Neuron
Article

Neural Activities in V1 Create a Bottom-Up Saliency Map

Xilin Zhang,[1] Li Zhaoping,[4] Tiangang Zhou,[5] and Fang Fang[1,2,3,*]
[1]Department of Psychology and Key Laboratory of Machine Perception (Ministry of Education)
[2]Center for Life Sciences
[3]IDG/McGovern Institute for Brain Research
Peking University, Beijing 100871, China
[4]Department of Computer Science, University College London, London WC1E 6BT, UK
[5]State Key Laboratory of Brain and Cognitive Science, Institute of Biophysics, Chinese Academy of Sciences, Beijing 100101, China
*Correspondence: ffang@pku.edu.cn
DOI 10.1016/j.neuron.2011.10.035

SUMMARY

The bottom-up contribution to the allocation of exogenous attention is a saliency map, whose neural substrate is hard to identify because of possible contamination by top-down signals. We obviated this possibility using stimuli that observers could not perceive, but that nevertheless, through orientation contrast between foreground and background regions, attracted attention to improve a localized visual discrimination. When orientation contrast increased, so did the degree of attraction, and two physiological measures: the amplitude of the earliest (C1) component of the ERP, which is associated with primary visual cortex, and fMRI BOLD signals in areas V1–V4 (but not the intraparietal sulcus). Significantly, across observers, the degree of attraction correlated with the C1 amplitude and just the V1 BOLD signal. These findings strongly support the proposal that a bottom-up saliency map is created in V1, challenging the dominant view that the saliency map is generated in the parietal cortex.

INTRODUCTION

Because neural resources are severely limited, only a very small fraction of visual inputs can reach all the way to perception. One of the main mechanisms of selection involves directing attention to a visual location, either overtly or covertly, without a shift in gaze. Attention may either be directed under voluntary control according to top-down goals, such as when directing gaze to an interesting book, or be attracted automatically by bottom-up stimuli, such as when the sudden appearance of a cat distracts one from reading. Throughout this study, we use the term salience to refer to this bottom-up attraction of exogenous attention. The regions of the brain responsible for top-down selection are well known, and include the frontal eye fields (FEF), dorsomedial prefrontal cortex, and posterior parietal cortex (PPC) (Corbetta and Shulman, 2002; Kastner and Ungerleider, 2000; Serences and Yantis, 2006). However, although bottom-up selection is typically faster and more potent (Jonides, 1981; Nakayama and Mackeben, 1989), there are controversies concerning the brain regions involved.

It is generally thought that the brain constructs a saliency map of visual space, with the activity at a location explicitly reporting the strength of its bottom-up attentional attraction (Koch and Ullman, 1985) so that it can be directly read out to guide attentional shifts before and after combining with top-down control factors. Based on neurophysiological and imaging studies, brain regions proposed to realize this saliency map have included the superior colliculus (Kustov and Robinson, 1996; Fecteau and Munoz, 2006), pulvinar (Shipp, 2004), parietal cortex (Bisley and Goldberg, 2010; Geng and Mangun, 2009; Gottlieb et al., 1998), V4 (Mazer and Gallant, 2003), and FEF (Serences and Yantis, 2007; Thompson and Bichot, 2005). However, neural activities in all these areas are also involved in top-down attentional direction. It is therefore unclear whether the observed neural correlates of saliency are relayed from brain regions upstream along the visual pathway, and whether they are the cause or the consequence of selection. In particular, because salient visual inputs typically enter awareness, it is difficult to determine whether the observed neural activities represent saliency as such, as opposed to being caused by the consequent perception of the selected stimuli.

A dominant view of the saliency map (Itti and Koch, 2001; Koch and Ullman, 1985; Wolfe, 1994) presumes that saliency results from pooling different visual features, being independent of whether the feature distinction making a location salient is in color, orientation, or other features. Hence, previous attempts to find the saliency map have typically concentrated in higher cortical areas, particularly the parietal cortex, whose neurons, unlike those in primary visual cortex (V1), are less selective to specific visual features.

By contrast, Li (1999, 2002) proposed that V1 (which, notably, projects directly and indirectly to all the previously proposed brain regions for the saliency map [Shipp, 2004]) creates a saliency map via intracortical interactions that are manifest in contextual influences (Allman et al., 1985). According to this responses to the other locations), regardless of the preferred feature of the most responsive neuron. Many psychophysical predictions arising from this proposal have been confirmed (Koene and Zhaoping, 2007; Zhaoping and May, 2007). One particularly interesting confirmation is that an eye of origin singleton, e.g., a bar presented to the left eye among many other bars presented to the right eye, can distract attention away from a very salient visual search target (e.g., a uniquely oriented bar presented to the right eye), even when observers cannot distinguish this eye of origin singleton from other items (Zhaoping, 2008). This supports the V1 theory, because the reason that observers cannot distinguish this singleton is that the eye of origin feature is not represented in any cortical area except V1. Indeed, Wolfe and Franzel (1988) reported that observers found it impossible to find a visual search target defined by its unique eye of origin. The apparent contradiction between the inaccessibility to search of the eye of origin feature, and yet its ability to attract attention can be resolved by realizing that attentional attraction by an input feature can be dissociable from the recognition of this feature needed for visual search.

To determine which cortical area realizes the saliency map, it is important to probe bottom-up attraction free from top-down influences (e.g., those arising from feature and object recognition). One way to do this is to use stimuli that are presented so briefly bars in a regular Manhattan grid in the lower visual field on a dark screen. All bars were identically oriented except for a foreground region of 2 × 2 bars of another orientation. The foreground region was at 7.2° eccentricity in either the lower left or the lower right quadrant. The orientation of the background bars was randomly chosen from 0° to 180°. There were five possible orientation contrasts between the foreground bars and the background bars: 0°, 7.5°, 15°, 30°, and 90°. A nonzero orientation contrast could possibly make the foreground region salient enough to attract attention. To isolate the bottom-up saliency signal, we minimized top-down influences by presenting the texture stimuli very briefly and subsequently masking them using a high luminance mask (Figure 1B). Subjects reported that they were unaware of the texture stimuli and could not detect even by forced choice which quadrant contained the foreground region. The percentages of correct detection (mean ± SEM) were 50.5 ± 0.8%, 50.0 ± 0.8%, 49.8 ± 0.8%, and 50.4 ± 0.7% for orientation contrasts of 7.5°, 15°, 30°, and 90°, respectively, statistically indistinguishable from the chance level (see Experimental Procedures).

Psychophysical Experiment

To assess the saliency (i.e., the degree of attentional attraction) of the invisible foreground region, we used a modified version of the Posner paradigm to measure the cueing effect induced by this foreground (Jiang et al., 2006; Posner et al., 1980), as shown in Figure 1C. The texture stimulus was presented for 50 ms (ms), followed by a 100 ms mask and then a 50 ms fixation on a blank screen. Afterward, a two-dot probe appeared for 50 ms at either the foreground location (the valid cue condition) or its contralateral counterpart (the invalid cue condition). Subjects were asked to press one of two buttons to indicate whether the upper dot was to the left or right of the lower dot (i.e., a vernier task). The saliency of the foreground region was quantified by the attentional cueing effect, i.e., the difference between the accuracy of the performance in the probe task in the valid cue condition, and that in the invalid cue condition. When there was an orientation contrast between the foreground

7.5°, 15°, and 90° (Figure 3D). C1 amplitude differences were submitted to one-way repeated-measures ANOVA, which showed that the main effect of orientation contrast was significant ($F_{2, 28} = 44.392$, $p < 0.001$). Post hoc paired t tests revealed that the C1 amplitude difference increased with the orientation contrast (7.5° versus 15°: $t_{14} = 4.793$, $p = 0.001$; 15° versus 90°: $t_{14} = 6.015$, $p < 0.001$), parallel to the attentional attraction in Figure 2. This suggests that the C1 amplitude and the attentional attraction might be closely related. An ERP experiment that was identical, except for relocating the stimuli from the lower to upper visual field, provided the same qualitative conclusion (Figure S2), while showing a reversal of the C1 polarity. This suggests that the C1 originates from V1 (Figure S349.5684Tm()Tj/T101Tf0.7098Tc89.6o ,5 significantly correlated with the C1 amplitude difference for orientation contrasts of 15° (r = 0.758, p = 0.001) and 90° (r = 0.798, $p < 0.001$), but not for the orientation contrast of 7.5° (r = 0.263, p = 0.343) (Figure 5A) (similar correlations were found using stimuli in the upper visual field; see Figure S4). It was also significantly correlated with the BOLD signal difference in V1 for orientation contrasts of 15° (r = 0.754, p = 0.012) and 90° (r = 0.924, $p < 0.001$), but not for the orientation contrast of 7.5° (r = 0.260, p = 0.468) (Figure 5B). However, no significant correlation was found between the attentional effect and the BOLD signal difference in the other cortical areas (Figure 5C). Moreover, for the orientation contrast of 90° (but not other contrasts), the correlation coefficient in V1 was (marginally) significantly larger than those in other areas (p = 0.076 for V2 and all

t
fr

mo

One should note that according to the V1 saliency hypothesis, saliency of a visual location is determined by its highest evoked V1 response relative to those evoked by other locations. In other words, saliency is determined by the relative rather than absolute levels of V1 responses. This perspective is necessary to understand why V1 responses to a non-salient conjunctive search target in an inhomogeneous background (e.g., a red-vertical bar among many green-vertical and red-horizontal bars) is not necessarily lower than those to a salient pop-out target against a homogeneous background (e.g., a red-vertical bar among red-horizontal bars, Hegde and Felleman, 2003). As explained in the analysis above, due to the intracortical iso-orientation suppression, and iso-feature (e.g., iso-color) suppression in general (Li, 1999), the V1 population responses to a homogeneous background are quite low, and lower than those to a less homogeneous background, such as the background for the conjunction target. Therefore, the unique feature target can be more salient than the unique conjunctive target even when the former evokes a lower V1 response, provided that the population responses to the homogeneous background of the unique feature target are sufficiently lower still. The dependence of saliency on the relative rather than the absolute levels of neural responses means that one has to look at the population responses, rather than a single neuron response, to assess saliency in a scene (Hegde and Felleman, 2003). Alternatively, one may compare the relative saliency of two items from their evoked V1 responses only when they share the same or comparable background stimuli. The latter is the case in our cueing stimuli, in which different pop-out foregrounds share the same homogeneous background texture.

Our data suggest that the neural correlates of saliency observed in intermediate and higher cortical areas, such as V4 or the parietal cortex, may be relayed from V1 rather than created within these areas. Parietal regions are known to integrate bottom-up and top-down attentional guidance (Bisley and Goldberg, 2010). Meanwhile, consistent with the idea that saliency is computed outside V4, V4 lesions impair the selection of the non-salient but not the salient objects in the scene (Schiller and Lee, 1991), and modulations in V4 responses to salient locations are eliminated when monkey prepares a goal related saccade elsewhere (Burrows and Moore, 2009). Similarly, lesions of the frontal eye field disrupt visual pursuit (Lynch, 1987) but barely affect input-driven saccades to salient locations (Schiller et al., 1987). Because neural correlates of saliency in these areas are generally evoked by highly visible inputs, and because the saliency signal was absent in IPS in our data which generated saliency using invisible stimuli, it remains unclear whether saliency is only relayed to parietal regions when the visual input responsible is perceptually visible.

Note that we distinguish a cortical area (V1) creating the saliency map from those that read out or inherit the saliency values from earlier regions along the visual pathway. Hence, for example, superior colliculus and parietal cortex, both receiving inputs from V1 directly or indirectly, may be viewed as areas reading out the saliency values to execute attentional shifts or to combine with top-down factors (note that retinal drives to SC do not lead to visual evoked saccades) (Schiller, 1998). Meanwhile, retina and LGN cannot be viewed as saliency maps. Of course, saliency values can be computed from their population responses (as indeed in the proposal that this happens via V1 intracortical mechanisms). However, the responses in these regions lack the significant context dependence required for saliency (e.g., that a vertical bar is salient in a background of horizontal, but not vertical, bars).

Our findings can be viewed as identifying V1 as the neural substrate of the early component of attentional selection. There has been over half a century of debate about the extent to which exogenous attentional selection occurs early or late, i.e., before or after visual inputs is perceptually identified (see Yantis and Johnston [1990] for a review). In principle, both top-down and bottom-up selection could occur at early or late stages. Most evidence discriminating early versus late selection has come from behavioral studies, whereas physiological evidence from ERP and single unit recordings has mainly implicated the extra-striate cortices in early selection (Luck et al., 1994; Moran and Desimone, 1985). V1 neurons are tuned only to primitive features rather than complex objects, and they respond even to stimulus features that are invisible to awareness. Thus, identifying V1 as the neural substrate of saliency confirms that selection can occur before input identification and awareness. Locating bottom-up selection in V1 invites us to re-evaluate the brain network for attention control.

EXPERIMENTAL PROCEDURES

Subjects

A total of 22 human subjects (7 male, 20 35 years old) were involved in the study. All of them participated in the psychophysical experiment. Sixteen and ten of them participated in the ERP and fMRI experiments, respectively. One subject in the ERP experiment was excluded because of frequent eye blinks. All subjects were naive to the purpose of the study except for two subjects (two of the authors). They were right-handed, reported normal or corrected to normal vision, and had no known neurological or visual disorders. They gave written, informed consent in accordance, and our procedures and protocols were approved by the human subjects review committee of Peking University.

Stimuli

Each texture stimulus (Figure 1A) had a regular Manhattan grid of 15 × 29 low-luminance bars (3.4 cd/m^2), presented in the lower visual field on a dark screen (1.6 cd/m^2). Each bar was a rectangle of $0.075^\circ \times 0.75^\circ$ in visual angle. The center-to-center distance between the bars was 1.13°. All bars were identically oriented except for a foreground region of 2 × 2 bars with another orientation in either the lower left or the lower right quadrant. The foreground region was centered at 7.2° eccentricity. The orientation of the background bars was randomly chosen from 0° to 180°. There were five possible orientation contrasts between the foreground bars and the background bars: 0°, 7.5°, 15°, 30°, and 90°

attention. Then a two-dot probe was presented for 50 ms at randomly either the foreground region (valid cue condition) or its contralateral counterpart a foreground region (i.e., 2 × 2 bars) like in our experiments. The model mechanisms include (1), direct inputs to V1 neurons from each bar according to the classical receptive fields, and (2), interactions between V1 neurons by the intracortical connections implementing contextual influences (such as surround suppression) of the surround to the neural responses. At each grid location, the maximum response from all pyramidal model neurons was obtained. This maximum was averaged over all simulation time steps within 50 ms (simulated by five membrane time constant of the model neurons). The saliency of each grid location is the Z-score of this maximum obtained as follows: take the difference between this maximum and the average of the maximums over all grid locations and then divide it by the standard deviation of all the maximums (Li, 1999). Saliency in the foreground region is the maximum of the Z-scores over the 4 × 4 bar region centered on the foreground region. The result for each orientation contrast (7.5°, 15°, 30°, and 90°) as plotted in Figure 2 was obtained by averaging the foreground region saliency from 24 simulations for 24 different background bar orientations evenly distributed between 0° and 180°. The saliency of the foreground region should be directly related to the strength of its attentional attraction (i.e., its cueing effect).

SUPPLEMENTAL INFORMATION

Supplemental Information includes four figures and can be found with this article online at doi:10.1016/j.neuron.2011.10.035.

ACKNOWLEDGMENTS

We are grateful to Peter Dayan for reading the manuscript with helpful comments and Yan Song for help with dipole source localization. This work was supported by the Ministry of Science and Technology of China (2011CBA00405 and 2010CB833903), the National Natural Science Foundation of China (Project 30925014, 30870762, 90920012, 30921064, and 90820307), the Fundamental Research Funds for the Central Universities, and the Gatsby Charitable Foundation.

Accepted: October 31, 2011
Published: January 11, 2012

REFERENCES

Ales, J.M., Yates, J.L., and Norcia, A.M. (2010). V1 is not uniquely identified by polarity reversals of responses to upper and lower visual field stimuli. Neuroimage 52, 1401–1409.

Allman, J., Miezin, F., and McGuinness, E. (1985). Stimulus specific responses from beyond the classical receptive field: neurophysiological mechanisms for local-global comparisons in visual neurons. Annu. Rev. Neurosci. 8, 407–430.

Bao, M., Yang, L., Rios, C., He, B., and Engel, S.A. (2010). Perceptual learning increases the strength of the earliest signals in visual cortex. J. Neurosci. 30, 15080–15084.

Bisley, J.W., and Goldberg, M.E. (2010). Attention, intention, and priority in the parietal lobe. Annu. Rev. Neurosci. 33, 1–21.

Buracas, G.T., and Boynton, G.M. (2002). Efficient design of event-related fMRI experiments using M-sequences. Neuroimage 16, 801–813.

Burrows, B.E., and Moore, T. (2009). Influence and limitations of popout in the selection of salient visual stimuli by area V4 neurons. J. Neurosci. 29, 15169–15177.

Clark, V.P., and Hillyard, S.A. (1996). Spatial selective attention affects early extrastriate but not striate components of the visual evoked potential. J. Cogn. Neurosci. 8, 387–402.

Clark, V.P., Fan, S., and Hillyard, S.A. (1995). Identification of early visually evoked potential generators by retinotopic and topographic analysis. Hum. Brain Mapp. 2, 170–187.

Corbetta, M., and Shulman, G.L. (2002). Control of goal-directed and stimulus-driven attention in the brain. Nat. Rev. Neurosci. 3, 201–215.

Di Russo, F., Martínez, A., Sereno, M.I., Pitzalis, S., and Hillyard, S.A. (2002). Cortical sources of the early components of the visual evoked potential. Hum. Brain Mapp. 15, 95–111.

Engel, S.A., Glover, G.H., and Wandell, B.A. (1997). Retinotopic organization in human visual cortex and the spatial precision of functional MRI. Cereb. Cortex 7, 181–192.

Fang, F., Boyaci, H., Kersten, D., and Murray, S.O. (2008). Attention-dependent representation of a size illusion in human V1. Curr. Biol. 18, 1707–1712.

Fecteau, J.H., and Munoz, D.P. (2006). Salience, relevance, and firing: a priority map for target selection. Trends Cogn. Sci. (Regul. Ed.) 10, 382–390.

Frey, H.P., Kelly, S.P., Lalor, E.C., and Foxe, J.J. (2010). Early spatial attentional modulation of inputs to the fovea. J. Neurosci. 30, 4547–4551.

Friston, K.J., Holmes, A.P., Worsley, K.J., Poline, J.B., Frith, C., and Frackowiak, R.S.J. (1995). Statistical parametric maps in functional imaging: a general linear approach. Hum. Brain Mapp. 2, 211–224.

Geng, J.J., and Mangun, G.R. (2009). Anterior intraparietal sulcus is sensitive to bottom-up attention driven by stimulus salience. J. Cogn. Neurosci. 21, 1584–1601.

Gilbert, C.D., and Wiesel, T.N. (1983). Clustered intrinsic connections in cat visual cortex. J. Neurosci. 3, 1116–1133.

Gottlieb, J.P., Kusunoki, M., and Goldberg, M.E. (1998). The representation of visual salience in monkey parietal cortex. Nature 391, 481–484.

Gratton, G., Coles, M.G.H., and Donchin, E. (1983). A new method for off-line removal of ocular artifact. Electroencephalogr. Clin. Neurophysiol. 55, 468–484.

Harrison, S.A., and Tong, F. (2009). Decoding reveals the contents of visual working memory in early visual areas. Nature 458, 632–635.

Hegde, J., and Felleman, D.J. (2003). How selective are V1 cells for pop-out stimuli? J. Neurosci. 23, 9968–9980.

Hupe, J.M., James, A.C., Girard, P., and Bullier, J. (2001). Response modulations by static texture surround in area V1 of the macaque monkey do not depend on feedback connections from V2. J. Neurophysiol. 85, 146–163.

Itti, L., and Koch, C. (2001). Computational modelling of visual attention. Nat. Rev. Neurosci. 2, 194–203.

Jeffreys, D.A., and Axford, J.G. (1972). Source locations of pattern-specific components of human visual evoked potentials. I. Component of striate cortical origin. Exp. Brain Res. 16, 1–21.

Jiang, Y., Costello, P., Fang, F., Huang, M., and He, S. (2006). A gender- and sexual orientation-dependent spatial attentional effect of invisible images.

Luck, S.J., Hillyard, S.A., Mouloua, M., Woldorff, M.G., Clark, V.P., and Hawkins, H.L. (1994). Effects of spatial cuing on luminance detectability: psychophysical and electrophysiological evidence for early selection. J. Exp. Psychol. Hum. Percept. Perform. 20, 887–904.

Lynch, J.C. (1987). Frontal eye field lesions in monkeys disrupt visual pursuit. Exp. Brain Res. 68, 437–441.

Marcus, D.S., and Van Essen, D.C. (2002). Scene segmentation and attention in primate cortical areas V1 and V2. J. Neurophysiol. 88, 2648–2658.

Martínez, A., Anllo-Vento, L., Sereno, M.I., Frank, L.R., Buxton, R.B., Dubowitz, D.J., Wong, E.C., Hinrichs, H., Heinze, H.J., and Hillyard, S.A. (1999). Involvement of striate and extrastriate visual cortical areas in spatial attention. Nat. Neurosci. 2, 364–369.

Mazer, J.A., and Gallant, J.L. (2003). Goal-related activity in V4 during free viewing visual search. Evidence for a ventral stream visual salience map. Neuron 40, 1241–1250.

Moran, J., and Desimone, R. (1985). Selective attention gates visual processing in the extrastriate cortex. Science 229, 782–784.

Nakayama, K., and Mackeben, M. (1989). Sustained and transient components of focal visual attention. Vision Res. 29, 1631–1647.

Nothdurft, H.C., Gallant, J.L., and Van Essen, D.C. (1999). Response modulation by texture surround in primate area V1: correlates of "popout" under anesthesia. Vis. Neurosci. 16, 15–34.

Posner, M.I., Snyder, C.R.R., and Davidson, B.J. (1980). Attention and the detection of signals. J. Exp. Psychol. 109, 160–174.

Ress, D., and Heeger, D.J. (2003). Neuronal correlates of perception in early visual cortex. Nat. Neurosci. 6, 414–420.

Rockland, K.S., and Lund, J.S. (1983). Intrinsic laminar lattice connections in primate visual cortex. J. Comp. Neurol. 216, 303–318.

Schiller, P.H. (1998). The neural control of visually guided eye movements. In Cognitive Neuroscience of Attention, J. Richards, ed. (Hillsdale, NJ: Lawrence Erlbaum Associates), pp. 3–50.

Schiller, P.H., and Lee, K. (1991). The role of the primate extrastriate area V4 in vision. Science 251, 1251–1253.

Schiller, P.H., Sandell, J.H., and Maunsell, J.H. (1987). The effect of frontal eye field and superior colliculus lesions on saccadic latencies in the rhesus monkey. J. Neurophysiol. 57, 1033–1049.

Serences, J.T., and Yantis, S. (2006). Selective visual attention and perceptual coherence. Trends Cogn. Sci. (Regul. Ed.) 10, 38–45.

Serences, J.T., and Yantis, S. (2007). Spatially selective representations of voluntary and stimulus-driven attentional priority in human occipital, parietal, and frontal cortex. Cereb. Cortex 17, 284–293.

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

Shipp, S. (2004). The brain circuitry of attention. Trends Cogn. Sci. (Regul. Ed.) 8, 223–230.

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

Swisher, J.D., Halko, M.A., Merabet, L.B., McMains, S.A., and Somers, D.C. (2007). Visual topography of human intraparietal sulcus. J. Neurosci. 27, 5326–5337.

Talairach, J., and Tournoux, P. (1988). Co-Planar Stereotaxic Atlas of the Human Brain: 3-Dimensional Proportional System: an Approach to Cerebral Imaging (New York: Thieme).

Thompson, K.G., and Bichot, N.P. (2005). A visual salience map in the primate frontal eye field. Prog. Brain Res. 147, 251–262.

Van Essen, D.C., Lewis, J.W., Drury, H.A., Hadjikhani, N., Tootell, R.B.H., Bakircioglu, M., and Miller, M.I. (2001). Mapping visual cortex in monkeys and humans using surface-based atlases. Vision Res. 41, 1359–1378.

Wolfe, J.M. (1994). Visual search in continuous, naturalistic stimuli. Vision Res. 34, 1187–1195.

Wolfe, J.M., and Frankel, S.L. (1988). Binocularity and visual search. Percept. Psychophys. 44, 81–93.

Yantis, S., and Johnston, J.C. (1990). On the locus of visual selection: evidence from focused attention tasks. J. Exp. Psychol. Hum. Percept. Perform. 16,