Spatial biases in viewing behavior

José P. Ossandón   Institute of Cognitive Science, University of Osnabrück, Osnabrück, Germany   ✉

Selim Onat   Institute of Cognitive Science, University of Osnabrück, Osnabrück, Germany
Institute of Systems Neuroscience, University Medical Center Hamburg-Eppendorf, Hamburg, Germany   ✉

Peter König   Institute of Cognitive Science, University of Osnabrück, Osnabrück, Germany
Institute of Neurophysiology & Pathophysiology, University Medical Center Hamburg-Eppendorf, Hamburg, Germany   ✉

Viewing behavior exhibits temporal and spatial structure that is independent of stimulus content and task goals. One example of such structure is horizontal biases, which are likely rooted in left-right asymmetries of the visual and attentional systems. Here, we studied the existence, extent, and mechanisms of this bias. Left- and right-handed subjects explored scenes from different image categories, presented in original and mirrored versions. We also varied the spatial spectral content of the images and the timing of stimulus onset. We found a marked leftward bias at the start of exploration that was independent of image category. This left bias was followed by a weak bias to the right that persisted for several seconds. This asymmetry was found in the majority of right-handers but not in left-handers. Neither low- nor high-pass filtering of the stimuli influenced the bias. This argues against mechanisms related to the hemispheric segregation of global versus local visual processing. Introducing a delay in stimulus onset after offset of a central fixation spot also had no influence. The bias was present even when stimuli were presented continuously and without any requirement to fixate, associated to both fixation- and saccade-contingent image changes. This suggests the bias is not caused by structural asymmetries in fixation control. Instead the pervasive horizontal bias is compatible with known asymmetries of higher-level attentional areas related to the detection of novel events.

Introduction

Viewing behavior is not determined only by the stimulus and task at hand; it is also influenced by other factors. Overt visual exploration is studied with eye-tracking experiments, which reveal the temporal and spatial structure of ocular movements responding to a variety of tasks and stimuli. The observed exploration patterns are highly variable and usually interpreted in terms of "goal-oriented" behavior: Locations on the visual field are selected based on their low- or high-level content in the context of task requirements (Betz, Kietzmann, Wilming, & König, 2010; Itti & Koch, 2001; B. Tatler & Hayhoe, 2011). Viewing behavior is nevertheless not exhausted by factors that depend solely on goals or stimulus content; eye movements display temporal organization and spatial biases that seem to be independent of such determinants (Kollmorgen, Nortmann, Schröder, & König, 2010).

For instance, temporal organization that is independent of stimulus content is present in fixation durations and saccade amplitudes. Fixation durations increase and saccade amplitudes decrease as a complex scene is explored. Because this pattern persists during different tasks, even when it is not the optimal viewing strategy, it has been proposed as evidence of a global-to-local visual exploration strategy (Over, Hooge, Vlaskamp, & Erkelens, 2007; Unema, Pannasch, Joos, & Velichkovsky, 2005).
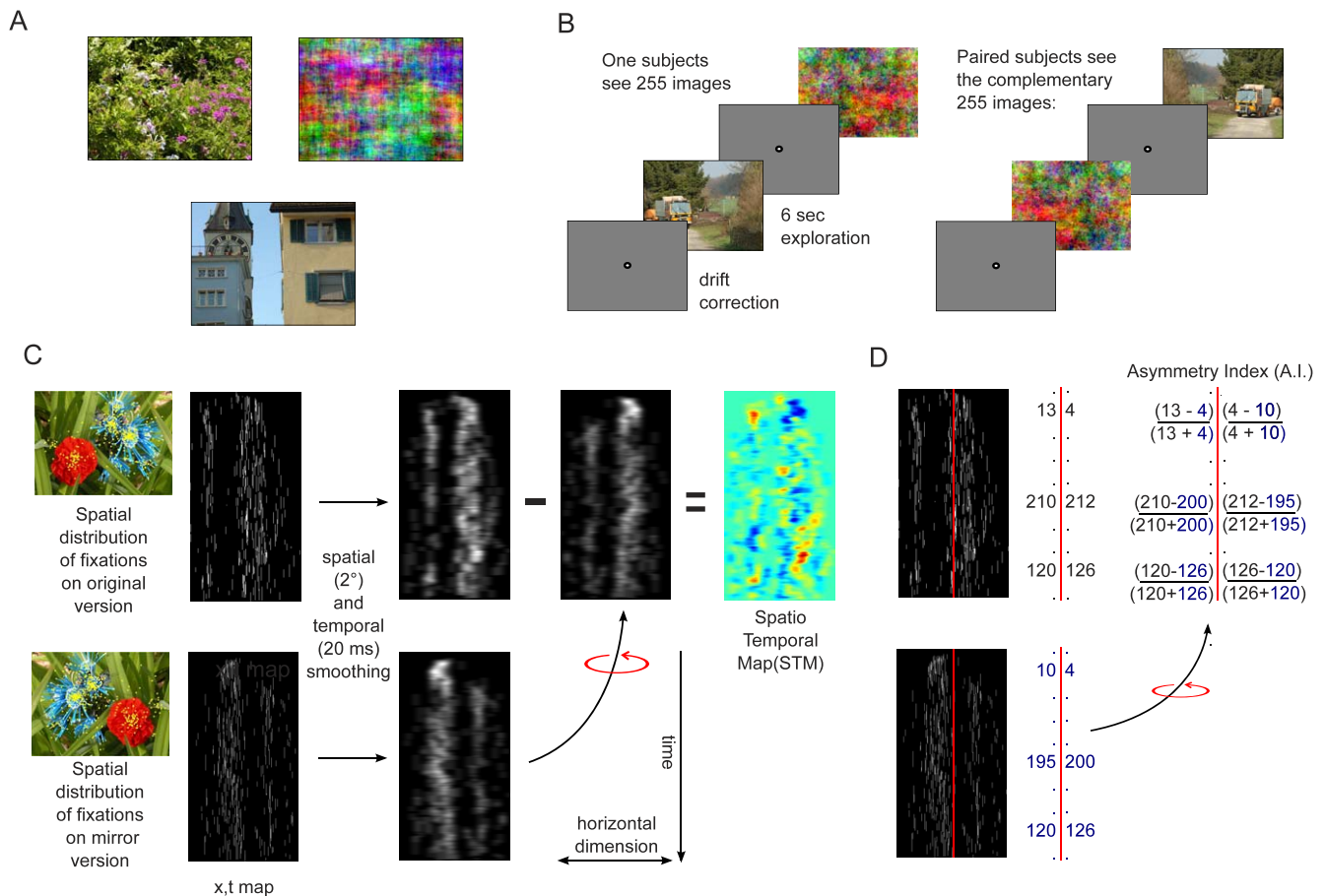
On the other hand, spatial structure in eye movements that is independent of stimulus and task can be defined as viewing bias. One spatial bias is the tendency to look at the center of visual stimuli during the free exploration of images (cf. B. Tatler, 2007; Tseng, Carmi, Cameron, Munoz, & Itti, 2009). Besides this

Figure 1. (A) Example of images from categories naturals, urban, and pink noise. (B) Experiment 1 procedure: Subject explored static images presented for 6 s. Images appeared suddenly after subjects fixated on the center of the screen to correct for drift. Images were presented in their original or mirror versions but never both for one subject. (C) Generation of STMs: All fixations on the original or mirror versions were included in 2-D matrices of size (trial duration) × (horizontal length) at their respective time and spatial bins. An example of such matrices is shown in the black boxes (second column, "x,t maps"), where every fixation is shown as a vertical line that marks its horizontal position and duration. Temporal and spatial filters smoothed original and mirror-version matrices to create STMs for original and mirror trials. Finally, we subtracted the flipped version of the mirror matrices from the original version, correcting for a potential bias in image content and getting the final difference STM used in the following figures. (D) We calculated the AI by collapsing data of each hemifield of the unsmoothed x,t maps, then subtracting fixation counts of the flipped mirror-version images from the originals and normalizing by the total of fixations in a given time. Final values are obtained from the average of both hemifields and were calculated for each time sample and also for successive periods of 1.5 s.

prominent bias, there is some evidence for an asymmetric horizontal spatial bias. Eye-tracking studies about face perception have shown that perceptual biases are often accompanied by an initial exploratory bias to the left (Barton, Radcliffe, Cherkasova, Edelman, & Intriligator, 2006; S. H. Butler & Harvey, 2005; Guo, Meints, Hall, Hall, & Mills, 2009; Guo, Tunnicliffe, & Roebuck, 2010; Leonards & Scott-Samuel, 2005; Mertens, Siegmund, & Grüsser, 1993; Phillips & David, 1997). Other studies have also shown this leftward bias in the initial exploration of complex scenes, but these studies were not investigating this and so did not control for image content asymmetry (Leonards & Scott-Samuel, 2005; see figure 8 in Parkhurst, Law, & Niebur, 2002; figure 3 in B. W.

Tatler, Baddeley, & Gilchrist, 2005). Only recently have two studies confirmed this early leftward bias with controlled stimuli: one on constructive memory errors (Dickinson & Intraub, 2009) and the other on the relationship between viewing bias and the perceptual bias of "pseudoneglect" (Foulsham, Gray, Nasiopoulos, & Kingstone, 2013).

This leftward bias could be the result of hemispheric lateralization, or dominance, in high-level brain areas. The cortical network involved in attention is one of the clearest examples of where hemispheric lateralization has the potential to bias visual exploration. Neuroimaging and lesion studies indicate this network involves regions in the parietal, frontal, and temporal lobes, roughly divided into two subsystems: a bilateral dorsal
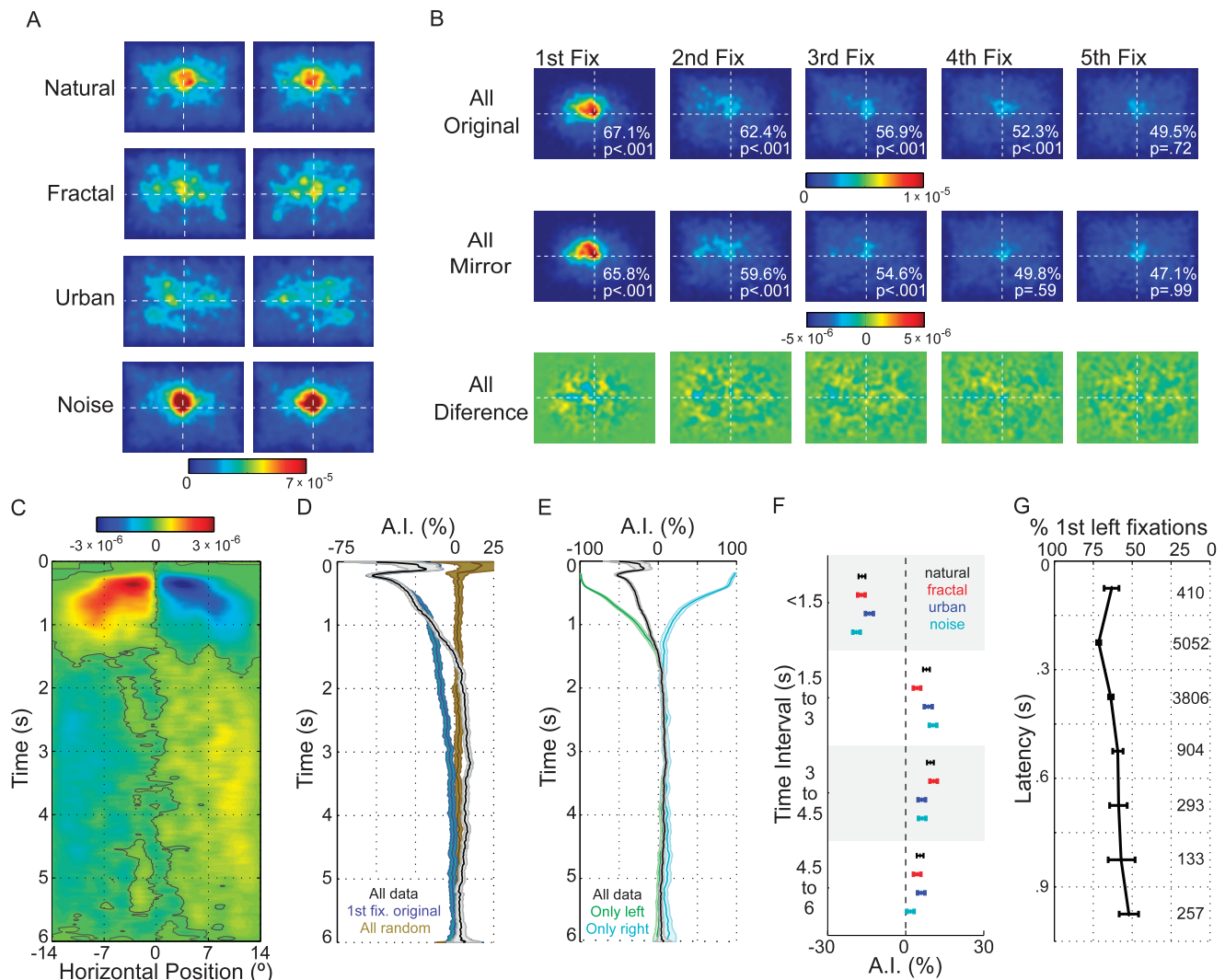
Figure 2. (A) Fixation-density maps for all images within a category separated by exploration of original (left column) or mirrored versions (right column). (B) Spatial distribution of fixation in both versions for different fixation orders after trial start. The bottom row shows the difference between both maps. Insets report the amount of fixations to the left of midline. *P* values are the probabilities associated with that fraction *k* assuming a binomial distribution *f(k; n, p)* with parameters *n* equal to the amount of fixations and *p* = 0.5. (C) Difference map between the STMs for all original images minus the horizontally flipped STMs of the mirror trials. Positive (red) values represent the excess of fixations that remain after removing fixations that are over the same stimulus content. (D) Continuous AI for original data and surrogated sets. The AI expresses the fraction of all fixations attributable to an excess of biased fixations to the left (negative) or right (positive) with corresponding bootstrap CI in light color. The surrogate sets preserve the temporal structure of the original trials but take the spatial information of saccade orientation and size randomly from the overall distribution of saccade orientations and amplitudes. The black line corresponds to the original data pooling across all images and subjects (corresponding to the difference STM in C). The dark blue line represents the surrogate set that preserves the spatial information of the first fixation; the brown line represents the set that does not. (E) Continuous AI for original data and subsets all-left (green) and all-right (cyan). We generated the subsets by taking only trial pairs in which the exploration in both the original and in the mirror versions started in the same hemifield. (F) Asymmetry index by time interval and for the different image categories. (G) Fraction of first saccades to the left of the midline by latency to move. Numbers on the right of the figure are the quantities of fixations in each temporal bin and error bars are the bootstrap *CIs*.

network dedicated to the voluntary control of overt and covert attention and a ventral network lateralized to the right hemisphere and involved in the detection of behaviorally relevant novel stimuli (Corbetta, Patel, & Shulman, 2008; Corbetta & Schulman, 2002). The disruption of this ventral subsystem leads to the severe inattention to and reduced exploration of the left hemifield seen in neglect syndrome (Corbetta & Schulman, 2011). Besides attention, hemispheric dominance of brain areas dedicated to the analysis of
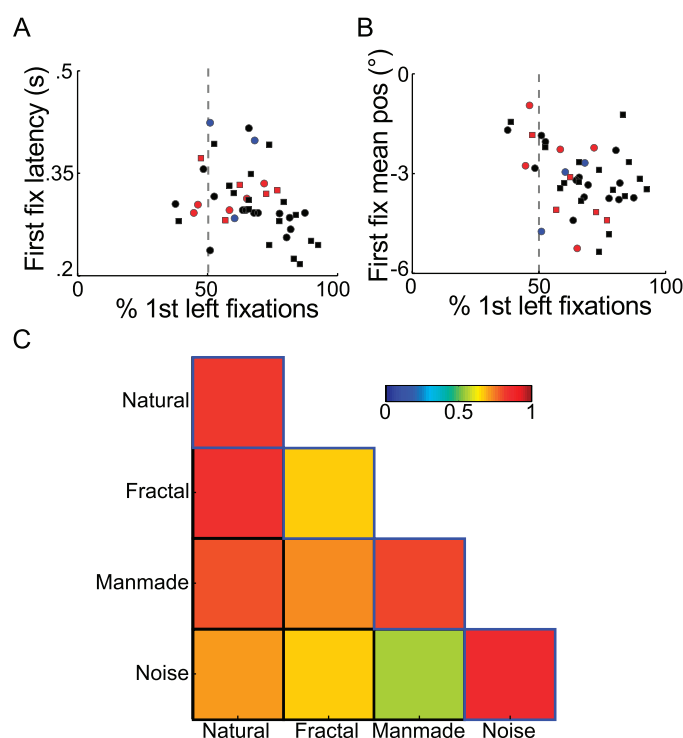
Figure 3. Subjects' spatial bias. Fraction of first movements to the left against mean latency (A) and mean horizontal position (B). Every dot represents the average value across trials for one subject (circles: female subjects, squares: male subjects; black: right ocular dominance, red: left ocular dominance, and blue: unclear) (C) Correlation of subjects' first fixation bias between different categories, and in the diagonal (boxes with blue borders) the half-split reliability for each category is shown (all correlation *p* values are below 0.005).

behavioral bias with bias of stimuli properties by comparing free-viewing behavior of static complex scenes with their mirror images. In Experiment 1, we run a baseline, in which many subjects freely explore static visual stimuli of different categories. In Experiment 2, we check if the horizontal bias is related to handedness or to general visual processes that are lateralized in the brain. In Experiments 3 and 4, we control for the possibility that the bias could be the result of asymmetries in voluntary inhibitory control caused by fixating a drift correction dot before each stimulus.

Experiment 1: Asymmetric spatial bias in the exploration of various visual stimuli

Introduction

Horizontal bias in viewing behavior has been reported mainly in face-viewing experiments. However, only two of these controlled for content asymmetry, either by using mirror-reversed versions (Mertens et al., 1993) or by artificially making the faces perfectly symmetric (S. Butler et al., 2005). These studies investigated only the first few fixations on an image and focused on perceptual bias in face recognition and not on the general structure or progression of viewing bias. In the case of real-world scenes, studies have found an early bias to the left using mainly indoor and outdoor scenes with manmade structures. This kind of stimuli activates ventral visual areas such as the parahippocampal and occipital place area. Although activation is usually bilateral, as with faces, activation is stronger on the right (Aguirre, Zarahn & D'Esposito, 1998; Epstein & Kanwisher, 1998). The associated neuropsychological deficits, landmark agnosia and anterograde disorientation, result from bilateral or right-hemispheric lesions, which agrees with the neuroimaging results (Aguirre & D'Esposito, 1999). With both faces and scenes, spatial bias may be caused by lateralization of a visual processing module to the right. Therefore, it is highly relevant to explore the generalization of bias to other types of stimuli. The goals of Experiment 1 are to confirm previous results about asymmetric bias in visual exploration, to evaluate the generalization of the bias to other kinds of complex stimuli that share low-level properties with complex scenes but lack their high-level cognitive content, and to describe in detail the bias' overall spatial and temporal pattern.

different visual content, such as text or faces, could also cause bias. Face processing is particularly interesting because it is usually right-dominant (Yovel & Freiwald, 2013) and because a series of perceptual biases for left-hemifield content has been associated with biases in viewing behavior. As these different functional systems, the attentional network and the modules for the processing of different visual content, may each cause bias, we cannot attribute viewing bias to the lateralization of a single brain area or functional system.

Regardless of the underlying cause of these biases, understanding their manifestations is essential to avoiding systematic experimental errors when studying viewing behavior by itself or as a marker of other cognitive processes.

Here we present a series of experiments to confirm horizontal asymmetry in the spatial structure of viewing behavior, independent of image structure. We further intend to characterize its properties and investigate contributing factors. We avoid confounding

Methods

Participants

Forty-three subjects (21 males, mean age 24.1 years, *SD* 6.1 years, range 19–48 years) with normal or corrected-to-normal vision participated in the study. Only right-handers were included. Additionally, ocular dominance was assessed by the Miles test (Miles, 1929). In all experiments presented here, an informed written consent was obtained from each participant. Experimental procedure conformed to the Declaration of Helsinki and national guidelines. Part of the data from Experiment 1 has been used in previous publications regarding limitations of models of fixation selection (Wilming, Betz, Kietzmann, & König, 2011) and as a comparison group in a study of low-level visual guidance on the free-viewing behavior of neglect patients (Ossandón et al., 2012).

Stimuli

We used four different kinds of visual stimuli (Figure 1A): natural, urban, fractal, and pink noise. The natural category included 64 scenes from the Calibrated Colour Image Database (Olmos & Kingdom, 2004) depicting outdoor scenes without man-made objects. The urban category included 64 high-resolution photos of public spaces around Zürich (taken with a Nikon D2X, Japan). The fractal category included self-similar computer-generated shapes with second-order statistics similar to real-world images from three different web databases: Chaotic N-Space Network (http://www.cnspace.net/html/fractals.html), Elena's Fractal Gallery (http://www.elena-fractals.it/, accessible in http://web.archive.org), and Maria's Fractal Explorer Gallery (http://www.mariagrist.net/fegal). We generated chromatic pink noise images from the images of the three other categories, transforming each to the Fourier space and combining their average power spectra with random phases taken from a uniform distribution to generate 63 noise images (21 per category). Mirror-reversing each image duplicated the complete set.

We presented the images at 80 cm on a 21-in. CRT monitor (Samsung SyncMaster 1100 DF, Samsung Electronics, Suwon, South Korea) at a refresh rate of 85 Hz and a resolution of 1280 × 960, corresponding to 45.6 pixels/° and a visual field of 28° × 21°.

Eye tracking

Eye movements were recorded with a head-mounted video-based eye-tracking system using binocular pupil tracking at 500 Hz (Eyelink II, SR Research Ltd., Mississauga, ON, Canada). Eye movements were defined using system default parameters, and a standard calibration procedure was performed to achieve an average error below 0.3° (Onat, Libertus, & König, 2007).

Procedure

We presented the 255 stimuli in sessions about 1 hr long. Subjects sat in a dark room in front of the monitor and were told to "study the images carefully." Each image was presented for 6 s (Figure 1B). First, a fixation dot appeared in the center of the screen, and the trial started after the eye-tracking system performed an automatic drift correction. Subjects explored a mixture of original and mirror-reversed images. Each explored one and only one version, original or reversed, of each image. Subjects were paired with one partner getting the original version and one getting the mirror version.

Analysis

The goal of the following analysis is to describe patterns of bias independent of spatial asymmetry in image content. We generated fixation-density maps that display the overall distribution of fixations on the images. We smoothed the maps with a circular convolution kernel, $FWHM_{(x,y)} = 0.5°$. We generated spatiotemporal maps (STMs) to display the temporal progression of horizontal exploration, $FWHM_{(x)} = 2°$, $FWHM_{(t)} = 20$ ms. Fixation-density maps and STMs were generated separately for both the normal and mirror-reversed viewing conditions. To evaluate the exploration bias, we computed the difference between the original STMs and horizontally flipped STMs of the mirror-reversed image (Figure 1C). We calculated an asymmetry index (AI) in the following fashion (Figure 1D): For each time point, we counted the difference in fixations between the left hemifield of the original image and the right of the mirrored one and, likewise, between the right hemifield of the original and left of the mirrored. These pairs of differences show the excess of fixations produced by spatial bias in the respective hemifields. Normalizing by the total amount of fixations for a given time gives an estimate of the fraction of spatially biased fixations over all fixations. Finally, we average the estimate of the left hemifield with the negative of the right hemifield to obtain a single AI value. Confidence intervals for the asymmetry index were calculated by bootstrapping (250 samples with replacement).

For further testing of asymmetries in viewing behavior, we calculated the AI for consecutive time windows of 1.5 s. In the different experiments presented here, we assessed significant differences between conditions with repeated measures or mixed ANOVAs of the AI. The unit of observation was images because individual subjects saw only one version of each. Prior

to statistical tests, we checked normality with the D'Agostino-Pearson test and sphericity with the Mauchly test. Of the 72 different data subgroups presented here (all experiments), only two were not normally distributed. This is fully compatible with the expected false positive rate, and neither of these two groups was part of a significant contrast. Hence, the ANOVA was an appropriate statistical method. Homogeneity of variance was preserved and sphericity violations (measured with Mauchly's test) corrected. We used custom MATLAB functions and the SPSS package for all analysis.

Results

All 43 subjects viewed each image either in its original or mirror-reversed version. Wilming et al. (2011) showed that a number of subjects higher than 20 do not noticeably increase intersubject predictability of fixation locations. Therefore, we considered the images' fixation-density maps to be stable descriptions of their viewing behavior. Inspection of fixation-density maps, obtained by pooling across all subjects, fixations, and images, revealed an overall mirrored pattern of exploration when comparing the exploration of the images' original and mirror versions (Figure 2A). Both image versions' explorations also showed a center bias. Its strength differed among categories, being stronger for the noise images and weaker for urban ones.

We then looked for general spatial asymmetries in exploratory behavior due to factors independent of image content. First, we looked at the horizontal center of gravity (mean horizontal position) of all fixations over each image (Figure 2A). The paired comparisons of centers of gravity across images showed no difference between original and mirror version trials (all images: $t = 0.9$, $p = 0.32$; natural: $t = -0.5$, $p = 0.59$; fractal: $t = 1$, $p = 0.32$; urban: $t = -1.53$, $p = 0.11$; noise: $t = -0.05$, $p = 0.96$). However, when examining in detail the first five fixations after trial start, we see that the first two fixations on the images were clearly biased to the left (Figure 2B). We then calculated STMs of image-viewing behavior (pooled across subjects and image category). Subtracting the horizontally flipped STM of the mirror version from the original version's STM (see methods, Figure 1A) cancels out the probability of fixation due to image structure but preserves the probability of fixation due to an asymmetric spatial bias. Figure 2C shows this difference map averaged over all images, and Figure 2D (black line) shows the continuous AI value as a function of time. Both STM and AI plots showed a marked initial spatial bias to the left for approximately the first 1.5 s. Afterward, a smaller bias to the right continues until the end of the trial. According to the

AI, up to 50% of fixations at the start of exploration can be attributed to the spatial bias to the left (the other half being distributed left/right according to chance). This demonstrates that, although there was no asymmetric bias in all fixations, there was a substantial bias to the left at the beginning of exploration, independent of image structure.

To further test the temporal progression of AI, we performed a mixed-effect ANOVA. The unit of observation was images, and we used one between-group factor for image category (four levels) and one repeated-measure factor for time interval (four levels). Additionally, we included a further repeated-measure factor to test gender differences in image viewing (two levels). Images with outlier values within an experimental group (>3 *SD*) were removed (3/64 natural, 3/64 fractal, 2/64 urban, and 1/63 noise images). We observed a main effect of time interval, $F(3, 726) = 275.6$, $p < 0.001$, and an interaction between time interval and image category, $F(9, 726) = 2.74$, $p = 0.004$. Gender was not significant, $F(1, 242) = 1.07$, $p = 0.3$. Post hoc tests showed significant differences only for the main effect of time interval between the first and all other intervals ($p < 0.05$ corrected, Figure 2F). There were no significant differences in direct contrasts between image categories within the same time interval. The difference closest to significance was between fractal and noise images in the second interval (corrected $p = 0.07$). Trend analysis indicated a cubic trend for the interaction between time and image category, $F(3, 242) = 4.82$, $p = 0.003$, thus reflecting the combined differences between image categories with respect to the strength of the early bias, the subsequent bias to the right, and its reduced strength at the end of the trial. This confirmed a temporally structured exploratory bias that is independent of image content and present in all categories with differences in fine-grain structure depending on image type. The bias was leftward starting at the beginning of exploration (<1 s), then switched sharply toward the right and remained slightly biased to the right until trial's end.

The early asymmetric bias could be mainly produced by a bias of the first fixation. To test this possibility, we created two surrogated data sets that preserved the temporal structure of the original data (fixation-saccade intervals) but shuffled the spatial structure. We did so by sampling saccade orientations and amplitudes from distributions generated with all saccades done from the fourth fixation on (fixation groups that did not show differences in AI, analysis not shown). In the first surrogated set, the random sampling was for every movement order. We generated the second set similarly but preserved the spatial information of the first-pair saccade fixation. Figure 2D shows the results. When all saccade amplitudes and orientations are taken randomly from their parent distributions (brown line),

there is no apparent bias at any moment. This holds both for the early strong leftward bias as well as the weaker rightward bias after 1.5 s. On the other hand, when the spatial information of the first fixation was preserved (dark blue line), the AI mimics the original data (black line) with a left bias at the beginning, then drifts back to the center more slowly than in the original data. Therefore, the swift return to no or right bias is somewhat independent of movement statistics. The early bias also depended on the latency to move: Movements started later after image presentation were less biased that those started in the first 300 ms (Figure 2G). These results show that the first saccade indeed produced most of the spatial bias, which depended on the latency of this first movement.

After discounting the initial leftward bias, the following rightward bias could be a consequence of the statistics of saccade orientation and amplitudes. We discarded this unlikely alternative, in which the saccades' parameters are decided randomly, independent of task or content, by the analysis of the surrogated set shown in Figure 2D (dark blue line): Starting from the initial leftward bias, randomly sampling saccade orientations and amplitudes does not produce a subsequent bias to the right. The second alternative is that the rightward bias compensates for the early leftward one in terms of information gathering. To test this alternative, we created two new data subsets based on whether initial movement was directed exclusively to the left or to the right in both original and mirror-version trials. Figure 2E shows the results, by definition in an initial AI of −100% and 100%, respectively. If the subsequent bias compensates for the initial one, the AI should drift to the opposite side. This is not the case; the left subset did not result in a stronger rightward bias, and the right subset did not result in a leftward bias. Instead, both data partitions result in a later bias to the right as in the complete data set. This result suggests that the late rightward bias is a noncompensatory, independent phenomenon.

We demonstrated a strong bias by comparing image-viewing between original and mirror-reversed versions; now we look at subject variability. Because subjects saw only one version of the images to avoid memory effects, we could not calculate the same STM and AI measures for individual subjects. However, as the first movement could explain most of the initial bias, we used the fraction of first fixations to the left of the midline of the image as a measure of each subject's bias. On average, the fraction of leftward-directed first movements was 66% (range 37%–92%, $SD = 14\%$), significantly different from 50%, $t(42) = 7.6$, $p < 0.001$. This fraction of first fixations is not the same as the AI used previously. The AI measures the percentage of *all* fixations in a given interval attributable to an asymmetric spatial bias as opposed to the percentage of *first* fixations. The fraction of first fixations takes into account all first movements, including biased but also content-responsive movements. As we had an equal number of original and mirror-version trials per image, the values should show the same tendency.

The strength of the leftward bias negatively correlated with subject latency to make the first saccade (Figure 3A, $N = 43$, $r = -0.381$, $p = 0.01$). The strength of leftward bias also correlated with the horizontal center of gravity of the endpoint of those leftward saccades (Figure 3B, $N = 43$, $r = -0.382$, $p = 0.01$). In other words, the subjects with more first movements to the left were also the ones in which those saccades to the left ended in more leftward locations, possibly indicating an increased guidance by low-frequency spatial content. Subjects showed high half-split reliability as well as high correlation between percentages of first fixation to the left across different image categories (Figure 3C). In summary, horizontally biased behavior was highly consistent.

By looking into a subject's measure of bias, we could also evaluate other factors that might be related to the bias, such as handedness (investigated in Experiment 2), ocular dominance, and gender. Subjects did vary with respect to their ocular dominance, so we explored the influence of this factor on the horizontal bias. In three subjects, this was not possible due to inconsistency between the two versions of the Miles test used. Of the remaining 40 subjects, 10 had left ocular dominance (Figure 3A, B). Subjects with left ocular dominance were less biased to the left ($n = 10$, 60%) than those with right ocular dominance ($n = 30$, 69%), which might be interpreted as a consequence of the monocular parts of the visual field at high eccentricity. However, this difference is not significant, $t(38) = 1.76$, $p = 0.08$, and we refrain from further discussion.

Patterns of brain lateralization and dominance usually differ in male and female subjects (Frederikse, Lu, Aylward, Barta, & Pearlson, 1999; Good et al., 2001; Kulynych, Vladar, Jones, & Weinberger, 1994; Welborn et al., 2009); therefore, we also looked into gender differences (Figure 3A, B squares and circles, respectively) but found none at the image level (see the above AI ANOVA results for the gender factor) or in percentage of first fixations to the left, M males = 69%, M females = 63%, $t(41) = 1.47$, p = 0.14. In summary, the analysis of subject bias confirmed the strong bias to the left at the beginning of exploration.

Discussion

Results from Experiment 1 show a marked horizontal bias to the left followed by a smaller one to the right that continues until the trial's end. The early bias was mainly due to the first saccade done in the image.

Because spatial bias changes during exploration, it was undetectable unless one took into account the temporal dimension; the mean horizontal position of all fixations was not biased to either side.

The leftward bias has been reported before, mainly in eye-tracking studies with face stimuli and, more recently, with complex scenes. However, the later bias to the right was an unexpected finding. Foulsham et al. (2013) reported the progression of the bias up to the 10th saccade, approximately 3.5 s into the trials in our experiment, long enough to detect the bias to the right. This difference with our study might be explained by the measures used (absolute location vs. gaze direction) and/or in the small size of the effect. The late rightward bias could explain some inconsistencies between previous reports that aggregate behavior over different time windows.

A common explanation of behavioral bias is that perceptual and exploratory biases follow the hemispheric dominance of specific visual-processing modules in the brain. For instance, in the case of faces, behavioral evidence shows that human subjects, presented with chimeric stimuli composed of two half-faces, report identity, gender, and emotion based on the features appearing in the left hemifield (Burt & Perrett, 1997; S. H. Butler & Harvey, 2005; Chiang, Ballantyne, & Trauner, 2000; Gilbert & Bakan, 1973; Heller & Levy, 1981; Levy, Heller, Banich, & Burton, 1983; Luh, Redl, & Levy, 1994; Mattingley, Bradshaw, Nettleton, & Bradshaw, 1994). In tasks with text stimuli, the right hemifield is dominant (Bryden, 1965; Heron, 1957; Kimura, 1966), and the left hemifield dominates in choices between identical but mirror-reversed asymmetrical images, such as those showing different gradients of brightness (Mattingley et al., 1994; Nicholls, Bradshaw, & Mattingley, 1999) or distributions of dots (Luh et al., 1994; Luh, Rueckert, & Levy, 1991). Interestingly, in contrast to these examples of left-hemifield bias, the bias in reporting of content is to the right when the task is to judge the aesthetics of pictures or paintings. Right-handers prefer images with the most important content located to the right (Chokron & De Agostini, 2000; De Agostini, Kazandjian, Cavézian, Lellouch, & Chokron, 2010; Levy, 1976). Some explanations for this discrepancy have been attempted, such as the idea that the rightward content of the picture balances the subject's leftward attentional bias (Levy, 1976) or that attracting the gaze to the right leaves most of the image in the left visual field to be evaluated by the right hemisphere (Beaumont, 1985). All these behavioral studies agree, though, that the left and right hemispheres process visual content differently.

Behavioral studies are consistent with neuroimaging experiments. Left-hemifield dominance for face content and right-hemifield dominance for written content matches the asymmetry of visual processing of faces producing higher activation in the right face fusiform area (e.g., Kanwisher, McDermott, & Chun, 1997; Puce, Allison, Asgari, Gore, & McCarthy, 1996) and text producing higher activation in the left occipito-temporal area (e.g., L. Cohen et al., 2000; Petersen, Fox, Snyder, & Raichle, 1990). These neuroimaging studies also agree with clinical studies that show lesions in the same areas produce deficits in facial and text recognition (e.g., L. Cohen, 2003; De Renzi, Perani, Carlesimo, Silveri, & Fazio, 1994).

In the present study, we investigate asymmetries in several general categories, including naturalistic photos, fractals, and pink noise images. The purpose of using such sets of images was to investigate whether the bias was general or restricted to faces and static real-world scenes. The images used in the previous studies that found a leftward bias as well as in most neuroimaging studies about scene recognition are usually similar to the images we included in our urban category. We included a natural category of landscapes with fewer or no man-made objects. More importantly, we include fractal and noise images, which share first- and second-order statistics with natural stimuli but none of their cognitive content. In this way, we show the bias is present in a broader variety of stimuli and not dependent on specific content, such as faces or human environments. All of the image categories show the same general bias structure although an interaction between image category and time is present, indicating differences of bias strength between categories. When our results are considered together with other stimulus studies, it is clear that a leftward bias exists for most stimuli. This may be due to lateralization of category-specific modules or lateralization of a more general visual-processing mechanism. The second alternative seems most likely because pink noise and fractals are not natural types, and it is improbable that category-specific modules exist for their processing. In Experiment 2, we explore one such general mechanism: the differential processing of global and local features through both hemispheres.

We found no gender differences in bias. Previous reports showed a stronger bias for males on other laterality effects. The biggest meta-analysis so far conducted on laterality effects, including 266 studies, confirmed gender differences in visual paradigms (Voyer, 1996). However, the consistency of the effects did not resist analysis for publication bias. Moreover, the small magnitude of the reported differences casts doubt on their relevance (Voyer, 1996). It is possible that the variability in the differences between males and females in visual bias depends on the menstrual cycle (e.g., Hausmann, 2005). No information about menstrual cycles or hormone levels was recorded in our

study, so it is not possible to address this hypothesis here.

In addition to the findings reported above, Experiment 1 also found lesser bias in first movements that were initiated later. Such diminution has been found before but only for short image presentations (500 ms) and not for longer presentations as used here (Dickinson & Intraub, 2009). This trade-off between bias and saccadic latency may reflect the processing speed of the different pathways involved in eye movements. Several pathways involved in visual processing and programming of eye movements have parallel components: subcortical versus cortical eye-movement control, magnocellular versus parvocellular pathways, and dorsal versus ventral streams. In Experiment 2, we explore the role of latency with a forced delay between image onset and the initiation of exploration, which we hypothesized would reduce bias.

In summary, in Experiment 1, we established a strong early leftward bias, which is consistent with previous studies. In the following three experiments, we attempted to uncover the possible mechanisms underlying it. To this end, we probed the influence of different visual processes known to show hemispheric lateralization or dominance and, therefore, which could cause bias.

Experiment 2: Brain dominance and viewing biases

Introduction

One possible general mechanism underlying viewing bias is the process of hierarchical evaluation of visual content. "Global precedence" is a phenomenon in which global visual features show priority over local features (Navon, 1977). Multiple studies have shown a behavioral advantage for processing global content presented in the left hemifield and for local content presented in the right (e.g., Christie et al., 2012; Sergent, 1982; Van Kleeck, 1989). Neuroimaging supports this pattern, showing a corresponding differential activation in the right hemisphere for globally directed attention and in the left for locally directed attention (Fink et al., 1996; Han et al., 2002; Martinez et al., 1997). Further evidence stems from clinical cases showing deficits in globally directed attention following right-hemisphere injury and deficits in locally directed attention following left-hemisphere injury (Delis, Robertson, & Efron, 1986; Ivry & Robertson, 1998; Robertson & Delis, 1986). Global and local visual features can usually be mapped to low- and high-frequency spatial content. Therefore, behavioral dif-

ferences in the processing of hierarchical stimuli could also be explained in terms of differential hemispheric processing of low and high spatial frequencies. This applies for both simple stimuli (Christman, 1989; Ivry & Robertson, 1998; Sergent, 1982) and complex natural scenes (Oliva & Schyns, 1997; Schyns & Oliva, 1994). Neuroimaging studies have also shown differential hemispheric responses for low and high spatial frequencies of naturalistic stimuli similar to those used here (Peyrin, Baciu, Segebarth, & Marendaz, 2004; Peyrin et al., 2005). This kind of stimuli follows a $1/f$ frequency spectrum (Field, 1987; Torralba & Oliva, 2003), concentrating most of the power in the lower frequencies. Therefore, exploratory bias could be rooted in differential hemispheric activation produced by heterogeneous spatial frequency distribution in stimuli. Furthermore, in Experiment 1, subjects with more biased behavior produced larger initial saccades. Because high-frequency content cannot be processed at high eccentricity, these saccades are probably driven by lower frequency content. If the right hemisphere processes lower frequency content, this would explain the saccades' leftward bias. To test this, Experiment 2 uses low-pass (LP) and high-pass (HP) filtered stimuli to change the availability of local or global content.

Experiment 2 evaluates not only right-handers, as in Experiment 1, but also left-handers. The latter present weaker perceptual asymmetries and higher between-subject variance (Bryden, 1965; Gilbert & Bakan, 1973; Heller & Levy, 1981; Levy et al., 1983; Luh et al., 1994). Moreover, identification of local versus global features depends on homologous areas in the posterior parietal cortex (PPC), the lateralization of which is opposite for left-handers (Mevorach, Humphreys, & Shalev, 2005). Focus on local information depends on the right PPC for left-handers and on the left PPC for right-handers. If the horizontal bias were dependent on differential activation of the hemispheres because of the processing of global and local features, we would expect the bias to be reversed for left-handers.

Experiment 2 also explores whether the salience of the sudden onset of stimuli might cause the bias. The reduction in bias at increased saccadic latencies seen in Experiment 1 could reflect other structural or functional constraints that shorten latency responses. Stronger bias at early latencies might indicate a bias produced by asymmetries in pathways with shorter latencies in the visual system, such as the direct subcortical path through the superior colliculus (SC) or the magnocellular pathway (Schroeder, Metha, & Givre, 1998; Schroeder, Tenke, Arezzo, & Vaughan, 1989). Alternatively, as mentioned, the bias might be caused by the asymmetry of the ventral attentional system for salient events (e.g., the presentation of a novel image), a system that seems situated along the faster visual dorsal stream (e.g., Schroeder et al., 1998).

In all cases, a delay between image onset and initiation of exploration could mitigate the competition between faster and slower mechanisms. Therefore, in Experiment 2, we included a condition in which we only allowed subjects to explore the image after a delay of 1 s following onset.

Methods

Participants

Forty-eight new subjects participated in the study. All had normal or corrected-to-normal vision and participated for either credits or monetary reward. Handedness was determined by subjects' self-report and additionally by the Edinburgh handedness inventory (EHI, 10 questions with a final score between −100 and 100; Oldfield, 1971). Subjects belong to two different groups: right-handers ($N = 31$, 15 males, mean age 22.5 years, *SD* 2.2 years, range 19–28 years) and left-handers ($N = 17$, nine males, mean age 22.8 years, *SD* 2.3 years, range 19–28 years).

Stimuli

We used images in the natural and urban categories described above and created two new versions of each image by spatial LP and HP filtering with a Gaussian filter with a cutoff of 0.6 c/° (Gonzalez & Woods, 2008). Such low cutoff changes eye-movement parameters (Groner, Groner, & von Mühlenen, 2008) but preserves clear visual content in both LP and HP images (Figure 4A). To avoid identifying differences in exploration due only to differences in overall luminance between LP and HP images, the HP version preserved the mean luminance of the original images. Image presentation and eye tracking was identical to Experiment 1.

Procedure

Procedures were similar to those of Experiment 1 with the exception that, in half of the trials, the fixation dot remained on for 1 s after the stimulus onset, and we requested subjects to keep fixating until it disappeared (Figure 4A). If a subject's gaze moved away from a radius of 1 visual degree from the center, the trial terminated, and a feedback message was delivered. We blocked delay and nondelay trials and balanced the order of blocks across subjects.

Results

Experiment 1 results came from a population of only right-handers; therefore, we wanted to investigate whether the bias was also present in left-handers. We looked at the overall pattern of exploration by making difference STMs as in the baseline experiment (Figure 4B). We reproduced the main result of the baseline experiment; the left spatial bias was visible for right-handed subjects but almost absent for left-handers. However, although left-handers did not present a leftward bias, they also did not present a mirrored bias.

We evaluated the role of handedness and image filtering in a repeated-measures ANOVA with factors subject group (right-handers and left-handers), filter (none, LP, HP), and the already known effect of time interval (four levels). Only in 93 of 128 images was there complete information for every level of the different factors. In the others, the general reduction in exploration with filtered images led to sparser data (Ossandón, Açık, & König, 2011), which could not be included in the analysis. The assumption of sphericity was violated in the main effect of time, Mauchly's test $\chi^2(5) = 13.9$, $p = 0.016$, and in the interaction between time and handedness, Mauchly's test $\chi^2(20) = 28.7$, $p = 0.001$; therefore, we corrected degrees of freedom using Greenhouse-Geisser estimates of sphericity ($\varepsilon = 0.9$ and 0.89, respectively). We found a main effect of time, $F(2.7, 249.2) = 12.5$, $p < 0.001$; handedness, $F(1, 92) = 10.0$, $p = 0.002$; and the interaction between the two, $F(2.6, 247.1) = 9.2$, $p < 0.001$ (Figure 4C). Notably, the filtering factor was not significant, $F(2, 184) = 1.86$, $p = 0.16$ (Figure 4C). For the interaction between time interval and group, we found significant differences between images explored by left- and right-handed subjects only in the first time interval, <1.5 s, $t(184) = 6.06$, $p < 0.001$. Image filtering did cause other changes in viewing behavior, especially in saccade amplitudes (Figure 4F). An ANOVA with a single factor, filtering, was significant, $F(2, 273) = 14.1$, $p < 0.001$, distinguishing HP images from normal, $t(273) = 3.18$, $p < 0.001$, and LP images, $t(273) = 5.01$, $p < 0.001$, but not normal from LP, $t(273) = 1.82$, $p = 0.03$ uncorrected. We conclude that only handedness but not spatial scale results in a significantly different exploration bias.

We then evaluated whether the spatial bias was related to the sudden presentation of the image. In half of the trials, we asked subjects to keep fixating on the middle of the screen for 1 s after image onset. When subjects failed to fixate on a central region of 1° radius, the trial stopped and the experiment continued with the next trial (7.2% of trials). Of the trials that continued, 8.7% still showed eye movement before the go signal, but this movement was smaller than 1°. In the no-delay condition, right-handers showed a strong initial bias to the left and left-handers remained unbiased. The introduction of a forced delay in movement after image appearance did not change the spatial bias pattern seen in Experiment 1 or in the no-delay condition (Figure 4D). The relationship between latency to move and amount of bias seen in Experiment 1 was also present in
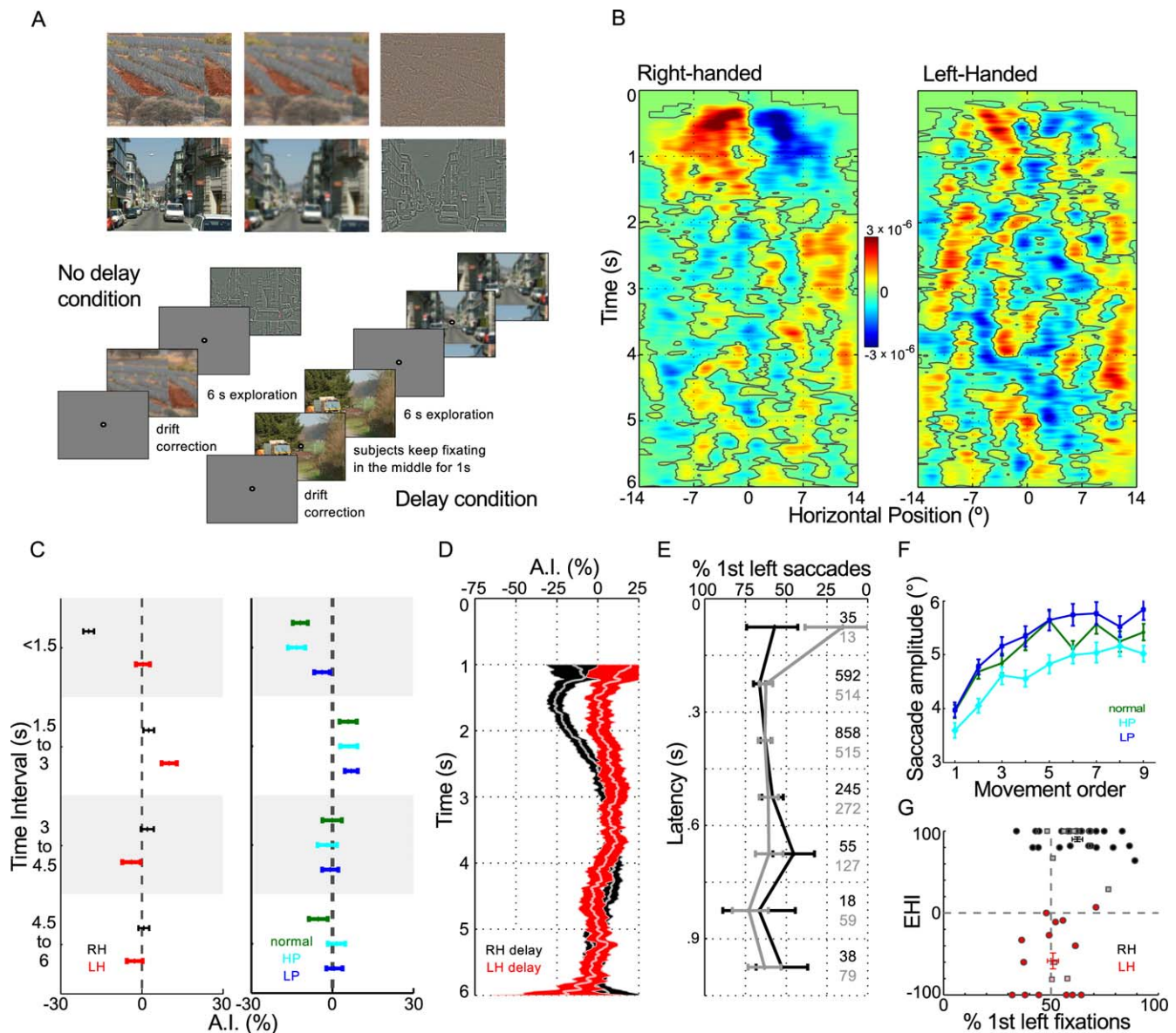
Figure 4. (A) Top: Examples of visual stimuli. Original images in the left column, LP in the middle, and HP in the right. Bottom: Subjects explored images after a drift-correction procedure. With the no-delay condition, the procedure was the same as in Experiment 1. With the delay condition, the dot used for drift correction remained visible for 1 s after image appearance, and subjects were instructed to keep fixating on it until its disappearance. (B) Difference STMs for right- and left-handers. (C) Asymmetry index by time interval divided by handedness (left) and image filtering (right) trials. (D) Continuous AI for the delay condition separated by handedness. (E) Fraction of first saccade to the left of the midline by latency to move. The latency is from image appearance in the no-delay condition (black line) and from fixation dot disappearance in the delay condition (gray line). Numbers to the right of the figure are the numbers of fixations in each temporal bin, and error bars represent bootstrap *CIs*. (F) Saccade amplitudes at different movement orders after image appearance in the three different filtering conditions. (G) Relationship between subjects' spatial bias and EHI values. Red and black markers identify left- and right-handers, respectively (according to the dominant hand used for writing). Square markers identify subjects with first-degree left-handed familiars. Dots with error bars show the groups' mean ±*SEM*.

the no-delay condition (Figure 4E, black line) in Experiment 2 but was absent when subjects had to withhold movement for 1 s (Figure 4E, gray line). We performed a second repeated-measures ANOVA for the delay condition data with the same factors as in the no-delay data but with the time interval factor reduced to only three levels. Only 80 of the 128 images could be included in the analysis due to the lost trials and the reduction of exploration of filtered images. The results for the delay data were in full concordance with the no-delay condition. We found a main effect of time, $F(2, 158) = 9.3$, $p < 0.001$; handedness, $F(1, 79) = 13.9$, $p <$

0.001; and an interaction between time and handedness, $F(2, 158) = 12.3$, $p < 0.001$. Introducing a delay in movement did not change the early leftward bias.

Finally, we evaluated how the results obtained using images as units of observation are expressed in terms of subjects' behavior. As in Experiment 1, we used the fraction of first fixations to the left as a measure of subject bias. This analysis revealed again a left bias in the first fixation with a mean percentage of left saccades of 58.2% (range 31.9%–89%, $SD = 13$). Percentages of first fixation to the left (Figure 4F) are significantly different from 50% for right-handers, $N = 31$, 62.2%, $t(30) = 5.0$, $p < 0.001$, but not for left-handers, $N = 17$, 50.9%, $t(16) = 0.35$, $p = 0.72$, and both groups also differed, $t(46) = 2.97$, $p = 0.004$. To better understand the relationship between handedness and viewing bias, we evaluated the correlation between the fraction of first fixations to the left and subjects' EHI value. To compare both groups, we compared the score of right-handers against the negative of the value of left-handers (grouped by self-report of dominant hand). Right-handers scored higher than left-handers, mean right-handers 89.9%, mean left-handers −58.4%, $t(46) = 3.87$, $p < 0.001$. Unsurprisingly, EHI and percentage of first saccades to the left correlated when accounting for both groups ($N = 47$, $r = 0.37$, $p = 0.009$). However, correlations within each group were not significant (right-handers $N = 31$, $r = 0.27$, $p = 0.13$; left-handers $N = 16$, $r = 0.21$, $p = 0.4$). This absence of correlation might be only an effect of the reduction in the number of subjects or in the within-group range of scores. In conclusion, although handedness was related to leftward bias, the bias strength was not clearly correlated with an index of motor dominance.

Discussion

In Experiment 2, we demonstrated that the leftward bias reported in Experiment 1 is observed only in right-handers and largely absent in left-handers. This agrees with behavioral studies showing differing visual perceptual biases between right- and left-handers (Bryden, 1965; Gilbert & Bakan, 1973; Heller & Levy, 1981; Levy et al., 1983; Luh et al., 1994). Those differences were not straightforward reversals. Likewise, here, the bias of left-handed subjects is not a reversal of the bias of right-handed subjects. Early bias strength did not correlate well with the EHI, suggesting that the bias is not the result of a pure motor effect. The EHI mainly measures motor dominance and not attentional biases, such as those found with the line-bisection task or cued-attention paradigms. We did not ask our subjects to perform either one of those tasks, so we cannot determine if they are correlated with the viewing bias shown here. However, Foulsham et al.'s (2013) subjects

that presented early leftward biases when exploring scenes also showed leftward error in line bisection. They also tended to start exploration from the left, supporting the idea that the leftward bias correlates with other attentional biases.

To investigate whether leftward bias results from right hemispheric dominance in the processing of global visual content, we presented filtered images. If it did, we would expect a decreased leftward bias for HP filtered images and an increased bias for LP images. The filtering cutoff used here is in the lowest range of spatial frequencies usually tested in contrast-sensitivity functions. It nevertheless clearly affects fixation frequency and saccade length. As shown previously with texture stimuli (Groner et al., 2008), HP images produced shorter saccades than LP images, suggesting that visible content in the periphery is necessary for saccades to that region. In other words, saccades seem not to be directed to image areas for which no information is available even if content seems likely to be there given normal scene structure (Ossandón et al., 2011). Image-filtering did not result in the expected change in bias pattern. The lateralization of spectral processing depends, however, not on the absolute frequencies present in the image but on their distribution (Christman, Kitterle, & Hellige, 1991; Hellige, 1996; Kitterle, Christman, & Hellige, 1990; Kitterle, Hellige, & Christman, 1992). Therefore, bias could still depend on the spectral content. Filtering does nevertheless effectively reduce the amount of global (HP filtered images) or local content (LP). This indicates that leftward bias cannot be explained in terms of opposing hemispheric processes oriented to global or local processing. Likewise, as magnocellular and parvocellular pathways are also segregated in their spectral response, with the faster magnocellular division being much more responsive to low-frequency content (Derrington & Lennie, 1984), our results suggest the bias is not due to differences in the processing speed or lateralization profile of these pathways.

Global precedence effects can also be reversed by making global features less salient (Fink et al., 1997; Fink, Marshall, Halligan, & Dolan, 1999; Han et al., 2002; Lamb & Yund, 1993; Mevorach, Humphreys, & Shalev, 2006). In a series of behavioral, transcranial magnetic stimulation, and neuroimaging studies, Mevorach et al. used modified hierarchical stimuli to independently assess the effects of local and global content and saliency (as determined by stimulus spectral power). This modification left differences in behavior and activity between right and left hemispheres better explained by lateralization, not of global or local processing, but of the processing of salience (Mevorach, Hodsoll, Allen, Shalev, & Humphreys, 2010; Mevorach et al., 2006; Mevorach, Shalev, Allen,

& Humphreys, 2009). The relevant cortical structure for this kind of control is within the PPC and not in the ventral stream where specific category processing modules are. Based on these results, an alternative hypothesis has been proposed to explain global precedence and hemispheric spectral precedence. This hypothesis holds that there are opposing, lateralized systems for the selection or avoidance of salient stimuli (Mevorach et al., 2006), a proposition compatible with the results shown here.

The presentation of a static visual scene, even after filtering, is a salient event and salient stimulus. Therefore, it could cause an attentional bias by activating right temporoparietal and frontal areas that are involved in the response to behaviorally relevant salient stimuli (Corbetta et al., 2008). As the lateralization of selection and avoidance of salient stimuli relates to handedness (Mevorach et al., 2005), the difference in bias we show here is to be expected. In summary, the exploratory bias could reflect attentional bias produced by the stimuli's overall salience.

The closer a saccade is to stimulus onset, the stronger the influence of salience (van Zoest & Donk, 2004, 2005). This results in a dependency between viewing bias and movement latency. This holds for the sudden onset of images in Experiment 1 and the no-delay condition of Experiment 2. However, a forced delay in movement initiation in Experiment 2 did not reduce the bias, and after a delay, the bias did not seem to depend on the latency of the first movement. These results cast doubts on the attentional explanation and raise the question of whether forced fixation before image appearance causes the early bias. We evaluate this question in Experiments 3 and 4.

Experiment 3: Bias and fixation control

Introduction

In the previous experiments, the images displayed directly after the disappearance of a fixation drift-correction point. Almost all of the cited reports on perceptual or exploratory biases use similar procedures. This explicit requirement to fixate on a visual anchor might result in inhibitory processes related to voluntary control that could underlie the observed bias.

Cortical and subcortical mechanisms involved in the voluntary inhibition of response seem also to be dominant in the right hemisphere. Multiple studies have implicated right frontal and right cingulate cortical areas in the inhibition of response, usually in go/no-go and stop-signal tasks (Rubia et al., 2001;

Swick, Ashley, & Turken, 2011). Subcortical pathways also show asymmetries. One of the main neural routes in the voluntary control of eye movements from the frontal cortex to the SC goes through the basal ganglia (Hikosaka, Takikawa, & Kawagoe, 2000). The latter circuit shows left-right asymmetries in dopamine content that have been found to correlate with other, nonocular, exploratory biases (de la Fuente-Fernández, Kishore, Calne, Ruth, & Stoessl, 2000; Zimmerberg, Glick, & Jerussi, 1974). If any of these asymmetries inhibits the left SC more than the right before the beginning of exploration, it will facilitate saccades to the left. As the inhibition will probably decay with time, saccades initiated later should be less biased.

One way to control for inhibition related to voluntary fixation is to introduce a gap between fixation and stimulus onset. This procedure reduces the latency of eye movements to the extent that a second population of very fast "express" saccades appears (Fischer & Ramsperger, 1984; Saslow, 1967). This gap effect is mediated by changes in the activation profiles of motor neurons in the SC (Dorris & Munoz, 1995; Dorris, Paré, & Munoz, 1997). Accordingly, it is absent after SC lesions (Schiller, Sandell, & Maunsell, 1987) and becomes more prominent after frontal cortical lesions (Braun, Weber, Mergner, & Schulte-Mönting, 1992; Guitton, Buchtel, & Douglas, 1985; Pierrot-Deseilligny, Rivaud, Gaymard, & Agid, 1991). We used the gap effect paradigm in Experiment 3 to evaluate the asymmetry-of-inhibition hypothesis as an explanation for the early bias described above.

Methods

Participants

Twenty-four new subjects participated in the study (18 females, mean age 22 years, *SD* 2.5 years, range 19–28 years). All subjects were right-handed, had normal or corrected-to-normal vision, and participated either for credits or monetary reward.

Stimuli

Natural and urban images from Experiment 1 were used. Image presentation and eye tracking were identical to Experiment 1.

Procedure

Procedures were similar to those in Experiment 1, but we introduced temporal gaps between fixation dot disappearance and image appearance, creating four experimental conditions: 0-ms no-gap, 300-ms gap, 600-ms gap, and 900-ms gap (Figure 5A). During the temporal gap, the screen was at the gray scale level of
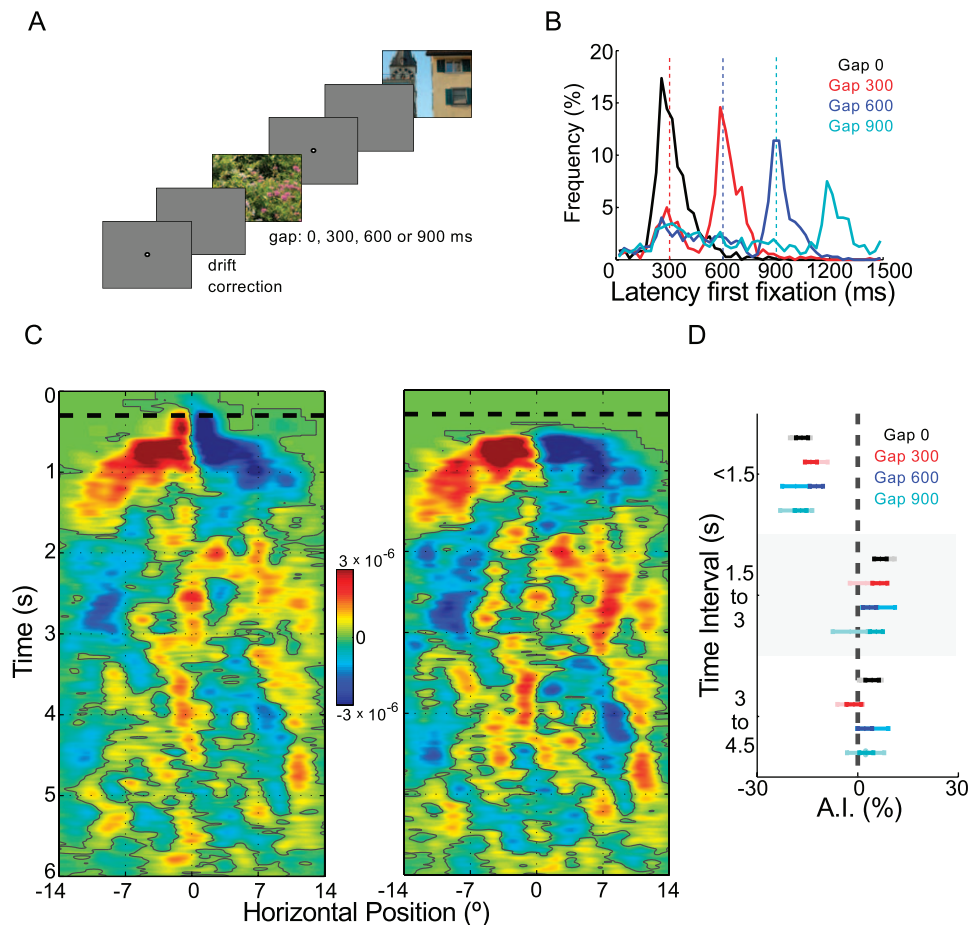
Figure 5. (A) Trials started with a requirement to fixate a dot in the center of the screen. Once subjects were fixating in the middle, the screen turned blank for a variable gap interval and then the image appeared. (B) Distribution of first movements' latency after fixation dot disappearance for the different gap conditions. Vertical dashed lines show moment of image appearance for the different conditions. (C) Difference STM for the 300-ms gap condition for the complete data set (left) and for only the trials without movement prior to image onset (right). (D) Asymmetry index by time interval and gap condition. The time interval starts at image onset. Saturated colors represent all trials, and the lighter colors are used for only the trials without movements prior to image onset.

the drift-correction period, and the gap duration was randomized across trials. Subjects did not receive any instruction in relation to the existence of a gap.

Results

In Experiment 3, we evaluated the role of inhibition control in the production of exploratory biases. Subjects' median latency to the first movement after image appearance (Figure 5B) was not different between any of the gap conditions (gap 0 = 297 ms, gap 300 = 320 ms, gap 600 = 314 ms, gap 900 = 317 ms, Kruskal-Wallis $\chi^2 = 1.28$, $p = 0.73$, data only from subjects with more than five events per gap). The first movement sometimes began during the gap period with increasing frequency as the gap lengthened (gap 300: 16.3%, gap 600: 37%, gap 900: 54.7%). These first movements done during the gap period peaked at a

similar time to the no-gap condition and then progressively decreased until about 150 ms after stimulus onset. The difference STM plot shows that introducing a gap did not change the overall pattern of bias after image appearance (Figure 5C, example for the 300-ms gap condition). The bias was also present for movements during the gap period.

We evaluated the role of the gap in a repeated-measures ANOVA with factors gap length (no-gap, 300 ms, 600 ms, and 900 ms) and time interval (three levels, starting at the moment of image appearance). The data from one image, >abs (3 SD), was considered as an outlier and removed from analysis. We found only a main effect of time, $F(2, 236) = 99.8$, $p < 0.001$, with a post hoc difference between the first interval and the other two (Figure 5D). There was no effect due to gap modification. As this analysis also included the trials in which an eye movement began before image appearance, we performed a second ANOVA only with trials

in which subjects refrained completely from eye movement until after image appearance (Figure 5D, light colors). The result was again only a significant main effect for time interval, $F(2, 102) = 28$, $p < 0.001$, similar to the one with the complete data. In summary, gaps between fixation dot disappearance and image appearance did not change the spatial bias.

Analysis based on a subject measure was performed for the fraction of first fixations to the left in two analyses: one if the movement was performed before image presentation and one for movement after. The fraction of first fixations after image presentation was biased to the left for all gap conditions, gap 0 = 68.6%, $t(18) = 5.2$, $p < 0.001$; gap 300 = 69.4%, $t(18) = 5.29$, $p < 0.001$; gap 600 = 66.8%, $t(18) = 5.09$, $p < 0.001$; and gap 900 = 67.8%, $t(18) = 6.0$, $p < 0.001$. A repeated-measures ANOVA with a main factor of gap condition did not show difference between the groups, $N = 19/24$, $F(3, 54) = 0.65$, $p = 0.58$. Saccades in the absence of stimuli during the gap period were also biased to the left in all conditions (gap 300 = 73.8%, gap 600 = 69.3%, gap 900 = 67.6%). A repeated-measures ANOVA with a main factor of gap condition did not show a difference between groups, $F(2, 16) = 0.42$, $p = 0.66$.

Discussion

In Experiment 3, we evaluated the role of fixation control by introducing a temporal gap between fixation and image onset. This modification reduces reaction time in reflexive saccade tasks. Despite our expectations, the gap did not reduce movement latencies or cause the appearance of a bimodal distribution. Although this was unlikely for the 600-ms and 900-ms gaps, a 300-ms gap is within the optimal gap range (200–300 ms) for producing express saccades in humans (Mayfrank, Mobashery, Kimmig, & Fischer, 1986; Saslow, 1967). The two longer latencies were tested to compare with the observed effect of movement latency seen in Experiment 1. Express movements initially appear only in a fraction of trials but increase greatly in frequency with training (Fischer & Ramsperger, 1986). However, most subjects do show short-latency saccades already in the first experimental session, so a lack of training with the task is unlikely to explain the lack of express movements in Experiment 3. This absence of latency reduction disagrees with the literature on reflexive-saccade experiments but agrees with one previous report about the gap effect in free viewing in monkeys (Schiller, Slocum, Carvey, & Tolias, 2004). In that experiment, a gap before stimulus in a free-viewing task using complex scenes also failed to reduce movement latency. Moreover, the sudden appearance of a complex background prevented monkeys from producing faster saccades to targets even after an optimal gap. Considering the long movement latency after onset compared to the movement latency in reflexive saccade paradigms and our absence of a gap effect, we speculate that the sudden onset of a complex scene increases inhibition of the motor layers of the SC and overrides the disinhibition elicited by a gap (Dorris & Munoz, 1995).

Regardless, the visual fixation anchor was removed for periods up to 900 ms, but the bias remained. Therefore, this result does not support the hypothesis that the exploratory bias is produced by the requirement to fixate in the center prior to exploration start. However, as no gap effect was produced, we cannot exclude the possibility that the inhibition remained despite the gap. For this reason, in Experiment 4, we tested the role of voluntary and explicit fixation control by entirely removing the requirement to fixate.

Experiment 4: Bias and continuous image presentation

Introduction

In Experiment 4, we tested the role of voluntary and explicit fixation control by changing the images unexpectedly during the exploration of a previous image. In this way, we eliminated resting intervals between trials and avoided the explicit requirement to fixate on the center of the screen before changing the images. This experimental setting also allowed us to test whether the bias effect was produced only by image changes occurring during a fixation period or also when the image appears during a saccade. This distinction allowed us to investigate whether the inhibition of visual processing during saccades influences the bias pattern.

Methods

Participants

Seventeen new subjects participated in the study (10 females, mean age 22.8 years, *SD* 2.5 years, range 19–29 years). All subjects were right-handed, had normal or corrected-to-normal vision, and participated for either credits or monetary reward.

Stimuli

In Experiment 4, we used different original images than in the three others, 165 images from the "LabelMe" database (Russell, Torralba, Murphy, &
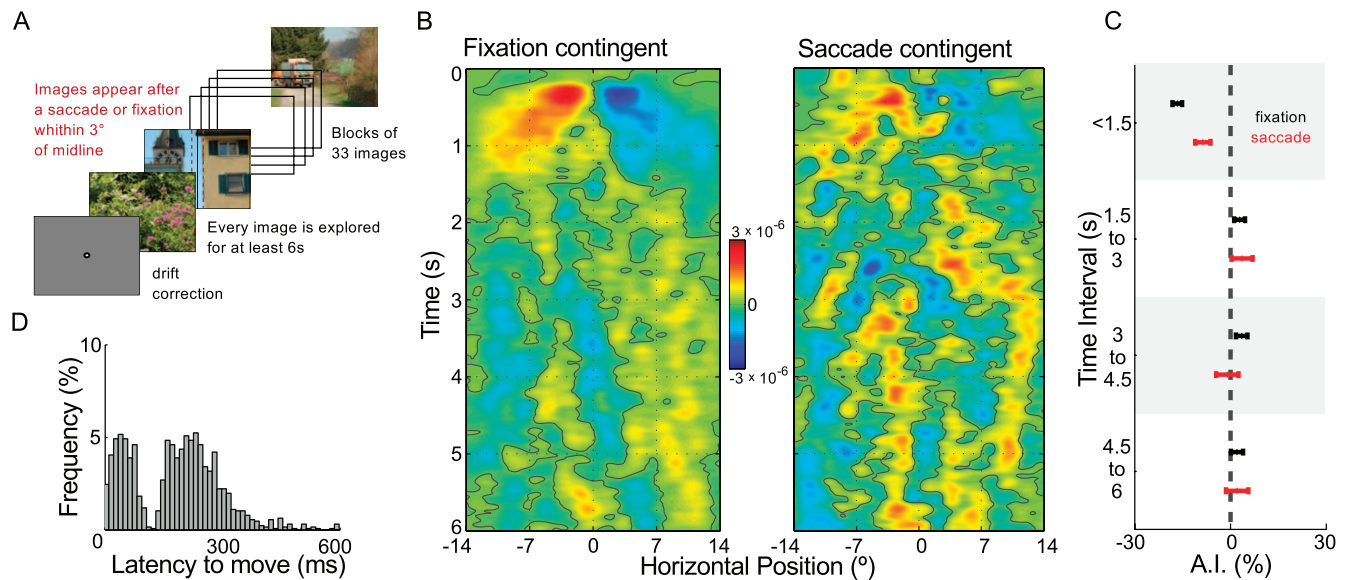
Figure 6. (A) Experiment 4 procedure. Images appeared in blocks of 33, one after another, without intervening blank screens or drift-correction procedures. After the first image in the block, successive image changes occurred after at least 6 s of exploration and contingent on the start of a fixation or saccade within 3° of the horizontal midline (shown in the third image by black and dashed red lines that were not present during image viewing). (B) Difference STM for the fixation and saccade condition. (C) AI by time interval for the two conditions. (D) Latency to move after image change in fixation-contingent trials.

Freeman, 2008) and mirror-reversed them as above. We did this to ensure the bias was not bound to a specific image set. We took care that the images did not include cues (e.g., text) that could make subjects aware that some images were mirror-reversed. Image presentation and eye tracking was identical to Experiment 1.

Procedure

Each experiment was completed in less than 1-hr sessions in which the 165 scenes were presented. Each session was divided into five blocks, which used 33 images each. Each block started with an image presented after a drift-correction point, but after that first image, the next 32 images appeared in sequence without intervening fixation points. The experiment was set to obtain image changes during a saccade half the time and, in the other half, changes during a fixation period (50 to 140 ms after fixation start). Image change occurred after two criteria had been fulfilled (Figure 6A): (a) The previous image was explored for at least 6 s, and (b) gaze was within 3 visual degrees of the image's horizontal center (fixation start position for fixation-change trials and previous fixation end position for saccade-change trials). The combination of criteria ensured that subjects could not predict exactly when a new image would appear. Subjects explored a set of original and mirror-reversed images with each exposed to only one version of each image, paired as in Experiment 1.

Due to hardware limitations and the uncertainty of when a saccade or fixation would end, saccade- or fixation-contingent changes did not always occur as planned. In only 44.3% of the saccade-contingent trials did the change occur during a saccade; the rest were right after the end of the saccade. Overall, change during a saccade occurred when the saccade was longer or during saccades associated with blinks. During fixation-contingent trials, in 92.6% of the trials, the change was achieved during a fixation. Data were reassigned offline to the correct saccade- and fixation-contingent conditions.

Results

In Experiment 4, we evaluated the role of fixation control in relation to the subjects' instruction in Experiments 1, 2, and 3 to fixate in the middle of the screen before exploration of the stimuli. In Experiment 4, image changes occurred suddenly while subjects explored the previous image. STM profiles show that this did not change the overall pattern of bias (Figure 6B), but it seems reduced in the saccade-contingent trials.

We evaluated the role of the sudden change of images during saccade or fixation periods with a repeated-measures ANOVA with factors time interval (four levels, starting at the moment of image appearance) and movement condition (two levels, change of

images during a fixation or during a saccade). Due to the fewer saccade-contingent trials, only 134 of 185 images yielded sufficient information on every level of the different factors to perform the repeated-measures analysis. We found only a main effect of time, $F(3, 399) = 16.5$, $p < 0.001$, with a post hoc difference between the first interval and the other three (Figure 6C). There was no significant difference between images appearing during a saccade or during a fixation period.

Analysis based on subject measures was performed for the percentage of first saccades to the left after image change in two different conditions: saccade- and fixation-contingent changes. The percentage was higher than chance in each condition, fixation = 60.3%, $t(16) = 4.27$, $p < 0.001$; saccade = 57.7%, $t(16) = 3.02$, $p = 0.008$, and similar in both, $t(32) = 0.72$, $p = 0.47$. During fixation-contingent trials, latency for the next movements showed a marked bimodal distribution (Figure 6D). Based on the literature of countermanding tasks in monkeys and humans, in which the time needed to cancel a movement is between 125 and 145 ms (Hanes & Carpenter, 1999), this bimodal distribution suggests that movements begun before 125 ms of image change were responses to targets in the previous image that could not be stopped. When taking into account only the movements in the fixation-contingent trials that started after 125 ms, the fraction of saccades to the left increased from 60.1% to 63.7%. Nevertheless, the comparison between fixation- and saccade-contingent trials remains nonsignificant, $t(32) = 1.43$, $p = 0.15$.

Discussion

The results of Experiment 4 confirmed that the exploratory bias is not caused by the explicit requirement to fixate. The pattern of viewing bias remained in both fixation- and saccade-contingent trials. However, after excluding the left-handed group of Experiment 2, the fraction of first fixations to the left was the smallest of all four experiments, and the saccade condition showed the smallest bias of all. It is important to note that Experiment 4 also differed from the other three in the image set used. Because the methods in all four experiments were chosen explicitly to demonstrate that the bias does not depend on actual content and we have already shown that the leftward bias is present in different types of images, we think the new image set is unlikely to have caused changes in bias.

The processing of visual stimuli is actively suppressed during eye movements. This is known as "saccadic suppression" (Ross, Morrone, Goldberg, & Burr, 2001). This inhibition makes the detection of major changes in visual scenes difficult (e.g., Grimes, 1996; Hollingworth & Henderson, 2002). If the bias is driven by visual attention, and saccadic suppression reduces the saliency of the onset of a new image, then changes during saccades should result in less bias. This was observed in our data. In agreement with this view, changes are detected faster in the left hemifield in the change-blindness paradigm (Lyilikci, Becker, Güntürkün & Amado, 2010; Spotorno & Faure, 2011). This has been shown in detection experiments in which scenes were flickered and has not yet been investigated in saccade-contingent paradigms. Neuroimaging and transcranial magnetic stimulation studies show that change-detection performance correlates with activity in the right parietal and right dorsolateral prefrontal cortex (Beck, Muggleton, Walsh, & Lavie, 2006; Beck, Rees, Frith, & Lavie, 2001). The fact that bias appears to be reduced in saccade-contingent trials compared to the first three experiments suggests that saliency could be the crucial factor driving the leftward bias.

General discussion

Summary

We presented four experiments that showed an asymmetric exploratory bias during the initial exploration of complex visual stimuli. This bias was robust to different experimental conditions. Across the four experiments, we tested a total of 132 subjects. The only ones who did not exhibit a leftward bias were the 17 left-handers of Experiment 2. A second bias to the right following the initial bias to the left and continuing until trial's end was evident in Experiment 1. These biases were independent of each other, of image asymmetries, and of image type. The rightward bias was small and could not be confirmed in the other three experiments: Its existence and relevance need to be confirmed before considering it a consistent effect. The first saccade mostly explains the early bias. This bias was unlikely to result from a predominance of global features or an asymmetry in inhibitory control. We found a trade-off between movement latency and the bias of the first movement. Importantly, the general bias pattern was not changed by a number of experimental manipulations that removed the explicit requirement to fixate in the center or that disentangled the first saccade from image onset. These experiments demonstrate a horizontal bias in visual exploration under a wide variety of experimental conditions. This is not explained by previously reported differences of hemispheric lateralization of the processing of visual content. Instead, the simplest explanation is that the bias is driven by hemispheric asymmetries in the attentional system.

Bias and stimulus

There are different ways in which spatial viewing bias can depend on stimulus content. For instance, one usual explanation of the center bias described in Experiment 1 is that the features of the stimuli itself are concentrated in the center. This is also known as the "photographer bias": The photographer centers the composition on the content rich in features. This can explain the observed centered distribution in at least two ways. In the first case, the empirical distribution is the direct result of visual selection being driven by the actual stimulus features, which, in most cases, are centered, and therefore, aggregated behavior will show it correspondingly. In this case, the real bias is the inhomogeneous distribution of features in the visual stimuli and not in the behavior. In the second case, the empirical distribution is truly biased, i.e., it does not entirely depend on the distribution of features in the currently presented stimulus but is a strategy based on learned stimuli statistics. Evidence supports both views with experiments showing that the empirical fixation distribution is dependent on the actual feature distribution (Tseng et al., 2009) or independent of it (B. Tatler, 2007).

The asymmetric bias described here cannot be explained by the location of features in the stimuli because mirror-reversing the images controls this. Therefore, we observed true behavioral bias. This bias could still be a learned strategy based upon the statistics of content distribution. However, it is also not the case that the overall exploration is biased to the left: The bias is restricted to the start of the exploration of a new scene. As a learned strategy this early bias might be useful for text or other kinds of structured stimuli, such as web pages (Betz et al., 2010).

As the biases shown here are asymmetric, there is another possibility of stimulus-driven bias: It may be caused by hemispheric dominance of visual-processing modules for specific stimulus content. We discuss in the next two sections both alternatives: strategic sampling of the stimulus as in the example of reading and lateralization of visual-processing modules.

Role of strategic sampling

The prime example of strategic sampling is reading scanning habits. Although we did not test this directly, several reasons make this explanation unlikely. First, left-handers would have the same reading bias; nevertheless, they do not show the same bias pattern. Second, 6-month-old humans and animals, such as monkeys and dogs, also present such viewing bias (Guo et al., 2009). Third, horizontal exploratory asymmetries also appear in other behaviors, such as head-turning

biases in neonates (e.g., L. B. Cohen, 1972; Liederman & Kinsbourne, 1980) or kissing (Güntürkün, 2003), which seem to have little to do with reading. Fourth, studies about the dependence of perceptual asymmetries on reading show that subjects still present leftward bias despite reading from right to left although the bias is often smaller, especially for subjects literate only in a right-to-left language (Chokron & De Agostini, 2000; Gilbert & Bakan, 1973; Heath, Rouhana, & Ghanem, 2005; Megreya & Havard, 2011; Nicholls & Roberts, 2002; Vaid & Singh, 1989). Finally, although a learned strategy from reading might generalize to other behavior, the stimuli in our and other experiments do not involve any text. Therefore, if viewing bias is secondary to reading habits, this implies that a strategy associated with reading has become an automatic process that cannot be overridden by task-specific requirements, at least in experiments that use sudden stimulation on computer monitors. It seems more plausible that, if bias were related to reading, it would be the result of spatial priming from reading instructions on the screen. Such a carryover effect has been shown before for successive unrelated tasks (e.g., Foulsham et al., 2013) and should be tested directly in further work. Altogether, these different considerations suggest that the viewing bias is not primarily based on learned reading strategy or normal monitor-scanning strategies.

Role of lateralization of visual-processing modules

The hemispheric specialization hypothesis is supported by perceptual bias experiments that show opposing hemifield advantages for different kinds of stimuli. The best examples are the advantage of the side of the face presented in the left hemifield and the advantage for text presented in the right hemifield in accordance with right and left hemisphere dominance for the respective stimuli. Moreover, when faces appear upside down, making recognition more difficult, exploratory biases shrink (Barton et al., 2006; S. H. Butler & Harvey, 2005; Coolican, Eskes, McMullen, & Lecky, 2008; Guo, Meints, Hall, Hall, & Mills, 2009; Leonards & Scott-Samuel, 2005). This suggests that hemispheric dominance does play a role in both perceptual and exploratory bias. On the other hand, perceptual bias seems to be highly dependent on exploratory patterns: The left-field bias for faces correlates with the number of fixations on the left (S. Butler et al., 2005), and free-viewing paradigms result in stronger perceptual biases than tachiscopically presented stimuli (S. H. Butler & Harvey, 2008). There is also less perceptual bias when images appear too briefly to be explored and when exploration time is

much longer than the period of leftward bias (S. H. Butler & Harvey, 2006; Phillips & David, 1997). Our results also argue against a simple effect of lateralization of visual-processing modules: The exploratory bias is present with a variety of stimuli, making hemispheric specialization as a single factor unlikely. Moreover, even for perceptual biases directed to the right hemifield, as in the case of text, there is still a left-hemifield bias when stimuli appear simultaneously in both fields (Heron, 1957). In summary, although the use of stimuli that is processed asymmetrically in the brain might modulate exploratory asymmetries, general evidence speaks against lateralization of specific visual-processing modules as the cause of bias.

Role of attentional control

An alternative cause of leftward bias is brain asymmetries in attentional control related to the salience of new stimuli. Attentional mechanisms are lateralized in the brain with the most striking example being neglect syndrome, in which one hemifield, usually the left, is unattended after injuries to the contralateral hemisphere. Healthy subjects present plenty of other behavioral evidence of attentional bias in different phenomena, such as spatial memory errors (Buschman, Siegel, Roy, & Miller, 2011; Della Sala, Darling, & Logie, 2010), boundary extension in scene memory tasks (e.g., Dickinson & Intraub, 2009), multitracking of stimuli (Alvarez & Cavanagh, 2005), and feature-based attention capture (Du & Abrams, 2010).

These different attentional or perceptual biases are observed in both tachiscopic and free-viewing conditions; thus, it is not easy to address whether attention or perceptual biases follow scanning biases or the other way around. For instance, in the line-bisection task, a standard test of attentional bias in clinical settings, healthy subjects consistently show a slight bias or "pseudoneglect," usually to the left side. However, there is large variability on this subtle bias, depending both on subject characteristics and task details (Jewell & McCourt, 2000). Structurally, it seems that the strength of bias in this task depends on interhemispheric asymmetries in the attentional network: Individual behavioral biases correlate both with neural activity asymmetries in frontoparietal areas (Szczepanski & Kastner, 2013) and with anatomical asymmetries in the white-matter tracts that connect the parietal and frontal cortices (Thiebaut de Schotten et al., 2011). One of the most relevant behavioral parameters that affects the bias direction and strength is whether visual scanning is allowed or not (Jewell & McCourt, 2000), making it possible to partly differentiate between contributions of covert and overt attention. Some of the largest effects in line bisection are seen in experiments that manipulate the

direction of scanning with the largest effect seen when subjects are forced to start scanning from the left (Brodie & Pettigrew, 1996; Ishiai, Furukawa, & Tsukagoshi, 1989). Similarly, the studies about perceptual asymmetries in face-perception bias show an enhancement of the bias for the left hemifield when scanning is allowed (S. H. Butler & Harvey, 2005). This suggests that attentional and perceptual biases follow viewing biases.

On the other hand, attentional and perceptual biases also appear when eye movements are not possible or can be dissociated from them. For instance, one study of change blindness showed faster detection of changes in the left hemifield but unrelated to early viewing biases (Lyilikci et al., 2010). In another example, boundary-extension errors appear only when subjects are prevented from exploring the images and not when they do explore, but a marked viewing bias to the left nevertheless remains (Dickinson & Intraub, 2009). In the case of asymmetries in the perception of visual stimuli, one study found that while controlling for premotor, scanning, and attentional biases, only attention could modify these biases (Nicholls & Roberts, 2002). Therefore, there is evidence for causation in both directions with covert attention and content processing on one side and overt eye movements on the other.

To differentiate between these two alternatives is experimentally and conceptually challenging because overt and covert attention are strongly linked. The cortical and subcortical networks of overt and covert attention overlap to a large extent (Corbetta et al., 1998; Nobre, Gitelman, Dias, & Mesulam, 2000). This organization results in both obligatory presaccadic shifts of attention being produced by the programming of eye movements (Deubel & Schneider, 1996) and small saccadic movement in the cued direction being produced by covert attention (Engbert & Kliegl, 2003; Hafed & Clark, 2002).

Different aspects of our results support an attentional explanation of the early leftward bias. The onset of a complex scene is a salient event, and a spontaneous delay in exploring a new image lessens bias. This agrees with the dependence of saccade latencies on low-level salience (van Zoest & Donk, 2004, 2005). Further support for this view is that the smallest bias occurs when the image appears during a saccade, a period in which processing of visual stimuli is actively inhibited and salience presumably reduced. However, this last conclusion needs to be taken with caution because the unexpected image change during saccade or fixation periods did not differ significantly in Experiment 4. Therefore, it is likely that the high saliency of the appearance of a new complex stimulus might partly explain the strong exploratory bias shown here. However, another manipulation that might have reduced the saliency of new stimuli by preventing subjects from exploring until 1 s after stimulus onset did

not change the bias pattern. We found a clear effect of handedness, which may be linked with asymmetries in the salience selection mechanisms in the PPC (Mevorach et al., 2006), which also supports an attentional cause. However, these are indirect post hoc explanations that need to be tested in the future by looking for evidence of an association between viewing bias and other attentional biases and between the viewing bias and structural or functional asymmetries in the subjects' attentional network.

Conclusion

Although the exploration of static scenes is a limited example of how visual stimuli are encountered in the real world, we have presented here evidence for a strong early leftward bias and a late rightward bias that are probably present in many other task contexts. Because the early leftward bias is a robust finding, we believe it will now be relevant to evaluate how it could affect the results of any research that includes visual attentional components. This is especially the case for tasks with noncontrolled asymmetric stimuli or when differences between left- and right-handers are found. Finally, these biases indicate asymmetries in the structure of the visual-selection system that might not have a functional role but that need, nevertheless, to be taken into account when modeling the organization of the visual system.

Keywords: spatial bias, free-viewing, eye movements

References

Aguirre, G. K., & D'Esposito, M. (1999). Topographical disorientation: A synthesis and taxonomy. *Brain, 122,* 1612–1628.

Aguirre, G. K., Zarahn, E., & D'Esposito, M. (1998). An area within human ventral cortex sensitive to "building" stimuli: Evidence and implications. *Neuron, 21,* 373–383.

Alvarez, G. A., & Cavanagh, P. (2005). Independent resources for attentional tracking in the left and right visual hemifields. *Psychological Science, 16*(8), 637–643, doi:10.1111/j.1467-9280.2005.01587.x.

Barton, J. J. S., Radcliffe, N., Cherkasova, M. V., Edelman, J., & Intriligator, J. M. (2006). Information processing during face recognition: The effects of familiarity, inversion, and morphing on scanning fixations. *Perception, 35*(8), 1089–1105, doi:10.1068/p5547In.

Beaumont, J. G. (1985). Lateral organization and aesthetic preference: The importance of peripheral visual asymmetries. *Neuropsychologia, 23,* 103–113.

Beck, D. M., Muggleton, N., Walsh, W., & Lavie, N. (2006). Right parietal cortex plays a critical role in change blindness. *Cerebral Cortex, 16,* 712–717, doi:10.1093/cercor/bhj017.

Beck, D. M., Rees, G., Frith, C. D., & Lavie, N. (2001). Neural correlates of change detection and change blindness. *Nature Neuroscience, 4*(6), 645–650.

Betz, T., Kietzmann, T. C., Wilming, N., & König, P. (2010). Investigating task-dependent top-down effects on overt visual attention. *Journal of Vision, 10*(3):15, 1–14, http://www.journalofvision.org/content/10/3/15, doi:10.1167/10.3.15. [PubMed] [Article]

Braun, D., Weber, H., Mergner, T., & Schulte-Mönting, J. (1992). Saccadic reaction times in patients with frontal and parietal lesions. *Brain, 115,* 1359–1386.

Brodie, E. E., & Pettigrew, E. L. (1996). Is left always right? Directional deviations in visual line bisection as a function of hand and initial scanning direction. *Neuropsychologia, 34*(5), 467–470.

Bryden, M. P. (1965). Tachistoscopic recognition, handedness, and cerebral dominance. *Neuropsychologia, 3*(1), 1–8, doi:10.1016/0028-3932(65)90015-1.

Burt, D. M., & Perrett, D. I. (1997). Perceptual asymmetries in judgements of facial attractiveness, age, gender, speech and expression. *Neuropsychologia, 35,* 685–693.

Buschman, T. J., Siegel, M., Roy, J. E., & Miller, E. K. (2011). Neural substrates of cognitive capacity limitations. *Proceedings of the National Academy of Sciences, USA, 108*(27), 11252–11255, doi:10.1073/pnas.1104666108.

Butler, S., Gilchrist, I. D., Burt, D. M., Perrett, D. I.,

Jones, E., & Harvey, M. (2005). Are the perceptual biases found in chimeric face processing reflected in eye-movement patterns? *Neuropsychologia, 43*(1), 52–59, doi:10.1016/j.neuropsychologia.2004.06.005.

Butler, S. H., & Harvey, M. (2005). Does inversion abolish the left chimeric face processing advantage? *Neuroreport, 16*(18), 1991–1993.

Butler, S. H., & Harvey, M. (2008). Effects of aging and exposure duration on perceptual biases in chimeric face processing. *Cortex, 44*(6), 665–672, doi:10.1016/j.cortex.2007.02.001.

Butler, S. H., & Harvey, M. (2006). Perceptual biases in chimeric face processing: Eye-movement patterns cannot explain it all. *Brain Research, 1124*(1), 96–99, doi:10.1016/j.brainres.2006.09.069.

Chiang, C. H., Ballantyne, A. O., & Trauner, D. A. (2000). Development of perceptual asymmetry for free viewing of chimeric stimuli. *Brain and Cognition, 44*(3), 415–424, doi:10.1006/brcg.1999.1202.

Chokron, S., & De Agostini, M. (2000). Reading habits influence aesthetic preference. *Cognitive Brain Research, 10,* 45–49.

Christie, J., Ginsberg, J. P., Steedman, J., Fridriksson, J., Bonilha, L., & Rorden, C. (2012). Global versus local processing: Seeing the left side of the forest and the right side of the trees. *Frontiers in Human Neuroscience, 6*(February), 28, doi:10.3389/fnhum.2012.00028.

Christman, S. (1989). Perceptual characteristics in visual laterality research. *Brain and Cognition, 11*(2), 238–257.

Christman, S., Kitterle, F. L., & Hellige, J. (1991). Hemispheric asymmetry in the processing of absolute versus relative spatial frequency. *Brain and Cognition, 16*(1), 62–73.

Cohen, L. (2003). Visual word recognition in the left and right hemispheres: Anatomical and functional correlates of peripheral alexias. *Cerebral Cortex, 13*(12), 1313–1333, doi:10.1093/cercor/bhg079.

Cohen, L., Dehaene, S., Naccache, L., Lehericy, S., Dehaene-Lambertz, G., Henaff, M., & Michel, F. (2000). The visual word form area: Spatial and temporal characterization of an initial stage of reading in normal subjects and posterior split-brain patients. *Brain, 123,* 291–307.

Cohen, L. B. (1972). Attention-getting and attention-holding processes of infant visual preferences. *Child Development, 43*(3), 869, doi:10.2307/1127638.

Coolican, J., Eskes, G. A., McMullen, P. A., & Lecky, E. (2008). Perceptual biases in processing facial identity and emotion. *Brain and Cognition, 66*(2), 176–187, doi:10.1016/j.bandc.2007.07.001.

Corbetta, M., Akbudak, E., Conturo, T. E., Snyder, A. Z., Ollinger, J. M., Drury, H. A., ... Shulman, G. L. (1998). A common network of functional areas for attention and eye movements. *Neuron, 21*(4), 761–773.

Corbetta, M., Patel, G., & Shulman, G. L. (2008). The reorienting system of the human brain: From environment to theory of mind. *Neuron, 58*(3), 306–324, doi:10.1016/j.neuron.2008.04.017.

Corbetta, M., & Shulman, G. L. (2002). Control of goal-directed and stimulus-driven attention in the brain. *Nature Reviews Neuroscience, 3*(3), 201–215, doi:10.1038/nrn755.

Corbetta, M., & Shulman, G. L. (2011). Spatial neglect and attention networks. *Annual Reviews Neuroscience, 34,* 569–599, doi:10.1146/annurev-neuro-061010-113731.

De Agostini, M., Kazandjian, S., Cavézian, C., Lellouch, J., & Chokron, S. (2010). Visual aesthetic preference: Effects of handedness, sex and age-related reading/writing directional scanning experience. *Writing Systems Research, 2*(2), 77–85, doi:10.1093/wsr/wsq006.

de la Fuente-Fernández, R., Kishore, A., Calne, D. B., Ruth, T. J., & Stoessl, A. J. (2000). Nigrostriatal dopamine system and motor lateralization. *Behavioural Brain Research, 112*(1–2), 63–68.

Delis, D., Robertson, L., & Efron, R. (1986). Hemispheric specialization of memory for visual hierarchical stimuli. *Neuropsychologia, 24*(2), 205–214.

Della Sala, S., Darling, S., & Logie, R. H. (2010). Items on the left are better remembered. *Quarterly Journal of Experimental Psychology, 63*(5), 848–855, doi:10.1080/17470211003690672.

De Renzi, E., Perani, D., Carlesimo, G. A., Silveri, M. C., & Fazio, F. (1994). Prosopagnosia can be associated with damage confined to the right hemisphere—An MRI and PET study and a review of the literature. *Neuropsychologia, 32*(8), 893–902.

Derrington, A. M., & Lennie, P. (1984). Spatial and temporal contrast sensitivities of neurons in lateral geniculate nucleus of macaque. *Journal of Physiology, 357,* 219–240.

Deubel, H., & Schneider, W. X. (1996). Saccade target selection and object recognition: Evidence for a common attentional mechanism. *Vision Research, 36*(12), 1827–1837.

Dickinson, C. A., & Intraub, H. (2009). Spatial asymmetries in viewing and remembering scenes: Consequences of an attentional bias? *Attention, Perception, & Psychophysics, 71*(6), 1251–1262, doi:10.3758/APP.71.6.1251.

Dorris, M. C., & Munoz, D. P. (1995). A neural correlate for the gap effect on saccadic reaction times in monkey. *Journal of Neurophysiology*, *73*(6), 2558–2562.

Dorris, M. C., Paré, M., & Munoz, D. P. (1997). Neuronal activity in monkey superior colliculus related to the initiation of saccadic eye movements. *Journal of Neuroscience*, *17*(21), 8566–8579.

Du, F., & Abrams, R. A. (2010). Visual field asymmetry in attentional capture. *Brain and Cognition, 72*(2), 310–316, doi:10.1016/j.bandc. 2009.10.006.

Engbert, R., & Kliegl, R. (2003). Microsaccades uncover the orientation of covert attention. *Vision Research, 43,* 1035–1045.

Epstein, R., & Kanwisher, N. (1998). A cortical representation of the local environment. *Nature, 392,* 598–601.

Field, D. J. (1987). Relations between the statistics of natural images and the response properties of cortical cells. *Journal of the Optical Society of America, A, Optics and Image Science, 4*(12), 2379–2394.

Fink, G. R., Halligan, P., Marshall, J., Frith, C. D., Frackowiak, R., & Dolan, R. J. (1996). Where in the brain does visual attention select the forest and the trees? *Nature, 382,* 626–628.

Fink, G. R., Halligan, P. W., Marshall, J. C., Frith, C. D., Frackowiak, R. S., & Dolan, R. J. (1997). Neural mechanisms involved in the processing of global and local aspects of hierarchically organized visual stimuli. *Brain, 120(10),* 1779–1791, doi:10. 1093/brain/120.10.1779.

Fink, G. R., Marshall, J. C., Halligan, P. W., & Dolan, R. J. (1999). Hemispheric asymmetries in global/ local processing are modulated by perceptual salience. *Neuropsychologia, 37*(1), 31–40.

Fischer, B., & Ramsperger, E. (1986). Human express saccades: Effects of randomization and daily practice. *Experimental Brain Research, 64,* 569–578.

Fischer, B., & Ramsperger, E. (1984). Human express saccades: Extremely short reaction times of goal directed eye movements. *Experimental Brain Research, 57*(1), 191–195.

Foulsham, T., Gray, A., Nasiopoulos, E., & Kingstone, A. (2013). Leftward biases in picture scanning and line bisection: A gaze-contingent window study. *Vision Research, 78,* 14–25, doi:10.1016/j.visres. 2012.12.001.

Frederikse, M. E., Lu, A., Aylward, E., Barta, P., & Pearlson, G. (1999). Sex differences in the inferior parietal lobule. *Cerebral Cortex, 9*(8), 896–901, doi: 10.1093/cercor/9.8.896.

Gilbert, C., & Bakan, P. (1973). Visual asymmetry in perception of faces. *Neuropsychologia, 11*(3), 355–362.

Gonzalez, R. C., & Woods, R. E. (2008). *Digital image processing*. Upper Saddle River, NJ: Prentice Hall.

Good, C. D., Johnsrude, I., Ashburner, J., Henson, R. N., Friston, K. J., & Frackowiak, R. S. (2001). Cerebral asymmetry and the effects of sex and handedness on brain structure: A voxel-based morphometric analysis of 465 normal adult human brains. *NeuroImage, 14*(3), 685–700, doi:10.1006/ nimg.2001.0857.

Grimes, J. (1996). On the failure to detect changes in scenes across saccades. In *Perception* (pp. 89–110). New York: Oxford University Press.

Groner, M. T., Groner, R., & von Mühlenen, A. (2008). The effect of spatial frequency content on parameters of eye movements. *Psychological Research, 72,* 601–608, doi:10.1007/ s00426-008-0167-1.

Guitton, D., Buchtel, H., & Douglas, R. M. (1985). Frontal lobe lesions in man cause difficulties in suppressing reflexive glances and in generating goal-directed saccades. *Experimental Brain Research, 58,* 455–472.

Güntürkün, O. (2003). Human behaviour: Adult persistence of head-turning asymmetry. *Nature, 421*(6924), 711, doi:10.1038/421711a.

Guo, K., Meints, K., Hall, C., Hall, S., & Mills, D. (2009). Left gaze bias in humans, rhesus monkeys and domestic dogs. *Animal Cognition, 12*(3), 409–418, doi:10.1007/s10071-008-0199-3.

Guo, K., Tunnicliffe, D., & Roebuck, H. (2010). Human spontaneous gaze patterns in viewing of faces of different species. *Perception, 39*(4), 533–542, doi:10.1068/p6517.

Hafed, Z. M., & Clark, J. J. (2002). Microsaccades as an overt measure of covert attention shifts. *Vision Research, 42,* 2533–2545.

Han, S., Weaver, J. A., Murray, S. O., Kang, X., Yund, E. W., & Woods, D. L. (2002). Hemispheric asymmetry in global/local processing: Effects of stimulus position and spatial frequency. *NeuroImage, 17*(3), 1290–1299, doi:10.1006/nimg.2002. 1255.

Hanes, D. P., & Carpenter, R. H. S. (1999). Countermanding saccades in humans. *Vision Research, 39,* 2777–2791.

Hausmann, M. (2005). Hemispheric asymmetry in spatial attention across the menstrual cycle. *Neu-*

ropsychologia, 43, 1559–1567, doi:10.1016/j. neuropsychologia.2005.01.017.

Heath, R. L., Rouhana, A., & Ghanem, D. A. (2005). Asymmetric bias in perception of facial affect among Roman and Arabic script readers. *Laterality, 10*(1), 51–64, doi:10.1080/13576500342000293.

Heller, W., & Levy, J. (1981). Perception and expression of emotion in right-handers and left-handers. *Neuropsychologia, 19*(2), 263–272.

Hellige, J. B. (1996). Hemispheric asymmetry for visual information processing. *Acta Neurobiologiae Experimentalis, 56*(1), 485–497.

Heron, W. (1957). Perception as a function of retinal locus and attention. *The American Journal of Psychology, 70*(1), 38–48.

Hikosaka, O., Takikawa, Y., & Kawagoe, R. (2000). Role of the basal ganglia in the control of purposive saccadic eye movements. *Physiological Reviews*, 80(3), 953–978.

Hollingworth, A., & Henderson, J. M. (2002). Accurate visual memory for previously attended objects in natural scenes. *Journal of Experimental Psychology: Human Perception & Performance, 28*(1), 113–136.

Ishiai, S., Furukawa, T., & Tsukagoshi, H. (1989). Visuospatial processes of line bisection and the mechanisms underlying unilateral spatial neglect. *Brain, 112,* 1485–1502.

Itti, L., & Koch, C. (2001). Computational modelling of visual attention. *Nature Reviews Neuroscience, 2*(3), 194–203, doi:10.1038/35058500.

Ivry, R. B., & Robertson, L. C. (1998). *The two sides of perception.* Cambridge, MA: MIT Press.

Jewell, G., & McCourt, M. E. (2000). Pseudoneglect: A review and meta-analysis of performance factors in line bisection tasks. *Neuropsychologia, 38,* 93–110.

Kanwisher, N., McDermott, J., & Chun, M. M. (1997). The fusiform face area: A module in human extrastriate cortex specialized for face perception. *Journal of Neuroscience, 17*(11), 4302–4311.

Kimura, D. (1966). Dual functional asymmetry of the brain in visual perception. *Neuropsychologia, 4*(3), 275–285, doi:10.1016/0028-3932(66)90033-9.

Kitterle, F. L., Christman, S., & Hellige, J. B. (1990). Hemispheric differences are found in the identification, but not the detection, of low versus high spatial frequencies. *Perception & Psychophysics, 48*(4), 297–306.

Kitterle, F. L., Hellige, J. B., & Christman, S. (1992). Visual hemispheric asymmetries depend on which spatial frequencies are task relevant. *Brain and Cognition, 20*(2), 308–314.

Kollmorgen, S., Nortmann, N., Schröder, S., & König,

P. (2010). Influence of low-level stimulus features, task dependent factors, and spatial biases on overt visual attention. *PLoS Comput Biol, 6*(5), e1000791, doi:10.1371/journal.pcbi.1000791.

Kulynych, J. J., Vladar, K., Jones, D. W., & Weinberger, D. R. (1994). Gender differences in the normal lateralization of the supratemporal cortex: MRI surface-rendering morphometry of Heschl's gyrus and the planum temporale. *Cerebral Cortex, 4*(2), 107–118, doi:10.1093/cercor/4.2.107.

Lamb, M., & Yund, E. W. (1993). The role of spatial frequency in the processing of hierarchically organized stimuli. *Perception & Psychophysics, 54*(6), 773–784.

Leonards, U., & Scott-Samuel, N. E. (2005). Idiosyncratic initiation of saccadic face exploration in humans. *Vision Research, 45*(20), 2677–2684, doi: 10.1016/j.visres.2005.03.009.

Levy, J. (1976). Lateral dominance and aesthetic preference. *Neuropsychologia, 14,* 431–445.

Levy, J., Heller, W., Banich, M., & Burton, L. (1983). Asymmetry of perception in free viewing of chimeric faces. *Brain and Cognition, 2,* 404–419.

Liederman, J., & Kinsbourne, M. (1980). The mechanism of neonatal rightward turning bias: A sensory or motor asymmetry? *Infant Behavior and Development, 3,* 223–238, doi:10.1016/ S0163-6383(80)80028-2.

Luh, K. E., Redl, J., & Levy, J. (1994). Left-and right-handers see people differently: Free-vision perceptual asymmetries for chimeric stimuli. *Brain and Cognition, 25,* 141–160.

Luh, K. E., Rueckert, L. M., & Levy, J. (1991). Perceptual asymmetries for free viewing of several types of chimeric stimuli. *Brain and Cognition, 16*(1), 83–103.

Lyilikci, O., Becker, C., Güntürkün, O., & Amado, S. (2010). Visual processing asymmetries in change detection. *Perception, 39,* 761–769, doi:10.1068/ p6623.

Martinez, A., Moses, P., Frank, L., Buxton, R., Wong, E., & Stiles, J. (1997). Hemispheric asymmetries in global and local processing: Evidence from fMRI. *Neuroreport, 8*(7), 1685–1689.

Mattingley, J. B., Bradshaw, J. L., Nettleton, N. C., & Bradshaw, J. A. (1994). Can task-specific perceptual bias be distinguished from unilateral neglect? *Neuropsychologia, 32*(7), 805–817.

Mayfrank, L., Mobashery, M., Kimmig, H., & Fischer, B. (1986). The role of fixation and visual attention in the occurrence of express saccades in man.

European Archives of Psychiatry and Clinical Neuroscience, *235*(5), 269–275.

Megreya, A. M., & Havard, C. (2011). Left face matching bias: Right hemisphere dominance or scanning habits? *Laterality, 16*(1), 75–92, doi:10.1080/13576500903213755.

Mertens, I., Siegmund, H., & Grüsser, O. J. (1993). Gaze motor asymmetries in the perception of faces during a memory task. *Neuropsychologia*, *31*(9), 989–998.

Mevorach, C., Hodsoll, J., Allen, H., Shalev, L., & Humphreys, G. (2010). Ignoring the elephant in the room: A neural circuit to downregulate salience. *Journal of Neuroscience, 30*(17), 6072–6079, doi:10.1523/JNEUROSCI.0241-10.2010.

Mevorach, C., Humphreys, G. W., & Shalev, L. (2005). Attending to local form while ignoring global aspects depends on handedness: Evidence from TMS. *Nature Neuroscience, 8*(3), 276–277, doi:10.1038/nn1400.

Mevorach, C., Humphreys, G. W., & Shalev, L. (2006). Opposite biases in salience-based selection for the left and right posterior parietal cortex. *Nature Neuroscience, 9*(6), 740–742, doi:10.1038/nn1709.

Mevorach, C., Shalev, L., Allen, H. A., & Humphreys, G. W. (2009). The left intraparietal sulcus modulates the selection of low salient stimuli. *Journal of Cognitive Neuroscience, 21*(2), 303–315, doi:10.1162/jocn.2009.21044.

Miles, W. R. (1929). Ocular dominance demonstrated by unconscious sighting. *Journal of Experimental Psychology, 12,* 113–126.

Navon, D. (1977). Forest before trees: The precedence of global features in visual perception. *Cognitive Psychology, 9,* 353–383.

Nicholls, M. E., Bradshaw, J. L., & Mattingley, J. B. (1999). Free-viewing perceptual asymmetries for the judgement of brightness, numerosity and size. *Neuropsychologia*, *37*(3), 307–314.

Nicholls, M. E., & Roberts, G. R. (2002). Can free-viewing perceptual asymmetries be explained by scanning, pre-motor or attentional biases? *Cortex; A Journal Devoted to the Study of the Nervous System and Behavior*, *38*(2), 113–136.

Nobre, A. C., Gitelman, D. R., Dias, E. C., & Mesulam, M. M. (2000). Covert visual spatial orienting and saccades: Overlapping neural systems. *NeuroImage, 11*(3), 210–216, doi:10.1006/nimg.2000.0539.

Oldfield, R. (1971). The assessment and analysis of handedness: The Edinburgh inventory. *Neuropsychologia, 9,* 97–113.

Oliva, A., & Schyns, P. G. (1997). Coarse blobs or fine edges? Evidence that information diagnosticity changes the perception of complex visual stimuli. *Cognitive Psychology, 34*(1), 72–107, doi:10.1006/cogp.1997.0667.

Olmos, A., & Kingdom, F. A. (2004). A biologically inspired algorithm for the recovery of shading and reflectance images. *Perception*, *33*(12), 1463–1473.

Onat, S., Libertus, K., & König, P. (2007). Integrating audiovisual information for the control of overt attention. *Journal of Vision*, *7*(10):11, 1–16, http://www.journalofvision.org/content/7/10/11, doi:10.1167/7.10.11. [PubMed] [Article]

Ossandón, J. P., Açık, A., & König, P. (2011). Low in the forest, high in the city: Visual selection and natural image statistics. *Perception, 40,* ECVP Abstract Supplement, 95.

Ossandón, J. P., Onat, S., Cazzoli, D., Nyffeler, T., Müri, R., & König, P. (2012). Unmasking the contribution of low-level features to the guidance of attention. *Neuropsychologia, 50*(14), 3478–3487, doi:10.1016/j.neuropsychologia.2012.09.043.

Over, E. A., Hooge, I. T., Vlaskamp, B. N., & Erkelens, C. J. (2007). Coarse-to-fine eye movement strategy in visual search. *Vision Research, 47*(17), 2272–2280, doi:10.1016/j.visres.2007.05.002.

Parkhurst, D., Law, K., & Niebur, E. (2002). Modeling the role of salience in the allocation of overt visual attention. *Vision Research*, *42*(1), 107–123.

Petersen, S. E., Fox, P. T., Snyder, A. Z., & Raichle, M. E. (1990). Activation of extrastriate and frontal cortical areas by visual words and word-like stimuli. *Science*, *249*(4972), 1041.

Peyrin, C., Baciu, M., Segebarth, C., & Marendaz, C. (2004). Cerebral regions and hemispheric specialization for processing spatial frequencies during natural scene recognition. An event-related fMRI study. *NeuroImage, 23*(2), 698–707, doi:10.1016/j.neuroimage.2004.06.020.

Peyrin, C., Schwartz, S., Seghier, M., Michel, C., Landis, T., & Vuilleumier, P. (2005). Hemispheric specialization of human inferior temporal cortex during coarse-to-fine and fine-to-coarse analysis of natural visual scenes. *NeuroImage, 28*(2), 464–473, doi:10.1016/j.neuroimage.2005.06.006.

Phillips, M. L., & David, A. S. (1997). Viewing strategies for simple and chimeric faces: An investigation of perceptual bias in normals and schizophrenic patients using visual scan paths. *Brain and Cognition, 35*(2), 225–238, doi:10.1006/brcg.1997.0939.

Pierrot-Deseilligny, C., Rivaud, S., Gaymard, B., &

Agid, Y. (1991). Cortical control of reflexive visually guided saccades. *Brain, 114,* 1473–1485.

Puce, A., Allison, T., Asgari, M., Gore, J. C., & McCarthy, G. (1996). Differential sensitivity of human visual cortex to faces, letter strings, and textures: A functional magnetic resonance imaging study. *Journal of Neuroscience, 16*(16), 5205–5215.

Robertson, L. C., & Delis, D. C. (1986). "Part-whole" processing in unilateral brain-damaged patients: Dysfunction of hierarchical organization. *Neuropsychologia, 24*(3), 363–370.

Ross, J., Morrone, M. C., Goldberg, M. E., & Burr, D. C. (2001). Changes in visual perception at the time of saccades. *Trends in Neurosciences, 24*(2), 113–121, doi:10.1016/S0166-2236(00)01685-4.

Rubia, K., Russell, T., Overmeyer, S., Brammer, M. J., Bullmore, E. T., Sharma, T., . . . Taylor, E. (2001). Mapping motor inhibition: Conjunctive brain activations across different versions of go/no-go and stop tasks. *NeuroImage, 13,* 250–261, doi:10.1006/nimg.2000.0685.

Russell, B. C., Torralba, A., Murphy, K. P., & Freeman, W. T. (2008). LabelMe: A database and Web-based tool for image annotation. *International Journal of Computer Vision, 77*(1–3), 157–173, doi:10.1007/s11263-007-0090-8.

Saslow, M. G. (1967). Effects of components of displacement-step stimuli upon latency for saccadic eye movement. *Journal of the Optical Society of America, 57*(8), 1024–1029.

Schiller, P. H., Sandell, J. H., & Maunsell, J. H. (1987). The effect of frontal eye field and superior colliculus lesions on saccadic latencies in the rhesus monkey. *Journal of Neurophysiology, 57*(4), 1033–1049.

Schiller, P. H., Slocum, W. M., Carvey, C., & Tolias, A. S. (2004). Are express saccades generated under natural viewing conditions? *The European Journal of Neuroscience, 20*(9), 2467–2473, doi:10.1111/j.1460-9568.2004.03663.x.

Schroeder, C. E., Metha, A. D., & Givre, S. J. (1998). A spatiotemporal profile of visual system activation revealed by current source density analysis in the awake macaque. *Cerebral Cortex, 8,* 575–592.

Schroeder, C. E., Tenke, C. E., Arezzo, J. C., & Vaughan, H. G. (1989). Timing and distribution of flash-evoked activity in the lateral geniculate nucleus of the alert monkey. *Brain Research, 477,* 183–195.

Schyns, P. G., & Oliva, A. (1994). From blobs to boundary edges: Evidence for time- and spatial-scale-dependent scene recognition. *Psychological Science, 5*(4), 195–200.

Sergent, J. (1982). The cerebral balance of power: Confrontation or cooperation? *Journal of Experimental Psychology: Human Perception and Performance, 8*(2), 253–272, doi:10.1037/0096-1523.8.2.253.

Spotorno, S., & Faure, S. (2011). Change detection in complex scenes: Hemispheric contribution and the role of perceptual and semantic factors. *Perception, 40,* 5–22, doi:10.1068/p6524.

Swick, D., Ashley, V., & Turken, A. U. (2011). Are the neural correlates of stopping and not going identical? Quantitative meta-analysis of two response inhibition tasks. *NeuroImage, 56,* 1655–1665, doi:10.1016/j.neuroimage.2011.02.070.

Szczepanski, S. M., & Kastner, S. (2013). Shifting attentional priorities: Control of spatial attention through hemispheric competition. *Journal of Neuroscience, 33*(12), 5411–5421, doi:10.1523/JNEUROSCI.4089-12.2013.

Tatler, B. (2007). The central fixation bias in scene viewing: Selecting an optimal viewing position independently of motor biases and image feature distributions. *Journal of Vision, 7*(14):4, 1–17, http://www.journalofvision.org/content/7/14/4, doi:10.1167/7.14.4. [PubMed] [Article]

Tatler, B., & Hayhoe, M. (2011). Eye guidance in natural vision: Reinterpreting salience. *Journal of Vision, 11*(5):5, 1–23, http://www.journalofvision.org/content/11/5/5, doi:10.1167/11.5.5. [PubMed] [Article]

Tatler, B. W., Baddeley, R. J., & Gilchrist, I. D. (2005). Visual correlates of fixation selection: Effects of scale and time. *Vision Research, 45*(5), 643–659, doi:10.1016/j.visres.2004.09.017.

Thiebaut de Schotten, M., Dell'Acqua, F., Forkel, S. J., Simmons, A., Vergani, F., Murphy, D. G. M., . . . Catani, M. (2011). A lateralized brain network for visuospatial attention. *Nature Neuroscience, 14*(10), 1245–1246, doi:10.1038/nn.2905.

Torralba, A., & Oliva, A. (2003). Statistics of natural image categories. *Network, 14*(3), 391–412.

Tseng, P., Carmi, R., Cameron, I. G., Munoz, D. P., & Itti, L. (2009). Quantifying center bias of observers in free viewing of dynamic natural scenes. *Journal of Vision, 9*(7):4, 1–16, http://www.journalofvision.org/content/9/7/4, doi:10.1167/9.7.4. [PubMed] [Article]

Unema, P., Pannasch, S., Joos, M., & Velichkovsky, B. (2005). Time course of information processing during scene perception: The relationship between saccade amplitude and fixation duration. *Visual Cognition, 12*(3), 473–494, doi:10.1080/13506280444000409.

Vaid, J., & Singh, M. (1989). Asymmetries in the perception of facial affect: Is there an influence of reading habits? *Neuropsychologia, 27*(10), 1277–1287, doi:10.1016/0028-3932(89)90040-7.

Van Kleeck, M. H. (1989). Hemispheric differences in global versus local processing of hierarchical visual stimuli by normal subjects: New data and a meta-analysis of previous studies. *Neuropsychologia, 27*(9), 1165–1178, doi:10.1016/0028-3932(89)90099-7.

van Zoest, W., & Donk, M. (2004). Bottom-up and top-down control in visual search. *Perception, 33,* 927–937.

van Zoest, W., & Donk, M. (2005). The effects of salience on saccadic target selection. *Visual Cognition, 12,* 353–375.

Voyer, D. (1996). On the magnitude of laterality effects and sex differences in functional literalities. *Laterality*, *1*(1), 51–83.

Welborn, B. L., Papademetris, X., Reis, D. L., Rajeevan, N., Bloise, S. M., & Gray, J. R. (2009). Variation in orbitofrontal cortex volume: Relation to sex, emotion regulation and affect. *Social Cognitive and Affective Neuroscience, 4*(4), 328–339, doi:10.1093/scan/nsp028.

Wilming, N., Betz, T., Kietzmann, T. C., & König, P. (2011). Measures and limits of models of fixation selection. *PloS One, 6*(9), e24038, doi:10.1371/journal.pone.0024038.

Yovel, G., & Freiwald, W. A. (2013). Face recognition systems in monkey and human: Are they the same thing? *F1000Prime Reports, 5*, doi:10.12703/P5-10.

Zimmerberg, B., Glick, S. D., & Jerussi, T. P. (1974). Neurochemical correlate of a spatial preference in rats. *Science*, *185*(4151), 623–623.