cd/m^2 ; darker: 585 cd/m^2), and the task of the participant was to indicate the direction of change by using an MR safe button box (fORP 904 fMRI trigger and response system, Current Designs, Philadelphia, PA, USA). In the “passive view” condition, participants were required to maintain fixation at the central mark without performing the fixation task. During the passive view scans, the fixation mark changed its brightness just as in the fixation task scans.

ROI localization

ROIs for areas lateral geniculate nucleus (LGN), V1, V2, V3, V3A/B, V4, and LO-1 were identified with square wave-modulated, contrast-reversing (8 Hz), black-and-white checks covering parts of the left and right visual fields as shown in Figure 3. The localizer runs were composed of alternating 12-s blocks of flickering checks and blank periods, repeated 10 times. Total duration of a localizer run was 250 s, including 10 s of a final blank period. Methods developed by Huk, Dougherty, and Heeger (2002) were used to localize the middle temporal complex, MT+. MT+ localizer stimulus was composed of small dots randomly placed inside a circular region of 6.75° of visual angle, centered at 9° to the left and right of the fixation mark. Each run started with stationary presentation of the dots for 12 s, followed by a 12-s block during which the dots in the left visual field moved radially inward and outward, alternating every second. During the next 12 s, the dots were stationary, followed by another 12-s block during which the dots on the right visual field were set in motion. In some participants, we could identify putative MST, which responds to ipsilat-

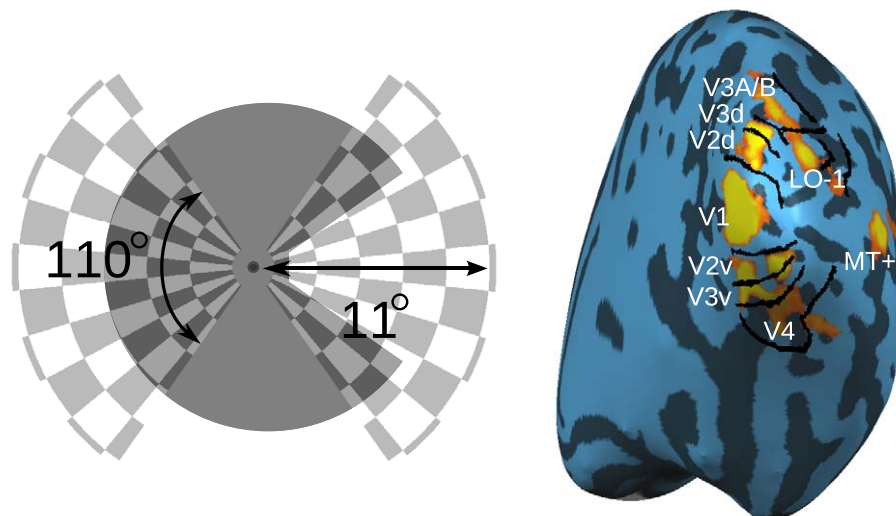


Figure 3. ROIs were identified using wedges texture-mapped with counter-phase contrast reversing checkerboard patterns in early visual areas (the Pac-man figure in the background is shown here for visualization purposes; it was not present in the actual experiment). For MT+, moving random dots were used as a localizer. Boundaries between early visual areas were drawn using the results of a separate retinotopic mapping session for each participant. The image on the right shows ROIs and visual area boundaries on an inflated brain of one participant.

eral stimulation, and MT separately (Huk et al., 2002; Morrone et al., 2000). However, this was limited to only a few subjects. Therefore, we present data averaged over the entire MT+.

Retinotopic mapping stimuli

All participants took part in a separate retinotopic mapping session. Results of this session were used to delineate borders between early visual areas. The stimuli were composed of rotating wedges and expanding and contracting rings with counter-phase flickering black-and-white checks. The wedges had an arc angle of 30° and rotated by 30° about the center of the screen every 10 s, sweeping the whole 360° in 12 steps. This cycle was repeated five times. There were six rings with a thickness of about 2° and an inner diameter ranging from 1° to 14° . Each ring was presented for 10 s. This cycle was repeated 10 times. For localizing the areas in the dorsal stream, namely V3A/B, LO-1, and LO-2 borders, we followed the convention used in Larsson and Heeger (2006) (see also Tootell et al., 1997). The structural images acquired during the retinotopic mapping session were used to obtain a 3-D inflated model of the cortex for each participant. Boundaries between retinotopic areas were drawn manually on the inflated cortices by inspecting the cross-correlation maps of the MR signal and the rotating wedges and expanding rings (Engel, Glover, & Wandell, 1997; Sereno et al., 1995).

MR data processing and analysis

Functional images were preprocessed using Brain-Voyager QX analysis software (Brain Innovation, Maastricht, The Netherlands). Preprocessing steps included slice scan time correction, 3-D head motion correction, linear trend removal, and temporal high-pass filtering (cutoff frequency 0.015 Hz) (A. M. Smith et al., 1999). No spatial smoothing was applied to the fMRI data. All subsequent functional images were spatially transformed, up-sampled, and aligned with the anatomical images obtained in the retinotopic mapping session. Functional images from ROI localizer scans were analyzed using the general linear model with Brain Voyager QX. Voxels that were significantly more active during corresponding dynamic blocks ($p < 10^{-4}$, corrected for multiple comparisons with false discovery rate method) were identified on the inflated cortex for each observer. Functional signals in experimental scans were extracted from these voxels, separate for each visual area, and further analyzed by our own numerical routines written in the Java programming platform. This step included converting the functional signals with arbitrary units to percentage change with the average of the entire scan serving as the baseline and event-related averaging for each stimulus condition. At each time point, the event-related average of the static condition is subtracted from that of the dynamic condition (Figure 5), and the average percentage signal change for the last three time points in each condition (from eighth to 12th second after the onset of the stimulus) was computed. After that, the

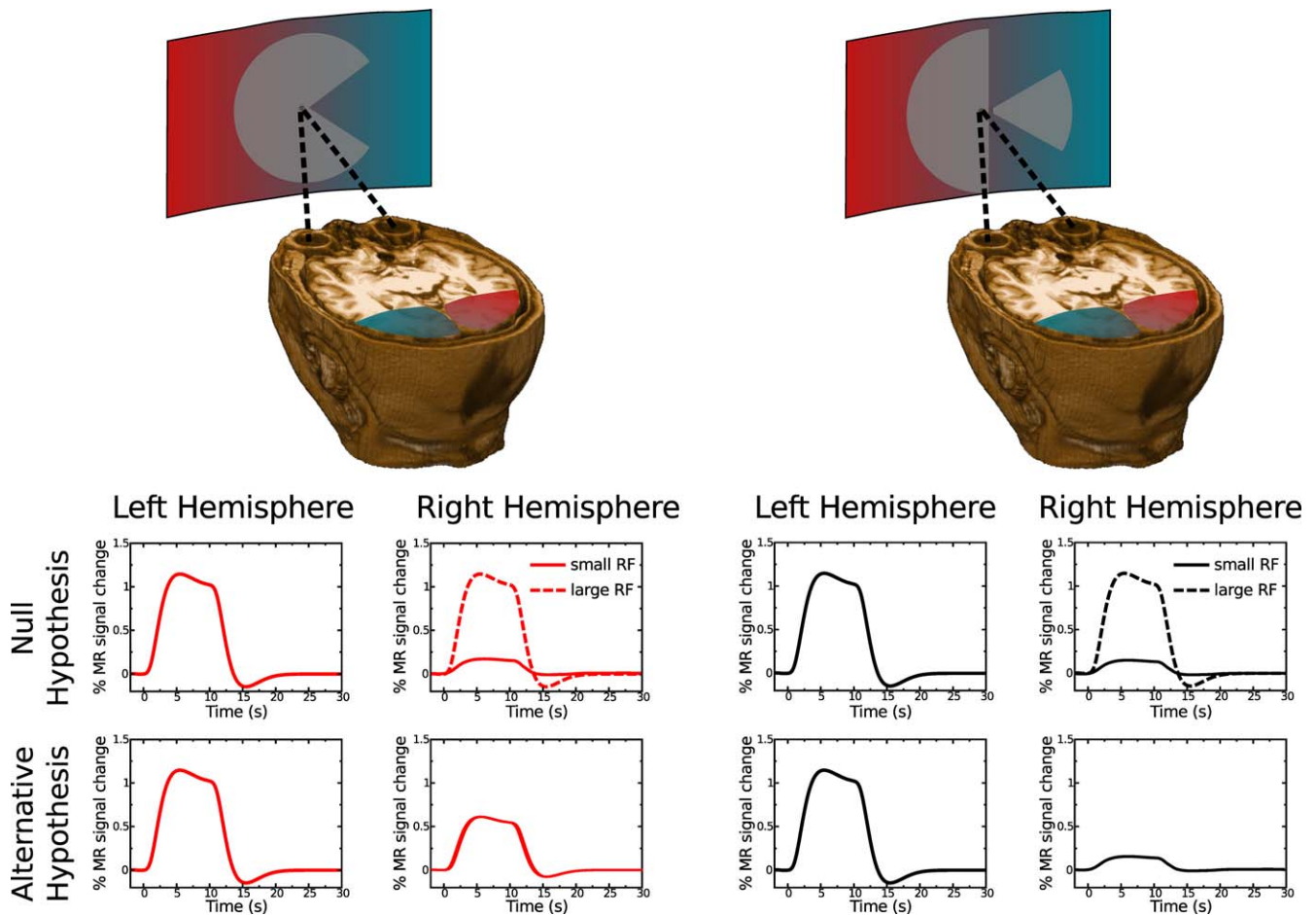


Figure 4. Possible outcomes. If the activity in a visual area is determined solely by localized motion signals on the retina, then we would expect approximately equal activity in that area under both stimulus conditions. This possibility is shown as the null hypothesis in the first row of functional plots. The common activity in the right hemisphere may be either vanishingly small (small RFs, restricted to contralateral VHF) or nonzero (large RFs, expanding into ipsilateral VHF). Alternatively, if the activity of an area depends on the perceived motion of an object unified across visual fields and not only on the localized physical motion signals, then we would expect a larger signal in the right hemisphere for the Pac-man condition than for the control condition. This possibility is presented in the last row. In both the null and alternative hypotheses, we would expect the activity in an area in the left hemisphere to be roughly equal in the Pac-man and control conditions because the local motion energy signals are approximately the same in the right VHF.

difference in percentage signal change between the Pac-man and control conditions were computed (Figure 6). Finally, statistical significance of the difference was tested with repeated measures t test (i.e., whether the signal change in the Pac-man condition was larger than that in the control condition).

Behavioral experiment

We assessed the perceptual effect of the illusory motion stimulus (Pac-man) through a simple behavioral experiment. Stimuli were those used in the fMRI and eye-tracking experiments (described below). Observers participated in four short experiments in which they viewed a given stimulus for 12 s. For this experiment only, dynamic stimuli were used. After each presentation, the

observer had to answer two questions: (a) Did any part of the stimulus *not* move? (b) If yes, please indicate on which side you perceived no motion (left/right). A total of 20 observers participated in the experiment, each performing a single trial (two stimulus conditions \times two attention conditions, five observers per condition).

Eye-tracking experiment

To assess potentially different fixation patterns across conditions (Pac-man–control, static–dynamic) and tasks (fixation task–passive view) eye movements were measured in separate behavioral experiments using an ASL Remote/Desktop Eye Tracking Optics, Model D6, with a sampling rate of 50 Hz. The visual angle of the stimuli were equated to that in the fMRI experiments, resulting

in a screen–eye distance of 64 cm. The observer’s head was stabilized using a custom-made chin rest. The experimental room was dimly lit to optimize pupil and corneal reflection detection by the eye tracker. Eye movements were recorded for the length of one run (250 s, see above) for each experimental condition, resulting in four experimental sessions. The order of sessions was randomized for each observer and usually completed on different days. Six observers participated in the experiment, two of which are authors. We analyzed the horizontal and vertical positions of eye fixations as a function of three factors (Pac-man–control, static–dynamic, fixation task–passive view), combined (MANOVA) and separate (ANOVAs).

Results

What would we expect if the neuronal activity in a cortical area were related solely to the physical characteristics of the image on the retina? In both Pac-man and control conditions, the part of the stimulus in the left VHF is static, and the motion energy in the right VHF is approximately the same. Thus, if receptive field (RF) sizes of neurons were small and restricted to the contralateral VHF in an area in the right hemisphere, we would expect to observe little or no response. Or, if the neurons have larger RFs that expand into the ipsilateral VHF, we would expect a nonzero response to both stimulus conditions. Critically, under both of these possibilities, we would expect the responses to be approximately the same across the two conditions. We call this the null hypothesis. Alternatively, if the neuronal activity were related to perceived motion of the object unified across the two VHFs, then we would expect to find a larger activity in visual areas in the right hemisphere in the dynamic Pac-man condition than in control condition. In both hypotheses, we expect a significant and approximately equal activity in the left hemisphere for both conditions because there is retinal motion in the right VHF with approximately equal local energy. Figure 4 summarizes these expected outcomes.

Figure 5 shows the time course of event-related averaged responses to dynamic Pac-man and control stimuli in the right and left hemisphere visual areas, averaged across all observers and all runs. The top two rows show the results from the right hemisphere; the bottom two rows show the results from the left hemisphere. The top row and the third row show results of the fixation-task condition, in which participants were performing a demanding fixation task to control for the effects of attention (fixation task results: 85% success for Pac-man, 76% for control [difference was significant at $\alpha = 0.05$ level],

RTs = 653 and 665 ms, respectively [difference was not significant at $\alpha = 0.05$ level]). The second and last rows show the results from the passive-view condition. Note that the negative MR signals measured in early visual areas in the right hemisphere are consistent with literature showing reduced blood-oxygen-level dependent activity in the ipsilateral hemisphere to visual stimulation (A. T. Smith et al., 2004; Tootell et al., 1998).

In order to quantitatively assess the effect, we computed the average responses in the last three time points (from the eighth to the 12th second after the onset of the dynamic stimulus) of the Pac-man and control stimuli and computed their difference. In other words, for each ROI, we tested whether the fMRI signal in the Pac-man condition was larger than that in the control condition. Results are presented in Figure 6. First, we notice that both in the fixation-task and the passive-view conditions, activity in the right hemisphere in the dorsal visual areas, V3A/B, LO-1, and MT+, is larger in the Pac-man condition. In the ventral pathway, however, in the fixation-task condition, there is no difference between the two stimulus conditions. The effect is more prominent in the passive-view condition, extending to ventral areas and to LGN. These results support the alternative hypothesis described above in the dorsal pathway in both attention conditions and in the ventral pathway when the attention is not directed away from the stimulus. In the left hemisphere, the responses to Pac-man and control stimuli are usually very similar (Figure 5), but in V1, responses in the control condition are statistically significantly larger than those in the Pac-man condition whereas in LO-1 and V3A/B the opposite is observed (at $\alpha = 0.05$ significance level). This indicates that even though the local physical motion signals were nearly the same, either small low-level differences or the perceived differences between the two stimulus conditions might have affected the activity in the left hemispheres, too.

Behavioral experiment

To establish the perceptual effect, we conducted a behavioral experiment in which we showed observers 12-s clips of oscillating Pac-man or control stimuli and asked (a) did any part of the stimulus *not* move? and (b) if yes, please indicate on which side you perceived no motion (left/right). Under the Pac-man passive-view condition, four out of five participants responded “no” (i.e., “No, there was no part that was *not* moving”); one participant responded “undecided.” Under the Pac-man fixation-task condition, two out of five participants responded “no,” one “undecided,” and two “yes.” All participants who said “yes” indicated that the left part

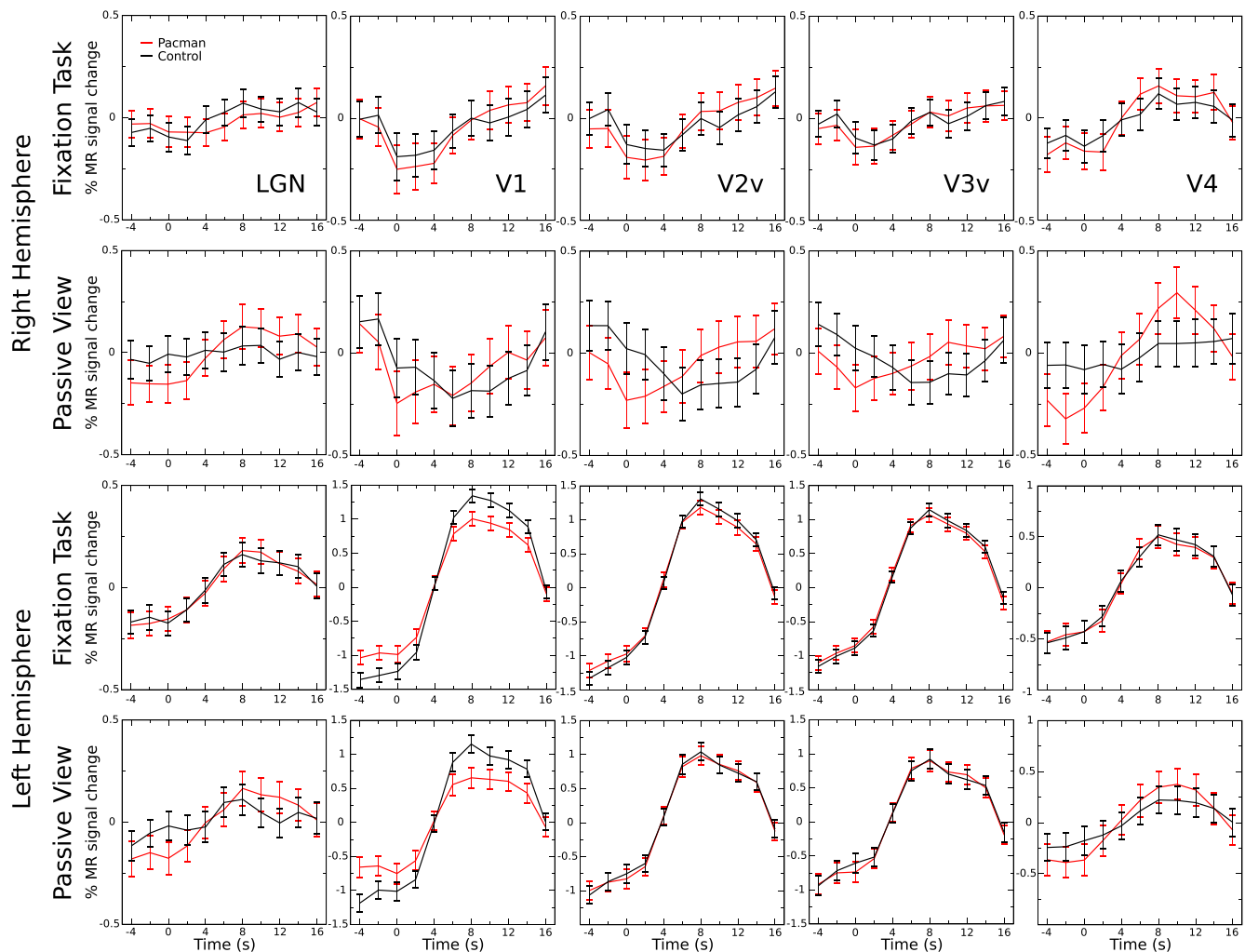


Figure 5. Event-related averages across all observers and all runs. Time point zero indicates the onset of the dynamic block. Red lines show the responses to the Pac-man stimulus; black lines show responses to the control stimulus. Error bars represent the 95% confidence interval. Note that in both conditions we often measured negative fMRI signal in right V1, V2, and V3. This kind of ipsilateral negative activity is consistent with earlier reports in literature.

seemed not to move. Under the control passive-view condition, all five participants responded “yes” and indicated that the left side did not appear to move. Under the control fixation-task condition, three of five participants responded “yes” and two responded “undecided.” Those who said “yes” indicated that the left side appeared to not move. In sum, the left side of the control stimulus is never perceived as moving whereas the left side of Pac-man is nearly always perceived as moving under the passive-view condition and nearly half of the time under the fixation-task condition.

Eye-tracking experiment

Using Wilks’ lambda, there was a significant effect of task (fixation task–passive view) on the horizontal and vertical fixation coordinates (in degrees of visual angle),

$\lambda = 0.947$, $F(2, 964) = 27.18$, $p < 0.0001$. No other factor yielded significant results, and there were no significant interactions at the $\alpha = 0.01$ level. The subsequent three-way ANOVAs for horizontal and vertical fixation coordinates, respectively, yielded a significant main effect of task (fixation task–passive view) on both horizontal, $F(1, 965) = 22.41$, $p < 0.0001$, and vertical, $F(1, 965) = 28.36$, $p < 0.001$, fixations. No other factor yielded significant results, and there were no significant interactions at the $\alpha = 0.01$ level. The mean horizontal fixation location was at -0.46° visual angle (0° being the center of the stimulus) ($SE = 0.03$) for passive viewing and -0.66° visual angle ($SE = 0.032$) for the fixation task. The mean vertical fixation location was at 0.77° visual angle ($SE = 0.042$) (0° being the center of the stimulus) for passive viewing and 0.45° visual angle ($SE = 0.044$) for the fixation task.

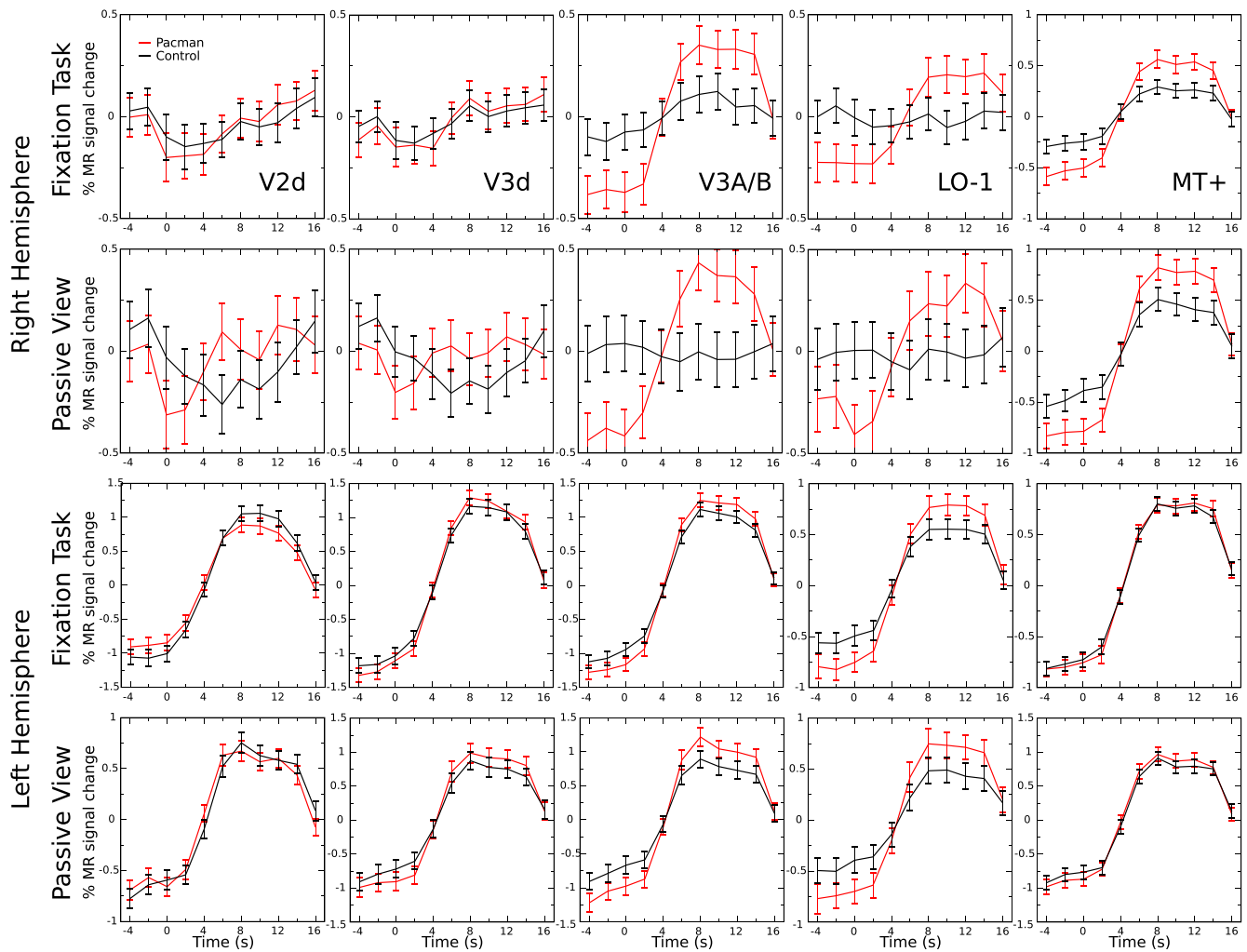


Figure 5. Continued.

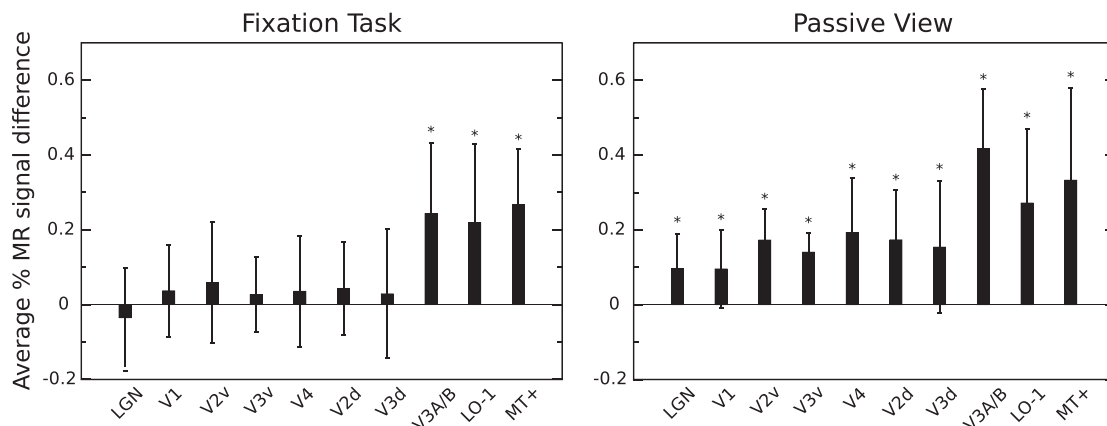


Figure 6. Difference between Pac-man and control conditions in the right hemisphere. The bars show the difference between the averaged signals from 8 to 12 s after the onset of the dynamic blocks for the Pac-man and control stimuli. Error bars are 95% confidence interval. A “*” indicates significance at $\alpha = 0.05$ level. Dorsolateral occipital areas are differentially more active during the presentation of oscillating Pac-man stimulus than that of control stimulus in both the passive-view and fixation-task conditions whereas early visual areas, including LGN, are differentially more active only in the passive-view condition.

Discussion

We found that when attention is directed away from the object, the right hemisphere dorsolateral occipital areas V3A/B, LO-1, and MT+ were differentially more active during the dynamic presentation of the Pac-man stimulus than during presentation of the control stimulus even though we expected no difference between them in the null hypothesis. When attention was not directed away from the object, all areas investigated in the right hemisphere, including LGN, were differentially more active to the oscillating Pac-man stimulus. In other words, we found that the neuronal activity correlated with perceived motion, not only retinal motion. These findings imply a strong interhemispheric integration, leading to perceptual experience of a unified global motion across VHFs in all areas investigated with the strongest effects observed in the dorsolateral occipital areas. The order of the effect is largely consistent with what has been reported in literature in response to actual motion (Tootell et al., 1997). Moreover, the results show that the effect is strongly attention-dependent in early visual areas. Lateral occipital areas, including MT+, on the other hand, are less affected by attention.

Lateral occipital areas are known to respond to ipsilateral stimulation (A. T. Smith et al., 2004; Tootell et al., 1998) and have been implicated to account for unified visual field perception in previous studies. Liu et al. (2009) found evidence that bilateral integration took place in both V1 and LOT regions, particularly in MT+, but the bilateral LOT activity preceded the bilateral V1 activity (see also Vanni et al., 2004). These results are consistent with our findings here; however, because of the coarser temporal sampling in fMRI, we do not have information about the timing of activity in different areas. MT+ is densely myelinated with thicker axons (Born & Bradley, 2005; Clarke & Miklosy, 1990) and has a very fast response rate to retinal input that is comparable to that in V1 (Born & Bradley, 2005; Lamme & Roelfsema, 2000). The fast connection from retina to MT+ could either be through the fast M pathway or direct inputs through superior colliculus, pulvinar, and LGN (Lamme & Roelfsema, 2000; Sincich, Park, Wohlgenuth, & Horton, 2004). Given the large receptive fields of its neurons and its suggested role in whole object motion perception and estimation of pattern motion by integrating V1 inputs (Born & Bradley, 2005), MT+ could be one of the first areas in which bilateral information is pooled (Vanni et al., 2004) and feedback is provided to earlier areas, including V1.

Surprisingly, we found that the activity of LGN is correlated with both perceived and retinal motion when attention is toward the object. The nature of this activity is not readily clear. There is a direct ascending

LGN–MT+ connection through the K pathway (Born & Bradley, 2005; Sincich et al., 2004), but this connection is not known to be symmetric. In an alternative route, extrastriate projecting LGN neurons receive input from the superior colliculus (SC), and the SC receives descending input from MT (Britten, 2004). Meanwhile, the pulvinar, a subcortical structure that is implicated with pattern motion processing, receives ascending input from the SC and has a symmetrical connection with MT (Britten, 2004; Casanova, 2004). It is possible that MT+ provides feedback to the SC and pulvinar, and as a result, the activity in LGN increases. The rise in the activity of these subcortical areas could partly be the cause of increased activity in V1, V2, and V3 in addition to direct feedback from MT to those cortical areas.

Callosal communications seem to be critical for an integrated visual perception as revealed by split-brain patient studies (Gazzaniga, 2000; Naikar & Corballis, 1996). In healthy humans, Genç, Bergmann, Singer, and Kohler (2011), using fMRI and DTI, have shown that the direction of perceived motion in a motion quartet stimulus depended strongly on callosal connections between the two MTs but not between the two V1s. This highlights the importance of MT for global motion perception in line with our results. Studies on callosal connections suggest rich connections at MT (Clarke & Miklosy, 1990; Genç et al., 2011) and at the V3–V3A/B border (Clarke & Miklosy, 1990) whereas V1, V2, and V3 have no callosal connections except regions retinotopically corresponding to vertical meridian (Clarke & Miklosy, 1990). This seems computationally efficient because the most important information for unifying the two VHFs lies along the vertical meridians. MT also has direct reciprocal connections with V1, and receives input from V2 and V3 (Born & Bradley, 2005; Britten, 2004). However, given the pattern of activity we found in ipsilateral V1, V2, and V3, the differentially increased activity in MT cannot be explained by these connections. Thus, the bilateral MT+ activity must be caused either by callosal interactions or direct subcortical input.

Even though motion is a salient stimulus and often perceived without attention, activity of MT+ is still affected by attention (Born & Bradley, 2005; Crespi et al., 2011; Culham, He, Dukelow, & Verstraten, 2001; O'Craven, Rosen, Kwong, Treisman, & Savoy, 1997; Saenz et al., 2002). Moreover, attention can more strongly modulate motion-related activity in early visual areas (Gandhi et al., 1999) as well as in LGN (O'Connor, Fukui, Pinsk, & Kastner, 2002). We found increased activity in ipsilateral early visual areas only when attention was not directed away from the stimuli, and participants reported being aware of perceiving global motion of a unified object only under this

attentional condition. Therefore, one can argue that the activity of early visual areas is critical for perceptual experience of global motion of an object unified across VHF's and that the activity of dorsolateral areas alone may not be enough for this perceptual experience. This argument is consistent with the results of previous studies in literature (Lamme & Roelfsema, 2000; Zeki & Ffytche, 1998).

Psychophysical studies suggest that RF sizes of MT neurons can be as large as 70° under some conditions (Burr, 2013; Burr, Morrone, & Vaina, 1998; Morrone, Burr, & Vaina, 1995). Moreover, the MT RF characteristics are very flexible, particularly RF size and position, and visual field representations are strongly affected by spatial attention (Burr et al., 2009; Crespi et al., 2011; Womelsdorf et al., 2006; also see Hansen et al., 2007). Moreover, object-based attention (O'Craven, Downing, & Kanwisher, 1999; Roelfsema, Lamme, & Spekreijse, 1998), distributed focus of spatial attention to multiple regions (McMains & Somers, 2004, 2005) or feature-based attention (Saenz et al., 2002; Treue & Trujillo, 1999) could all be important mechanisms for combining the visual stimuli across VHF's in MT.

Our results are not in complete agreement with the results of Ban et al. (2006), who found correlates of interhemispheric integration in context-dependent shape perception in early visual areas, including the primary visual cortex, as well as in V2d and V3d when attention was directed away from the object. This indicates that the cortical mechanisms underlying interhemispheric integration in shape perception may be different than those for motion perception.

Results of behavioral experiments show that, under the passive-view condition, the left side of Pac-man but not of the control stimulus is perceived as moving. In parallel to this finding, there are differences in fMRI signal in all visual areas. On the other hand, under the fixation-task condition, the left side of Pac-man is not always perceived as moving, and the fMRI signal difference between Pac-man and control is reduced in nearly all cortical areas investigated.

We found no difference in eye-movement patterns across the static and dynamic conditions of the control and Pac-man stimuli, only attention has modulated the eye fixations, bringing them closer to the center of the stimulus when observers performed a demanding fixation task. However, it is still possible that, even though the eye movements are similar, they might have affected the signal differently across conditions. This could have affected results, especially in areas with very small RF sizes, such as V1/2, leading to the differences between our study and the Ban et al. (2006) study. Note that there was a small but statistically significant difference between the success rates of the fixation task under Pac-man and control conditions (85% for pac-

man, 76% for control) but not for reaction times. This suggests that the fixation task could be slightly easier for the Pac-man condition and have influenced the outcomes under the fixation-task condition (this could affect only the conclusions in areas in which the Pac-man signal was measured larger than control, i.e., in LOT areas V3A/B, MT+, and LO1). However, given that there were no differences in eye movements and little effect of spatial attention on the results in LOT areas, it is unlikely that this difference played any major role in the results.

Conclusions

Taken together, our results imply that bilateral activity of both dorsolateral occipital areas and early areas play a role in interhemispheric integration and perceptual experience of a unified visual field. Our results are consistent with a model in which first lateral occipital areas V3A/B, LO-1, and MT+ respond bilaterally (through callosal connections or through subcortical input), and their feedback signals lead to increased bilateral neuronal responses in early areas.

Keywords: global motion perception, interhemispheric integration, fMRI, visual brain, perceptual experience of unified visual field

Acknowledgments

Supported by the Scientific and Technological Research Council of Turkey “1001” grant (108K398), European Commission “Marie Curie International Reintegration” grant (PIRG-GA-2008-239467), and Turkish Academy of Science “Distinguished Young Investigator” award. An earlier pilot version of the study was supported by the University of Minnesota, Center for Magnetic Resonance Research through the NIH Neuroscience Blueprint Interdisciplinary Center Core Grant (P30 NS057091). HB and KD were on sabbatical leave supported by a Fulbright fellowship in University of California, San Diego at the time of publication of the study.

Commercial relationships: none.

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