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 & Miklossy, 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 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 VHFs should be differentially more active in the

$30^\circ \times 22^\circ$ of visual angle. The maximum luminance

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;

seemed not to move. Under the control passive-view

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 & Miklossy, 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 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 VHFs 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). Moreoever, 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 VHFs 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.

O'Craven, K. M., Rosen, B. R., Kwong, K. K., Treisman, A., & Savoy, R. L. (1997). Voluntary attention modulates fMRI activity in human MT MST. Neuron, 18(4), 591–598.

Roelfsema, P. R., Lamme, V. A., & Spekreijse, H. (1998). Object-based attention in the primary visual cortex of the macaque monkey. Nature, 395(6700), 376–381.

Saenz, M., Buracas, G. T., & Boynton, G. M. (2002). Global effects of feature-based attention in human visual cortex. Nature Neuroscience, 5(7), 631–632.

Sereno, M., Dale, A., Reppas, J., Kwong, K., Belliveau, J., Brady, T., . . . Tootell, R. (1995). Borders of multiple visual areas in humans revealed by functional magnetic resonance imaging. Science, 268(5212), 889–893.

Sincich, L. C., Park, K. F., Wohlgemuth, M. J., & Horton, J. C. (2004). Bypassing V1: A direct geniculate input to area MT. Nature Neuroscience, 7(10), 1123–1128.

Smith, A. M., Lewis, B. K., Ruttimann, U. E., Ye, F. Q., Sinnwell, T. M., Yang, Y., . . . Frank, J. A. (1999). Investigation of low frequency drift in fMRI signal. Neuroimage, 9(5), 526–533.

Smith, A. T., Williams, A. L., & Singh, K. D. (2004). Negative bold in the visual cortex: Evidence against blood stealing. Human Brain Mapping, 21(4), 213–220.

Tootell, R. B., Mendola, J. D., Hadjikhani, N. K., Ledden, P. J., Liu, A. K., Reppas, J. B., . . . Dale A. M. (1997). Functional analysis of V3a and related areas in human visual cortex. The Journal of Neuroscience, 17(18), 7060–7078.

Tootell, R. B., Mendola, J. D., Hadjikhani, N. K., Liu, A. K., & Dale, A. M. (1998). The representation of the ipsilateral visual field in human cerebral cortex. Proceedings of the National Academy of Sciences, USA, 95(3), 818–824.

Tootell, R. B., Switkes, E., Silverman, M. S., & Hamilton, S. L. (1988). Functional anatomy of macaque striate cortex. II. Retinotopic organization. The Journal of Neuroscience, 8(5), 1531–1568.

Treue, S., & Trujillo, J. C. M. (1999). Feature-based attention influences motion processing gain in macaque visual cortex. Nature, 399(6736), 575–579.

Vanni, S., Dojat, M., Warnking, J., Delon-Martin, C., Segebarth, C., & Bullier, J. (2004). Timing of interactions across the visual field in the human cortex. Neuroimage, 21(3), 818–828.

Womelsdorf, T., Anton-Erxleben, K., Pieper, F., & Treue, S. (2006). Dynamic shifts of visual receptive fields in cortical area MT by spatial attention. Nature Neuroscience, 9(9), 1156–1160.

Zeki, S., & Ffytche, D. (1998). The Riddoch syndrome: Insights into the neurobiology of conscious vision. Brain, 121(1), 25–45.