

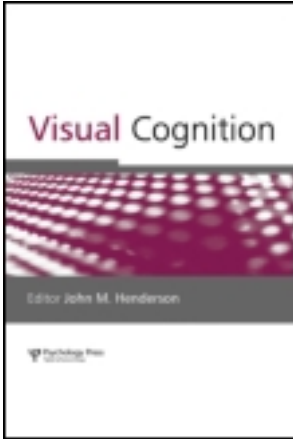
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Eccentricity biases of object categories are evident in visual working memory

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In high-order object areas, face-selective areas prefer centrally presented stimuli, whereas building-selective areas prefer peripherally presented stimuli (Levy et al., 2001). We investigated whether this eccentricity bias was also evident in visual working memory. In Experiment 1, we found that working memory performance for faces decreased towards the periphery while the performance for buildings remained unchanged across different eccentricities. To rule out the possibility that lower level features influence these results, we manipulated the spatial frequency of faces and buildings (Experiment 2) and the spatial layout information of the buildings (Experiment 3). In both of the experiments, we replicated the results of Experiment 1, even when these lower level features of stimuli were controlled. Consistent with previous findings, the current results suggest that each object category is processed in a different manner depending on the eccentricity. This eccentricity bias is likely the result of how the high-order object areas represent different object categories.

Keywords: Eccentricity; Eccentricity bias; High-order object area; Object category; Visual working memory.

We encounter various objects in daily life and use different strategies to recognize them depending on their categories. For instance, we focus on other's faces because we need visual details to identify them or to infer their

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internal states. On the other hand, we simply glance at buildings because we can recognize them by their coarse outlines most of the time. Thus, it appears that each object category requires a different degree of perceptual acuity. This tendency is closely related to the contrast between central and peripheral vision. Specifically, spatial resolution on the retina drops steeply towards the periphery (Anstis, 1974). This occurs because the density of the cones is much greater in central vision than in peripheral vision (Rolls & Cowey, 1970; Weymouth, 1958). Furthermore, more cells in both the lateral geniculate nucleus (LGN) and the primary visual cortex (V1) are allocated for central vision than for peripheral vision (cortical magnification; Tootell, Switkes, Silverman, & Hamilton, 1988; van Essen, Newsome, & Maunsell, 1984). Owing to these neurobiological factors, central vision is optimal for processing fine details, whereas peripheral vision is appropriate for processing coarser features.

Previous studies investigated this retinotopic organization in relatively early visual cortices from V1 to V4 (de Yoe et al., 1996; Tootell et al., 1997). Recently, however, it was shown that high-order object areas also have the retinotopic organization and that this organization is associated with the object category. An fMRI study found that face-selective regions showed preferential responses to centrally presented objects, whereas building-selective regions were more activated by peripherally presented objects (Levy, Hasson, Avidan, Hendler, & Malach, 2001). Behavioural results also support this finding. Face identification deteriorates in peripheral vision even after compensating for the poor resolution of the periphery (Mäkelä, Näsänen, Rovamo, & Melmoth, 2001), and the gist of a scene is processed better by the peripheral vision owing to large-scale integration (Larson & Loschky, 2009).

In the current study, we investigated the relationship between eccentricity and object categories using a visual working memory task. Levy et al. (2001) did not investigate the behavioural consequences of the eccentricity bias on object recognition. They only showed the bias in the patterns of fMRI responses depending on the object category. In addition, other behavioural studies used simple perception tasks, for instance, face identification (Mäkelä et al., 2001) or scene gist recognition (Larson & Loschky, 2009). Unlike these studies, we used a visual working memory task to measure the eccentricity bias at higher stages of visual processing.

In Experiment 1, we contrasted the visual working memory performance for faces and buildings. Based on neurophysiological (Levy et al., 2001) and behavioural (Larson & Loschky, 2009; Mäkelä et al., 2001) evidence, we hypothesized that the visual working memory performance for faces will be better in central vision than in peripheral vision. In contrast, the visual working memory performance for buildings will be mostly preserved, even in peripheral vision. In Experiments 2 and 3, we ruled out lower level factors

that could explain these results by modulating the spatial frequency of face and building images and the spatial layout information using new building images, respectively.

GENERAL METHODS

Participants

Twelve, 19, and 13 paid students at Yonsei University participated in Experiments 1, 2, and 3, respectively. All participants had normal or corrected-to-normal vision and were unaware of the purpose of the experiments. The Institutional Review Committee of Yonsei University approved the experimental protocol and signed informed consent forms were obtained from all participants.

Apparatus and stimuli

The stimuli were created using MATLAB and the Psychophysics Toolbox (Brainard, 1997; Pelli, 1997) and were presented on a linearized Samsung 21-inch monitor (resolution, 1600×1200 ; refresh rate, 85 Hz). The participants performed the experiments in a dark room. The position of each participant's head was stabilized by a head- and chinrest and the viewing distance to the monitor was 60 cm.

Seven different object categories were used as stimuli, and each category contained 100 images. Except for the faces and buildings, the other object categories were task-irrelevant distractors. We selected face images from the FERET database (Phillips, Moon, Rizvi, & Rauss, 2000; Phillips, Wechsler, Huang, & Rauss, 1998). The mean luminance (13.88 cd/m^2) and the root mean square (RMS) contrast (48.34%) were equated across all images. The luminance of the grey background used here was 14.43 cd/m^2 .

Task and procedure

Figure 1 depicts the experimental procedure. The participants were asked to fix their eyes on a fixation cross presented in the centre of the screen during all of the experiments. The fixation cross was presented only in the beginning of a trial in the fovea condition because the images were presented in the centre of the screen in this condition. Unlike the fovea condition, the images were presented in one of four locations (the upper, lower, right, and left visual fields) in the parafovea and periphery conditions. The position changed every 30 trials and an arrow briefly appeared to indicate this change. Every trial began when the participants pressed the spacebar. After doing this, six images were presented sequentially. In each image sequence, the first and the last images were task-irrelevant distractors and the four

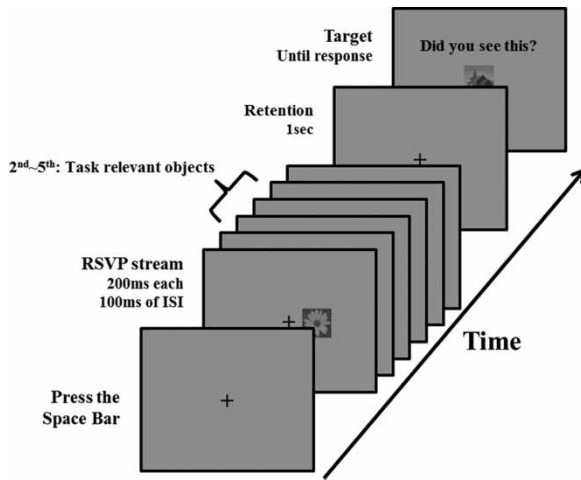


Figure 1. Experimental procedure. This shows an example of the parafovea condition when an RSVP stream is presented in the right visual field. The participants were asked to report whether a target was in an RSVP stream.

in-between images were either faces or buildings. Each image in the sequence was presented for 200 ms with 100 ms of ISI. After a delay of 1 s, a target image appeared in the centre of the screen. The target was included in an image sequence in half of the trials. The participants were asked to report whether or not the target was in the sequence by pressing “1” or “2” on a numeric keypad, respectively. The target remained on the screen until the participants responded. When the participants’ responses were incorrect, immediate auditory feedback was given.

Analysis

The dependent variable was the accuracy percentage corrected for guessing (Green & Swets, 1966). The accuracy percentage was obtained by the following formula: Accuracy (corrected for guessing) = $100 \times (\text{Hit rates} - \text{False alarm rates}) / (1 - \text{False alarm rates})$.

Experiment 1

In this experiment, face images had frontal views and building images typically had frontal views but they varied in terms of viewpoint more than the face images. Image sizes were scaled across eccentricity conditions. Images were presented in the centre of the screen and were subtended $1.8^\circ \times 1.8^\circ$ in the fovea condition. In the parafovea and periphery conditions, images were subtended $2^\circ \times 2^\circ$ at an eccentricity of 3.5° and $8.5^\circ \times 8.5^\circ$ at an eccentricity of 15.75° , respectively. The image sizes and eccentricities were equivalent to those

in Levy et al. (2001). The eccentricity conditions were blocked and consisted of 120 trials. Hence, the participants performed 360 trials in total.

Experiment 2

We replicated Experiment 1 with an addition of one independent variable, the spatial frequency of the images. The original images were fast-Fourier transformed and multiplied by Gaussian high-pass and low-pass filters. The high-pass cutoff was 24 cycles/image and the low-pass cutoff was 8 cycles/image (Oliva & Torralba, 2006; Schyns & Oliva, 1999). Subsequently, these images were inverse-fast-Fourier transformed. The mean luminance of the low-pass filtered images was 28.47 cd/m^2 ($SD = 5.01 \text{ cd/m}^2$) and that of the high-pass filtered images was 31.35 cd/m^2 ($SD = 2.59 \text{ cd/m}^2$). To equate the spatial frequency amplitude across different eccentricity conditions, the lengths and widths of the images in the fovea condition were doubled and quintupled in a pixel-wise manner for the parafovea and periphery conditions, respectively. Nevertheless, the image sizes in all eccentricity conditions did not significantly change as compared to those in Experiment 1 (fovea: $1.7^\circ \times 1.7^\circ$ at an eccentricity of 0° , parafovea: $3.3^\circ \times 3.3^\circ$ at an eccentricity of 4.15° , and periphery: $8.3^\circ \times 8.3^\circ$ at an eccentricity of 15.65°).

Experiment 3

All aspects of this experiment were identical to those in Experiment 1 except for the building images. Each building image contained the entire contour of a building and more background and thus contained more spatial layout information. Figure 2 shows examples of the face and building images used in Experiments 1 and 3. Previous studies showed that the extraction of the

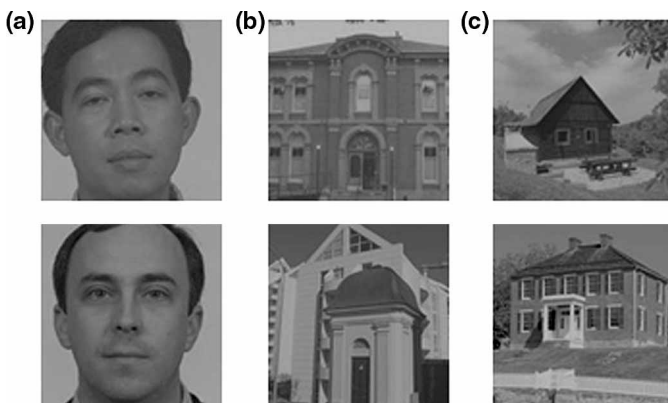


Figure 2. Examples of the visual stimuli used in Experiments 1 and 3: (a) The face images used in both Experiments 1 and 3; (b) and (c) the building images used in Experiments 1 and 3, respectively.

spatial layout information is rapid and accurate (Navon, 1977; Rousselet, Joubert, & Fabre-Thorpe, 2005; Schyns & Oliva, 1994) and that this information can facilitate subsequent scene and object recognition (Oliva & Torralba, 2006; Sanocki, 2003; Sanocki & Epstein, 1997). In addition, spatial layout information is considered as an intermediate-level feature, which is processed at a higher stage than the spatial frequency (Oliva, 2005; Velisavljević & Elder, 2008). Therefore, if the eccentricity bias is also sensitive to intermediate-level features, adding more spatial layout information may change the pattern of the results found in Experiment 1.

RESULTS

Experiment 1

We hypothesized that the working memory performance for faces decreases in the periphery whereas that for buildings does not deteriorate—even in the periphery. We conducted a 3×2 (Eccentricity \times Object category) repeated-measures analysis of variance (ANOVA). Figure 3 shows the results of Experiment 1. The main effects of eccentricity, $F(2, 22) = 5.539$, $p < .011$, and of object category, $F(1, 11) = 15.716$, $p < .002$, were significant. These results suggest that the overall accuracy decreased with the eccentricity and that it was higher for faces than for buildings. Importantly, the interaction between eccentricity and object category was significant, $F(2, 22) = 4.859$, $p < .018$. One-sample t -tests showed that the performance level of the participants was well above the chance level in all conditions (all $ps < .001$). In separate analyses of the faces and buildings, accuracy for faces decreased significantly as eccentricity increased, $F(2, 22) = 13.267$, $p < .001$, whereas accuracy for buildings did not change with the eccentricity, $F(2, 22) = .634$, $p = .540$. These results suggest that eccentricity affects visual working memory for faces and buildings in a different manner.¹

One may think that the pattern of the results observed in Experiment 1 is due to eye movements. To rule out this possibility, we compared the overall accuracy among the four different visual fields both in the parafovea and periphery conditions. Paired-samples t -tests showed that there were no significant accuracy differences among these visual fields, indicating that the participants maintained fixation, as we asked. Furthermore, if the participants had moved their eyes, accuracy for faces should not have changed with the eccentricity, like that for buildings. Therefore, it is unlikely that the eccentricity bias found in this experiment is due to eye movements.

¹We also analysed our data using d' (Green & Swets, 1966) and found essentially the same patterns of the results described here.

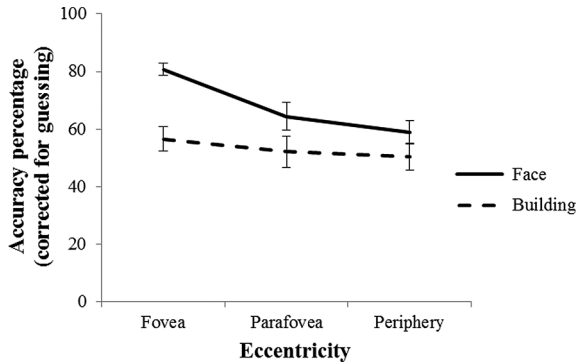


Figure 3. Accuracy for faces (solid line) and buildings (dashed line) depending on different eccentricities. The accuracy for faces decreased towards the periphery, whereas the accuracy for buildings did not change across different eccentricities. The error bars indicate the standard error of the mean (SEM).

Experiment 2

In this experiment, we investigated whether the results of Experiment 1 could change depending on the spatial frequency of the images. The results for each spatial frequency condition are shown in Figure 4. The performance level was again well above the chance level in all conditions (all $ps < .001$). The main effect of spatial frequency was significant, $F(1, 18) = 7.634$, $p < .013$, indicating that accuracy for LSF images was higher than that for HSF images. These results may be due to the fast extraction of the object identity through the LSF information. Because low spatial frequencies are processed rapidly through the dorsal pathway and facilitate object recognition in a top-down manner (Bar et al., 2006), the LSF information can facilitate object recognition, especially under the short exposure duration of 200 ms in this experiment.

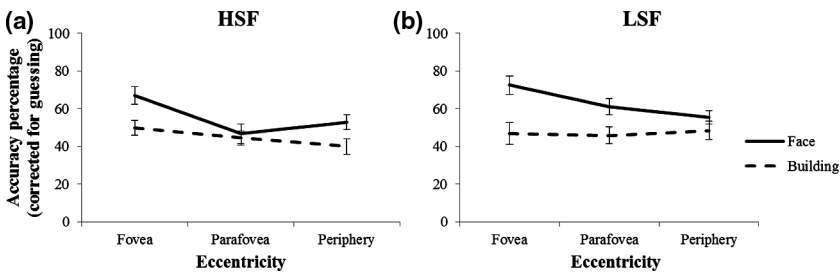


Figure 4. Accuracy for faces (solid line) and buildings (dashed line): (a) and (b) The visual working memory performance when high- and low-spatial frequency images were used, respectively. The results were similar for these two spatial frequency conditions.

The main effects of eccentricity, $F(2, 36) = 9.400$, $p < .001$, and object category, $F(1, 18) = 22.115$, $p < .001$, were also significant. In terms of two-way interaction, only the interaction between eccentricity and object category was significant, $F(2, 36) = 5.029$, $p < .012$, which again suggests the eccentricity bias, as in Experiment 1. Finally, the three-way interaction among spatial frequency, eccentricity, and object category was not significant, $F(2, 36) = 1.503$, $p = .236$. Therefore, the relationship between eccentricity and object category was not affected by different spatial frequencies. Further analyses showed that the accuracy patterns for faces and buildings were identical to those in Experiment 1. In the HSF condition, accuracy for faces decreased in the periphery, $F(2, 36) = 9.636$, $p < .001$, whereas accuracy for buildings did not change across eccentricities, $F(2, 36) = 1.667$, $p = .203$. In the LSF condition, accuracy for faces deteriorated towards the periphery, $F(2, 36) = 7.851$, $p < .001$, whereas accuracy for buildings remained unchanged regardless of the eccentricities, $F(2, 36) = 0.087$, $p = .917$.

EXPERIMENT 3

We examined whether the spatial layout information could affect the results of Experiment 1. Figure 5 illustrates the results of Experiment 3. The performance level was significantly higher than the chance level in all conditions (all $ps < .001$). The main effects of eccentricity, $F(2, 24) = 4.530$, $p < .021$, and object category, $F(1, 12) = 50.223$, $p < .001$, were significant. Although the interaction between eccentricity and object category was not significant, $F(2, 24) = 0.100$, $p = .905$, separate ANOVAs showed that accuracy for faces decreased significantly towards the periphery,

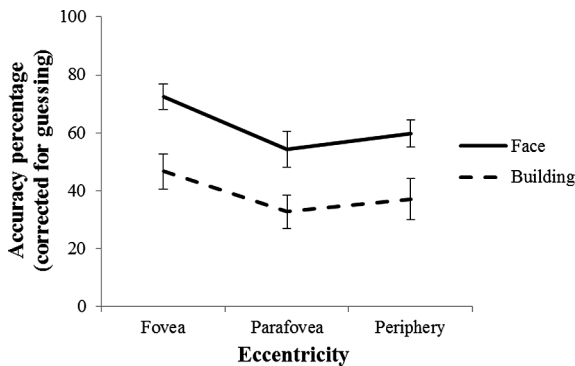


Figure 5. Accuracy for faces (solid line) and buildings (dashed line) when the spatial layout information was added to the new building images. As in Experiment 1, accuracy for faces deteriorated in the periphery, whereas accuracy for buildings remained unchanged across different eccentricities.

$F(2, 24) = 5.356, p < .012$. However, accuracy for buildings was maintained across different eccentricities, $F(2, 24) = 1.318, p = .286$. These results replicate the findings of Experiments 1 and 2, suggesting that the eccentricity bias is independent of the spatial layout.

The different patterns of the two-way interactions compared to those of the previous two experiments appear to arise from the different global configuration processing depending on the eccentricity. Previous studies demonstrated that peripheral vision is insensitive to the global configuration as compared to central vision (Hess & Dakin, 1997; Velisavljević & Elder, 2008). In this experiment, adding spatial layout information enhanced the global configuration and may have increased the accuracy for buildings in the fovea. This increased accuracy in the fovea may have produced weak interaction between the two object categories.

DISCUSSION

We investigated whether working memory performance is sensitive to how the brain is organized. Specifically, we tested whether the eccentricity bias found in high-level areas (Levy et al., 2001) was manifested in visual working memory. We found that accuracy for faces decreased in peripheral vision, whereas accuracy for buildings did not change across different eccentricities. These results indicate that the relative importance of central versus peripheral vision is different depending on the object category.

The current study demonstrated that the eccentricity bias is independent of various lower level features (e.g., the stimulus size, mean luminance, and RMS contrast in all experiments, the spatial frequency in Experiment 2, and the spatial layout in Experiment 3). These results are consistent with a previously reported eccentricity bias for faces, even with stimulus size scaling (Mäkelä et al., 2001). On the other hand, Rousselet, Husk, Bennett, and Sekuler (2005) showed that size scaling can offset decreased face-sensitive ERP (i.e., N170) responses in the periphery. However, in another study (Mäkelä et al., 2001), both size and contrast scaling are necessary to compensate for poor face identification in the periphery. Therefore, the results are inconclusive regarding the effects of scaling on a face eccentricity effect. Given that Levy et al. (2001) also showed that the eccentricity bias in high-order object areas is independent of the distribution of lower level features, eccentricity biases are unlikely to be produced due to lower level factors alone; rather, they reflect higher order processing.

One may argue that the location differences between targets and RSVP streams in the parafovea and periphery conditions can influence the eccentricity bias. However, this factor does not appear to be critical as

regards our results, as it was applied to both faces and buildings and because the patterns of the results in these two object categories were clearly dissociated in this study. If the encoding and retrieval of the stimuli had occurred at the same location, the overall performance level could have been better than that in the current results. Nevertheless, it is evident that the eccentricity bias will be preserved considering our current results.

In the present study, an eccentricity bias was reflected in a visual working memory task. This bias is likely the result of how the brain represents different object categories. Specifically, it is known that the load of the working memory pertaining to faces and scenes is affected by the activities of face- and place-selective areas, respectively (Gazzaley, Cooney, McEvoy, Knight, & D'Esposito, 2005). Moreover, these higher areas are known to have the eccentricity bias (Hasson, Levy, Behrmann, Hendler, & Malach, 2002; Levy et al., 2001). Larson and Loschky (2009) also demonstrated that central vision requires more information than expected by a V1 cortical magnification factor to achieve scene recognition performance equal to that of peripheral vision. This result suggests that higher scene-selective areas (i.e., the PPA), where cortical magnification is attenuated and where peripheral-bias representation can arise, play a more important role in scene gist recognition. Therefore, our results suggest that the eccentricity bias reflected in working memory is involved in the processing of high-order object areas.

REFERENCES

- Anstis, S. M. (1974). A chart demonstrating variations in acuity with retinal position. *Vision Research*, *14*, 589–592.
- Bar, M., Kassam, K. S., Ghuman, A. S., Boshyan, J., Schmid, A. M., Dale, A. M., et al. (2006). Top-down facilitation of visual recognition. *Proceedings of the National Academy of Sciences of the USA*, *103*, 449–454.
- Brainard, D. H. (1997). The Psychophysics Toolbox. *Spatial Vision*, *10*, 433–436.
- De Yoe, E. A., Carman, G. J., Bandettini, P., Glickman, S., Wieser, J., Cox, R., et al. (1996). Mapping striate and extrastriate visual areas in human cerebral cortex. *Proceedings of the National Academy of Sciences of the USA*, *93*, 2382–2386.
- Gazzaley, A., Cooney, J. W., McEvoy, K., Knight, R. T., & D'Esposito, M. (2005). Top-down enhancement and suppression of the magnitude and speed of neural activity. *Journal of Cognitive Neuroscience*, *17*, 507–517.
- Green, D. M., & Swets, J. A. (1966). *Signal-detection theory and psychophysics*. New York, NY: Wiley.
- Hasson, U., Levy, I., Behrmann, M., Hendler, T., & Malach, R. (2002). Eccentricity bias as an organizing principle for human high-order object areas. *Neuron*, *34*, 479–490.
- Hess, R. F., & Dakin, S. C. (1997). Absence of contour linking in peripheral vision. *Nature*, *390*, 602–604.
- Larson, A. M., & Loschky, L. C. (2009). The contributions of central versus peripheral vision to scene gist recognition. *Journal of Vision*, *9*, 1–16.

- Levy, I., Hasson, U., Avidan, G., Hendler, T., & Malach, R. (2001). Center-periphery organization of human object areas. *Nature Neuroscience*, *4*, 533–539.
- Mäkelä, P., Näsänen, R., Rovamo, J., & Melmoth, D. (2001). Identification of facial images in peripheral vision. *Vision Research*, *41*, 599–610.
- Navon, D. (1977). Forest before trees: The precedence of global features in visual perception. *Cognitive Psychology*, *9*, 353–383.
- Oliva, A. (2005). Gist of the scene. In L. Itti, G. Rees, & J. K. Tsotsos (Eds.), *Neurobiology of attention* (pp. 251–256). San Diego, CA: Elsevier.
- Oliva, A., & Torralba, A. (2006). Building the gist of a scene: The role of global image features in recognition. *Progress in Brain Research*, *155*, 23–36.
- Pelli, D. G. (1997). The video toolbox software for visual psychophysics: Transforming numbers into movies. *Spatial Vision*, *10*, 437–442.
- Phillips, P. J., Moon, H., Rizvi, S. A., & Rauss, P. J. (2000). The FERET evaluation methodology for face-recognition algorithms. *IEEE Transactions on Pattern Analysis and Machine Intelligence*, *22*, 1090–1104.
- Phillips, P. J., Wechsler, H., Huang, J., & Rauss, P. J. (1998). The FERET database and evaluation procedure for face-recognition algorithms. *Image and Vision Computing*, *16*, 295–306.
- Rolls, E. T., & Cowey, A. (1970). Topography of the retina and striate cortex and its relationship to visual acuity in rhesus monkeys and squirrel monkeys. *Experimental Brain Research*, *10*, 298–310.
- Rousselet, G. A., Husk, J. S., Bennett, P. J., & Sekuler, A. B. (2005). Spatial scaling factors explain eccentricity effects on face ERPs. *Journal of Vision*, *5*, 755–763.
- Rousselet, G. A., Joubert, O. R., & Fabre-Thorpe, M. (2005). How long to get to the “gist” of real-world natural scenes? *Visual Cognition*, *12*, 852–877.
- Sanocki, T. (2003). Representation and perception of scenic layout. *Cognitive Psychology*, *47*, 43–86.
- Sanocki, T., & Epstein, W. (1997). Priming spatial layout of scenes. *Psychological Science*, *8*, 374–378.
- Schyns, P. G., & Oliva, A. (1994). From blobs to boundary edges: Evidence for time- and spatial-scale-dependent scene recognition. *Psychological Science*, *5*, 195–200.
- Schyns, P. G., & Oliva, A. (1999). Dr. Angry and Mr. Smile: When categorization flexibly modifies the perception of faces in rapid visual presentations. *Cognition*, *69*, 243–265.
- Tootell, R. B., Switkes, E., Silverman, M. S., & Hamilton, S. L. (1988). Functional anatomy of macaque striate cortex. II. Retinotopic organization. *Journal of Neuroscience*, *8*, 1531–1568.
- Tootell, R. B. H., Mendola, J. D., Hadjikhani, N. K., Ledden, P. J., Liu, A. K., Reppas, J. B., et al. (1997). Functional analysis of V3A and related areas in human visual cortex. *Journal of Neuroscience*, *17*, 7060–7078.
- Van Essen, D. C., Newsome, W. T., & Maunsell, J. H. R. (1984). The visual field representation in striate cortex of the macaque monkey: Asymmetries, anisotropies, and individual variability. *Vision Research*, *24*, 429–448.
- Velisavljević, L., & Elder, J. H. (2008). Visual short-term memory for natural scenes: Effects of eccentricity. *Journal of Vision*, *8*, 1–17.
- Weymouth, F. W. (1958). Visual sensory units and the minimal angle of resolution. *American Journal of Ophthalmology*, *46*, 102–113.

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