PERCEPTION

Neural Correlates of Perceptual Grouping Under Conditions of Inattention and Divided Attention

Tiffany A. Carther-Krone [ID]
Perception and Action Lab, Department of Psychology, University of Manitoba, Winnipeg, Canada

Jane M. Lawrence-Dewar
Thunder Bay Regional Health Research Institute, Ontario, Canada

Sarah Shomstein, Joseph C. Nah and Andrew J. Collegio
Department of Psychology, George Washington University, Washington, USA

Jonathan J. Marotta [ID]
Perception and Action Lab, Department of Psychology, University of Manitoba, Winnipeg, Canada

Abstract

Grouping local elements of the visual environment together is crucial for meaningful perception. While our attentional system facilitates perception, it is limited in that we are unaware of some aspects of our environment that can still influence how we experience it. In this study, the neural mechanisms underlying the Ponzo illusion were examined under inattention and divided-attention conditions using functional magnetic resonance imaging to investigate the brain regions responsible for accessing visual stimuli. A line discrimination task was performed in which two horizontal lines were superimposed on a background of black and white dots that, on occasion, induced the Ponzo illusion if perceptually grouped together. Our findings revealed activation for perceptual grouping in the frontal, parietal, and occipital regions of the brain and activation in the bilateral frontal, temporal, and cingulate gyrus in response to divided attention compared with inattention trials. A direct comparison between grouping and attention showed involvement of the right

---

Corresponding author:
Tiffany A. Carther-Krone, Perception and Action Lab, Department of Psychology, University of Manitoba, 190 Dysart Rd, Winnipeg, MB R3T 2N2, Canada.
Email: lazart@myumanitoba.ca

supramarginal gyrus in grouping specifically under conditions of inattention, suggesting that even during implicit grouping complex visual processing occurs. Given that much of the visual world is not represented in conscious perception, these findings provide crucial information about how we make sense of visual scenes in the world.

To make sense of the visual scenes we encounter, meaningful perception relies on our ability to quickly and efficiently organize visual information. The visual system is able to group elements using principles first introduced by Gestalt psychologists, including similarity, proximity, and closure (Wertheimer, 1923). This allows incoming information to be organized and integrated from meaningless and fragmented input into coherent, whole objects and backgrounds. Behavioral research has demonstrated that visual object representations not only occur in situations in which such objects are attended or task-relevant but also take place when they are unattended and task-irrelevant (Lamy et al., 2006; Moore & Egeth, 1997; Müller et al., 2010; Russell & Driver, 2005). Previous research using visual illusions, in which susceptibility depends on grouping incoming information together, as well as grouped patterns, has established that individuals are susceptible to grouping even when they are unable to explicitly report the elements being grouped (Carther-Krone et al., 2016; Driver et al., 2001; Kimchi & Peterson, 2008; Kimchi & Razpurker-Apfeld, 2004; Lamy et al., 2006; Moore & Egeth, 1997; Russell & Driver, 2005; Shomstein et al., 2010). This suggests that perceptual grouping may occur relatively automatically and independently of top-down attentional selection. This is further supported by studies involving patients with neurological disabilities such as hemispatial neglect (Russell & Driver, 2005; Shomstein et al., 2010; Vuilleumier & Landis, 1998; Vuilleumier et al., 2001) and simultanagnosia (Huberle & Karnath, 2006; Karnath et al., 2000), who show an ability to implicitly group elements despite difficulties explicitly reporting the global configurations. However, it is unclear which brain regions are responsible for grouping unattended stimuli and whether access to a visual stimulus, even if unattended, activates the same regions.

While previous research has established that perceptual grouping can occur without attention, there is little research examining the neural mechanisms underlying grouping in this context and how it might differ from grouping under conditions of explicit attention. Of the research that exists, much of it focuses on grouping under varying conditions of attention, pointing to areas V1 and V2 of the visual cortex (Ross et al., 2000), the inferior parietal cortex, middle temporal gyrus, and prefrontal cortex (Seymour et al., 2008) as regions responsible for grouped compared with ungrouped visual information. Furthermore, research has suggested that different Gestalt properties rely on different neural mechanisms (Han et al., 2001, 2005; Vidal et al., 2006) and that these properties may be driven differentially by local and global processing strategies (Han et al., 2001; Prieto et al., 2014). As a result, there is a considerable divergence of findings regarding perceptual grouping, and most research on perceptual grouping has explicitly involved the

recruitment of attentional mechanisms to some extent. Neuroimaging research examining grouping without attention has focused mainly on comparing grouped with ungrouped stimuli. One line of work has examined the visual suppression that occurs between simultaneously presented proximal visual elements to show that these competitive interactions appear to occur automatically, without attention, in the early visual cortex (Kastner et al., 1998; Reynolds et al., 1999). Another study comparing grouped with ungrouped visual information pointed to the inferior parietal lobe as important in perceptual grouping when grouping was task-irrelevant and participants were unaware of the stimuli to be grouped (Xu & Chun, 2007). Although the limited amount of research examining perceptual grouping without attention points to the early visual cortex and inferior parietal lobe as an important marker of grouping under conditions of inattention, there has to date been no within studies comparisons of the neural correlates activated in response to perceptual grouping under conditions of inattention compared with when attentional processes are recruited.

To determine whether distinct brain regions are recruited for perceptual grouping without attention compared with grouping under conditions of divided attention, a functional magnetic resonance imaging (fMRI) investigation was conducted in which we used a version of the Ponzo illusion (Ponzo, 1910) that superimposed two horizontal lines over a background of black and white dots. When the black dots were grouped, they formed the two converging lines of the Ponzo illusion (Moore & Egeth, 1997). Inattentive processing was examined by requiring participants to determine which of two horizontal lines was longer after a brief presentation of the illusion. If participants consistently judged the line placed at the converging end of the illusion as longer, this would indicate that they were processing the illusion without attention. Following the inattention trials, divided attention was investigated by instructing participants to attend to the background while performing the same line judgment task as previously administered in the inattention condition.

If grouping without attention and under conditions of divided attention result in similar activations, then these overlapping regions would suggest a general processing mechanism is responsible for perceptual grouping regardless of whether or not it is perceived. However, if distinct regions of activation are found for grouping stimuli without attention, then this would suggest that input that is not explicitly reported is driven by those regions and that attention may serve as a modulating factor in differentiating between implicit and explicit grouping.

Here, we report novel findings comparing brain regions activated during perceptual grouping without attention and under conditions of divided attention. While previous research has examined the brain regions activated in response to perceptual grouping in general, the extent to which attention modulates these regions has mainly focused on paradigms requiring divided or selective attention. The current study not only examines the brain regions involved in perceptual grouping under conditions of inattention but also provides a direct comparison of grouping under inattention and divided-attention conditions in the same study. While activity related to perceptual grouping was found within previously reported regions of the occipital lobes, frontal lobes, and left parietal lobe, activation was also observed in the right supramarginal gyrus for grouping specifically in the inattention condition. This inferior parietal activation is consistent with previous research (Xu & Chun, 2007) but further demonstrates that it is unique to grouping under conditions of inattention by comparing grouping mechanisms with those resulting when attention is explicitly recruited, in which this activation is no longer found. The specific activation of the right supramarginal gyrus under conditions of inattention

suggests that this region is directly involved in grouping only when we do not explicitly attend to a stimulus.

Methods

Participants

The study protocol was approved by the Psychology/Sociology Human Research Ethics Board at the University of Manitoba and Thunder Bay Regional Health Sciences Center Ethics Board. The number of participants was preset to 20 to 25 based on comparable recent research using fMRI to study visual illusions (He et al., 2015; Mikellidou et al., 2016; Selles et al., 2014) and attention (Kok et al., 2016; Salo et al., 2017; Santangelo et al., 2010). Twenty-eight typically developing individuals were recruited and provided written informed consent. Inclusion criteria included normal or corrected-to-normal vision and no preclusions for MRI. Participants received $25.00 to compensate them for any transportation expenses to the study. There were several sources of data attrition: One participant could not be tested due to technical difficulties with the MRI and was excluded without data collection, data from one participant were discarded due to problems with the MRI in acquiring the T1-weighted anatomical scan, three participants were discarded due to excess (greater than 2 mm in any direction) head motion, and behavioral data from one participant were discarded due to problems acquiring responses using the MRI compatible trackball. Thus, the final sample consisted of 22 right-handed participants (13 females) aged 31 ± 6.85 (mean ± 1 SD).

Apparatus and Stimuli

Stimuli were generated on a 12.7″ Dell Tablet using E-Prime software (Psychology Software Tools, Pittsburgh, PA) and projected onto a screen that was viewed by subjects via a mirror measuring 13 cm × 8 cm (50° × 32° in visual angle) mounted on the head coil. The approximate distance from the participants eye to the screen was 14 cm (depending on individual head size and position in the head coil). The spatial resolution of the computer was 1,024 × 768 pixels, and the refresh rate was 60 frames per second.

Each trial began with a black 0.8° × 1° fixation cross presented in the center of a gray background (luminance: 106 cm/m²). Trial displays consisted of a matrix of 21 columns and 13 rows of black and white dots subtending approximately 18.4° × 19.2°, centered on the gray background, with two horizontal black line segments superimposed over the dot matrix. Each dot had a diameter of 0.6°. Dots within a row were separated by 1° (center to center), and those within a column were separated by 1.5° (center to center). The line segments were 0.4° wide. Line segments were centered horizontally within the matrix and positioned approximately one third of the way down from the top of the matrix (between the fifth and sixth rows of dots) and one third of the way up from the bottom of the matrix (between the eighth and ninth rows of the dots).

Trials consisted of either random matrix or pattern matrix trials. Random matrix trials consisted of dot matrices in which a random 8% of the dots were black and the rest were white. The line segments superimposed over the matrix were presented so that one line segment was slightly longer than the other, and the lengths were randomly chosen from three short–long pairs: (8.3°, 7.3°), (8.7°, 7.7°), and (9.3°, 8.3°). In these trials, the longer line segment was presented equally often in the top and bottom positions (Figure 1). Pattern matrix trials consisted of dot matrices in which the dots formed a pattern based on grouping
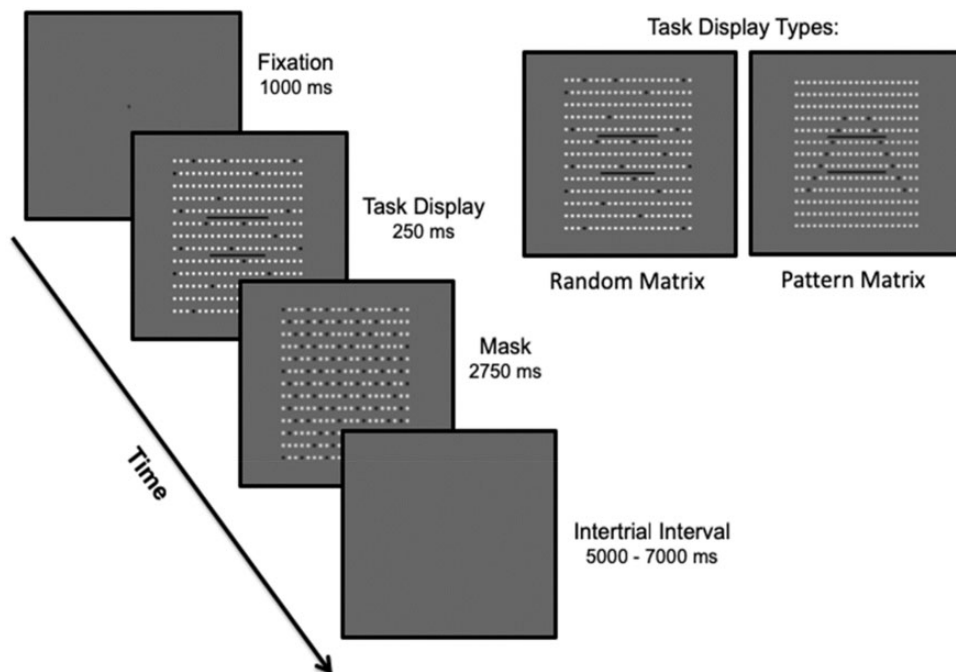
Figure 1. Stimulus Backgrounds and Time Course of Trial Events.

by similarity. In these trials, the line segments were equal in length (9.1°). Each trial was immediately followed by a mask consisting of a dot matrix in which a random 30% of the dots were black and the rest were white.

Procedure

Each participant was tested individually in one session lasting approximately 1 hour. The length of the line discrimination task was approximately 20 minutes, with the rest of the time allocated to preparing and informing the participant for the MRI (i.e., filling out the consent and demographics forms), MRI safety prescreening, ensuring comfort of the participant in the scanner, and acquiring anatomical scans.

Before going into the scanner, participants were given instructions about the line discrimination task. They were told that each trial would begin with a fixation cross, followed by the brief presentation of a dot matrix with two horizontal line segments superimposed on it. Participants were instructed to indicate whether they thought the top or bottom line was longer by making their response using the MRI compatible trackball, where a left click indicated that the top line was longer and a right click indicated that the bottom line was longer. Participants were asked to take a best guess if they were unsure which line was longer.

Once participants were comfortable with the task instructions, they were given an opportunity to perform 10 random matrix practice trials on a computer outside the scanner to ensure they were able to see the two line segments. Following these practice trials, participants completed the experimental trials in the MRI.

For the experimental trials, each participant completed the task four times (four runs), with each run starting with a 4,000 ms gray screen (Figure 1). Subsequently, the first trial

began with a fixation cross shown for 1,000 ms, followed by a trial display for 250 ms, which was immediately replaced by a mask display that remained on the screen for 2,750 ms, allowing participants to indicate their response. A jittered intertrial interval ranging from 5,000 to 7,000 ms in intervals of 250 ms with an average of 6,000 ms followed, appearing as a gray background, after which the next trial was presented. In each run, 36 trials were randomly presented (18 pattern and 18 random). The intertrial interval was jittered to increase variance for blood-oxygen-level-dependent deconvolution analysis.

Each run ended with a random matrix trial, and following the last trial of the second run, participants were presented with two surprise questions (direct query and forced choice) regarding the background pattern. For the direct query question, participants were asked, "Did you notice a pattern in the background of dots on any of the preceding trials?" Following the direct query, participants were shown two versions of the Ponzo illusion (converging lines toward the top of the screen and converging lines toward the bottom of the screen) and asked to indicate the pattern they observed, taking a best guess if no pattern was seen. Participants were always shown the illusion with the lines converging toward the top of the screen so they could be queried about the background over the whole block of trials rather than only the last pattern trial preceding the direct query and forced-choice questions. These questions served the purpose of examining whether participants were viewing the stimuli without attending the background. Following these two questions, participants were asked to complete two more runs of the same task but were instructed to also observe the background pattern while carrying out the line discrimination task. After the last pattern matrix trial of the final run, participants were once again asked the same two questions. Consistent with previous research (Moore & Egeth, 1997), participants were able to see and identify the background pattern, indicating that participants were completing the task under divided attention.

fMRI Image Acquisition

Imaging was performed on a 3 Tesla Philips Achieva MRI scanner (Philips, Amsterdam, the Netherlands) equipped with an eight-channel Sensory Element (SENSE) head coil (Philips). Participants were positioned in a supine position on the scanner bed with their right index and middle fingers positioned on the appropriate response buttons of a response box. Stimuli were back projected onto a screen mounted at the rear end of the scanner, and participants viewed the display via a mirror attached on the head coil. To minimize head motion, the head was fitted with memory foam cushions. Whole-brain functional images were acquired using a T2*-weighted single-shot two-dimensional gradient echo-planar pulse sequence (179 volumes, 30 slices, slice thickness = 4 mm, field of view = 240×240 mm, voxel size = $3.75 \times 3.75 \times 4.0$ mm^3, TR/TE = 2,000/30 ms, flip angle = 90°), while participants performed the task. The fMRI scans were repeated four times (one for each run of the task). After functional imaging, structural data were acquired for each participant using a T1-weighted MPRAGE sequence for detailed reconstruction of anatomy with isotropic voxels ($1 \times 1 \times 1$ mm) in a 240-mm field of view (256×256 matrix, 160 slices, TR = 8.1 ms, TE = 3.7 ms).

fMRI Data Preprocessing

Brain image preprocessing and statistical analyses were performed using BrainVoyager 2.8 (Brain Innovation, Maastricht, the Netherlands; Goebel et al., 2006). The first two volumes of each fMRI scan were discarded to allow the MRI signal to reach a steady state.

Images from each functional run were slice time corrected, motion corrected, and then temporally high-pass filtered using a general linear model with Fourier basis set to remove low- and high-frequency noise in the functional time series. All anatomical images were interpolated into 1-mm isotropic voxels and corrected for inhomogeneity and then coregistered to the mean functional image and transformed into the standardized Talairach and Tournoux (1988) atlas space using an AC/PC transform. These images were then spatially smoothed with a Gaussian kernel with a full width at half maximum of 6 mm, and the 6 motion predictors from each functional run were z-transformed and added into the general linear model as predictors.

Behavioral Data Analysis

In this study, perceptual grouping abilities under conditions of inattention (Runs 1 and 2) and divided attention (Runs 3 and 4) were examined by assessing participants' susceptibility to the Ponzo illusion in the perceptual grouping task. Random matrix and pattern matrix trials were analyzed separately in each attentional condition by first calculating the percentage of correct responses for each participant across the trials in each condition and then averaging these results across all participants to obtain the mean percentage of correct responses for each trial type in each attentional condition. The random matrix trials served to ensure that the participants could in fact make perceptual judgments based on line lengths, and a *correct* line judgment was coded when participants chose the longer line in the random matrix trials (i.e., the line that was physically longer) or indicated an illusion-based response in the pattern matrix trials (i.e., chose a physically identical line that was consistent with the illusory percept). Perceptual grouping abilities were assessed by comparing illusion susceptibility to a chance level (50%) for the pattern matrix condition. Similarly, line discrimination abilities were assessed by comparing accuracy in the random matrix trials (i.e., the percentage of trials in which participants successfully chose the longer of the two lines) to a chance level (50%). All analyses were carried out using alpha $= .05$.

General Linear Model First-Level Analysis

Data were analyzed for each subject using the general linear model. A contrast was applied to examine regions of statistically greater activation for the pattern matrix condition in comparison with the random matrix condition. The random matrix condition included all of the components of the pattern matrix condition except for the requirement of grouping the black dots together to perceive the illusion. Thus, the subtraction of the random matrix condition from the pattern matrix condition should reveal areas actively involved with perceptual grouping. Statistical analysis at the first level involved generating within-subject parametric activation maps for this contrast in both inattention and divided-attention conditions and modeling stimulus onsets using the hemodynamic response function.

General Linear Model Group Analysis

Random-effects general linear models were performed at the group level to determine regions significantly activated in association with perceptual grouping in both inattention and divided-attention conditions. Groupwise statistical maps were determined using the random-effects general linear model and cluster threshold estimation was calculated for each cluster of voxels ($p_{uncorr} < .01$) to correct for multiple comparisons and eliminate

false positives. This correction method incorporates the observation that neighboring voxels activate in clusters and calculates the likelihood of obtaining different cluster sizes (Forman et al., 1995). Main effects were calculated first by contrasting pattern matrix trials with random matrix trials across both attentional conditions (Grouping Type), as well as contrasting pattern and random matrix trials in the inattention condition with pattern and random matrix trials in the divided-attention condition (Attentional Type). The interaction was also examined to test whether any brain regions related to perceptual grouping were activated specifically in each attentional condition. Finally, simple effects analyses involved two separate analyses of variance (ANOVAs) contrasting pattern to random matrix trials for each attentional condition, as well as a 2 (Trial Type: Pattern, Random) × 2 (Attentional Condition: Inattention, Divided Attention) ANOVA to determine how much activation in response to pattern compared with random matrix trials differed between attentional conditions. Significant areas of activation in each condition were localized using the Talairach atlas.

Results

Behavioral Results

In this study, a line discrimination task was performed in which two horizontal lines were superimposed on a background of black and white dots organized so that, on occasion, the black dots induced the Ponzo illusion if perceptually grouped together. Trials in which the background dots were randomly configured confirmed that participants were able to make perceptual judgments based on the line lengths. A *correct* line judgment was coded when participants chose the longer line in the random matrix trials (i.e., the line that was physically longer) or indicated an illusion-based response in the pattern matrix trials (i.e., chose a physically identical line that was consistent with the illusory percept). Perceptual grouping abilities were examined both under conditions of inattention (i.e., before participants were aware of the illusion inducing elements in the background) and under conditions of divided attention (i.e., when participants had their attention directed to both the background elements and the line judgment task).

Participants showed high accuracy in line discrimination ability in the random matrix trials in both inattention and divided-attention conditions (Figure 2), identifying the longer line segment on 95.6% ($\pm6.02\%$) of the trials in the inattention condition and 96.48% ($\pm4.59\%$) of the trials in the divided-attention condition, both of which differed significantly from a 50% chance result, $t(21) = 74.074$, $p < .001$, Cohen's $d = 2.93$ and $t(21) = 98.021$, $p < .001$, Cohen's $d = 8.74$, respectively (values of the form $x \pm y$ refer to a 95% confidence interval of y, surrounding a mean of x). The results from the pattern matrix trials were consistent with previous research (Carther-Krone et al., 2016; Moore & Egeth, 1997), showing that participants were influenced by the background pattern in both inattention and divided-attention conditions, reporting the line toward the converging end of the patterned lines on 90.21% ($\pm15.31\%$) of the trials in the inattention condition and 95.57% ($\pm5.27\%$) of the trials in the divided-attention condition, both of which differed significantly from a 50% chance result, $t(21) = 27.479$, $p < .001$, Cohen's $d = 1.72$ and $t(21) = 84.591$, $p < .001$, Cohen's $d = 8.59$, respectively. Furthermore, a 2 (Attentional Condition: Inattention, Divided Attention) × 2 (Trial Type: Pattern, Random) repeated measures ANOVA revealed that there were no significant main effects of attentional condition, $F = 4.14$, $p = .06$, trial type, $F = 2.404$, $p = .136$, or interaction between the two, $F = 1.494$, $p = .235$. Taken together, these findings demonstrate that participants were able to complete the line judgment task
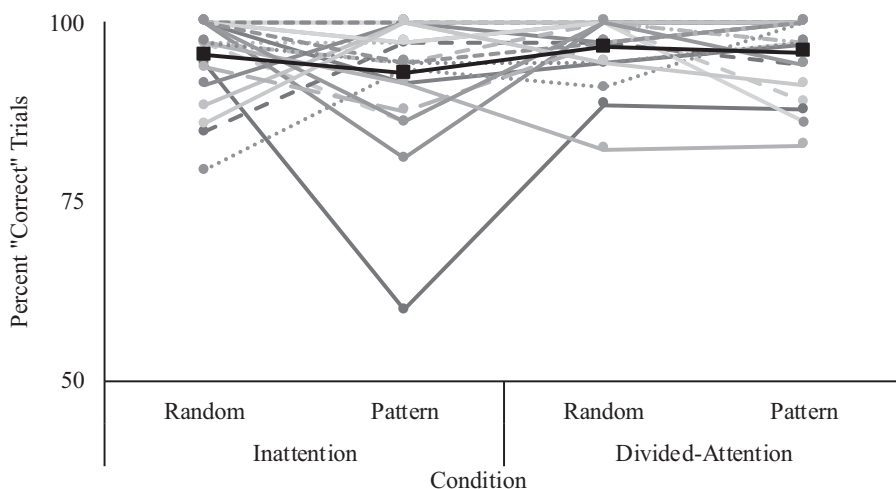
Figure 2. Behavioral Results of the Perceptual Grouping Task. The percent *correct* trials indicate the percentage of trials that each participant correctly chose the longer line in the random matrix trials (i.e., the line that was physically longer) and the percentage of trials that each participant indicated an illusion-based response in the pattern matrix trials (i.e., chose a physically identical line that was consistent with the illusory percept). Each line represents one participants' data ($N = 22$), and due to the distributional characteristics of the data being very similar among most participants, some of the lines overlap. Participants showed high accuracy in their ability to complete the behavioral task, further emphasized by the mean for each condition (represented by the black square).

with high accuracy regardless of trial type or attentional condition. Thus, it is highly unlikely that any brain activations in response to perceptual grouping in inattention or divided-attention conditions are due to differences in ability to perform the grouping task.

Direct Query and Forced-Choice Results

For the direct query, 50% of the participants (11 out of 22 participants) reported noticing a pattern after the inattention trials. However, more than 80% of participants (18 out of 22 participants) reported seeing the pattern after the divided-attention trials. In the forced-choice measure, of the participants who reported seeing the pattern after the inattention trials, 55% of them (6 out of 11 participants) were able to accurately identify the pattern, which did not differ significantly from a chance finding, $t(10) = 0.289$, $p = .779$. Of the total sample, 36% of participants (8 out of 22 participants) were able to accurately identify the pattern, which also did not differ significantly from a chance finding, $t(21) = -1.299$, $p = .208$. Of the participants who reported seeing the pattern after the divided-attention trials, all of them were able to accurately identify the pattern. There were four participants who reported not being able to see the pattern in response to the direct query question following the divided-attention trials; however, of these four participants, three of them were still able to correctly identify the pattern.

Correlation Between Forced-Choice Responses and Illusion Susceptibility

For all participants, a point-biserial correlation was calculated between the accuracy of the forced-choice response (0 = *incorrect*, 1 = *correct*) and the percentage of pattern matrix trials in which a response consistent with the illusion was reported (i.e., reporting the line at the

converging end of the illusion as longer) for both inattention and divided-attention trials. A significant positive correlation would suggest that a high percentage of illusion-based responses may have been due to those participants who happened to notice the pattern on the illusion-based trials. The results showed that the correlation did not differ significantly from zero for both inattention, $r = .163$, $p = .403$, and divided-attention, $r = -.188$, $p = .403$, trials. A second point-biserial correlation was also calculated between the accuracy of the direct query response and the percentage of pattern matrix trials in which a response consistent with the illusion was reported for both inattention and divided-attention trials. Again, the correlation did not differ significantly from zero for both inattention, $r = -.302$, $p = .172$, and divided-attention, $r = -.144$, $p = .524$, trials. Together, these results suggest that the high percentage of illusion susceptibility was not due to those participants who happened to notice the pattern during the inattention trials, which is further verified by a similar nonsignificant correlation in the divided-attention trials.

fMRI Results

A whole-brain analysis examining the brain regions involved in perceptual grouping was performed by testing the main effects of grouping and attention as well as the interaction between the two variables, using follow-up post hoc analyses of the simple effects to determine when attention influences grouping. First, pattern matrix trials were contrasted with random matrix trials (pattern > random) across both attentional conditions (Grouping Type). Activation in response to pattern matrix trials was found within the inferior gyrus of the left occipital lobe, middle frontal gyrus of the left frontal lobe, inferior region of the left parietal lobe, and cingulate gyrus of the right limbic lobe (Figure 3). Next, pattern and random matrix trials in the inattention condition were contrasted with pattern and random matrix trials in the divided-attention condition (Attentional Type). Activation specific to pattern and random matrix trials in the inattention condition was found in the parahippocampal gyrus of the left limbic lobe, while activation specific to these trials in the divided-attention condition was found bilaterally in the superior temporal gyrus, inferior frontal gyrus of the frontal lobe, and cingulate gyrus of the limbic lobe (Figure 3).

Following tests of the main effects, the interaction between grouping and attention was examined to test whether any brain regions related to perceptual grouping were activated specifically in each attentional condition. A 2 (Trial Type: Random, Pattern) × 2 (Attentional Condition: Inattention, Divided Attention) ANOVA revealed a significant interaction in the supramarginal gyrus of the right parietal lobe, $F(1, 21) = 12.689$, $p = .002$ (Figure 4). Post hoc comparisons involving the beta values revealed significantly stronger activation for pattern matrix trials in the inattention compared with divided-attention conditions, $p = .021$.

Finally, a simple effects analysis was performed involving two separate 2 (Grouping Type: Pattern, Random) × 2 (Attentional Condition: Inattention, Divided Attention) ANOVAs contrasting pattern to random matrix trials for each attentional condition. Activation in response to perceptual grouping in the inattention condition revealed activation within the inferior gyrus of the left occipital lobe, middle frontal gyrus of the right frontal lobe, inferior region of the left parietal lobe, and supramarginal gyrus of the right parietal lobe. Activation in response to perceptual grouping in the divided-attention condition revealed activation in the right medial frontal gyrus and in the lingual gyrus of the occipital cortex bilaterally (Figure 4). The peak location and cluster sizes for the main effects, interaction, and post hoc analyses are summarized in Table 1. Significant areas of activation in each condition were localized using the Talairach atlas.
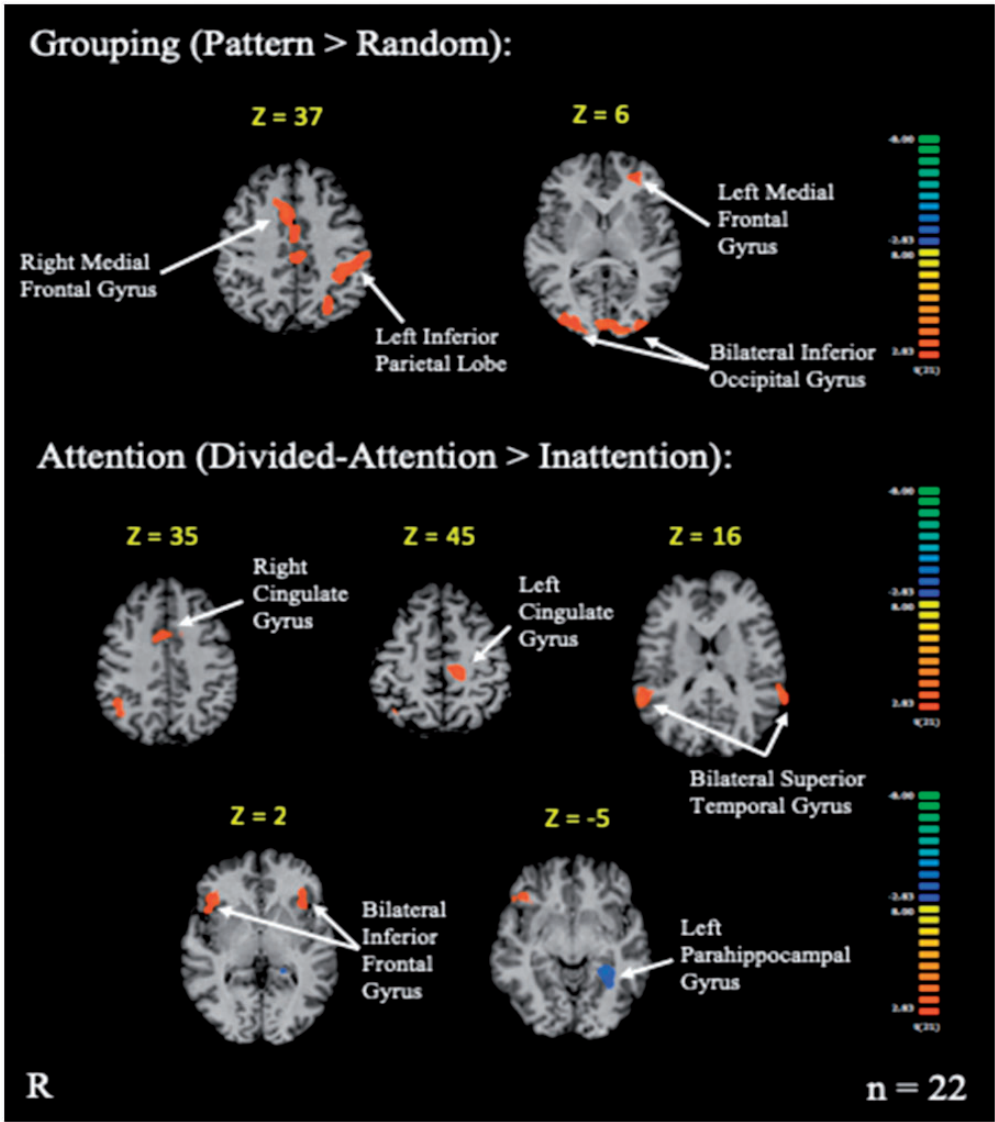
Figure 3. Main Effects Analysis. Images are presented in radiological orientation. Whole-brain axial slices of the average activation from all participants ($n = 22$) are shown. Multiple comparisons were corrected using cluster threshold estimation ($p_{uncorr} = .01$). Activations in the grouping condition are the result of contrasting pattern ($+$) trials with random ($-$) trials across both attention conditions. Activations in the attention condition are the result of contrasting pattern and random matrix trials in the divided-attention ($+$) condition with pattern and random matrix trials in the inattention ($-$) condition. In testing the main effect of attention, orange activations represent stronger activation in the divided-attention trials, while blue activations represent stronger activation in the inattention trials.
Note: Please refer to the online version of the article to view the figures in colour.

Discussion

The aim of the present experiment was to explore and further clarify the neural areas affected by perceptual grouping using a line discrimination task that allowed us to directly
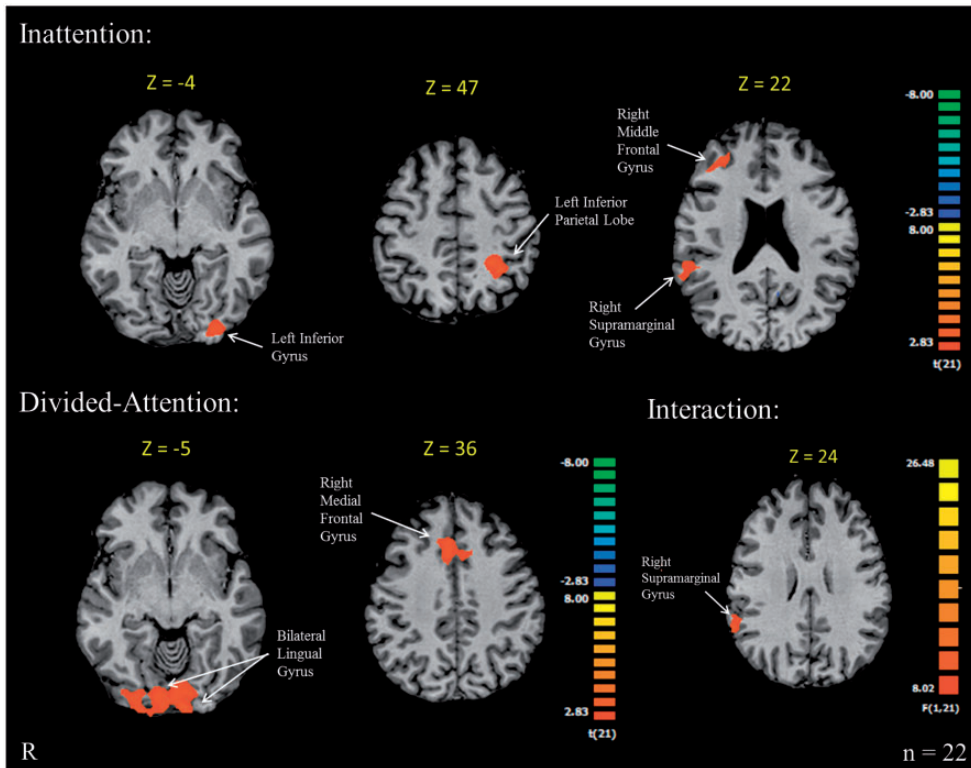
Figure 4. Interaction and Simple Effects. Images are presented in radiological orientation. Whole-brain axial slices of the average activation from all participants ($n = 22$) are shown. Multiple comparisons were corrected using cluster threshold estimation ($p_{uncorr} = .01$). Activations are the result of general linear model predictor contrast of the random (−) and pattern (+) conditions during perceptual grouping under conditions of inattention, divided attention, and the interaction between trial type (random (−) and pattern (+)) and attentional type (inattention (+), divided attention (−)).
Note: Please refer to the online version of the article to view the figures in colour.

compare grouping ability under conditions of inattention to grouping ability under conditions of divided attention. The behavioral data clearly indicated that participants perceived the Ponzo illusion during fMRI scanning: They perceived the horizontal line at the converging end of the illusion as longer than the horizontal line at the diverging end. This effect did not occur when no illusion was presented in the background, and in this case, participants were able to accurately identify the longer of the two different horizontal lines.

Perceptual Grouping and Attention

Our findings revealed activation in the frontal, parietal, and occipital regions of the brain in response to grouping in general, consistent with previous research involving perceptual grouping (Ross et al., 2000; Seymour et al., 2008). Furthermore, activation in the bilateral frontal, temporal, and cingulate gyrus in response to divided-attention trials compared with inattention trials is consistent with the increased cognitive demands resulting from carrying out the line discrimination task while attending to the background (Fink et al., 1996; Herath et al., 2001), as well as mechanisms related to encoding and retrieving

Table 1. Activation Regions in Response to Grouping Stimuli Under Inattention and Divided-Attention Conditions.

Location	Side	Brodmann area	TAL coordinates			Voxels (1 × 1 × 1 mm)
			x	y	z	
Main effects						
Stimulus (pattern vs. random)						
Inferior occipital gyrus (occipital lobe)	L	18	−27	−88	−8	29,600
Cingulate gyrus (limbic lobe)	R	24	3	−10	31	6,202
Inferior parietal lobe (parietal lobe)	L	40	−39	−31	46	9,953
Medial frontal gyrus (frontal lobe)	L	9	−24	44	10	1,794
Attention (inattention > divided attention)						
Parahippocampal gyrus (limbic lobe)	L	36	−27	−40	−5	1,541
Attention (divided attention > inattention)						
Superior temporal gyrus (temporal lobe)	R	22	60	−46	19	4,450
Inferior frontal gyrus (frontal lobe)	R	44	48	17	10	3,483
Cingulate gyrus (limbic lobe)	R	24	6	8	37	1,350
Cingulate gyrus (limbic lobe)	L	31	−15	−25	43	1,477
Inferior frontal gyrus (frontal lobe)	L	45	−36	29	7	1,569
Superior temporal gyrus (temporal lobe)	L	22	−54	−49	10	1,627
Interaction						
Supramarginal gyrus (parietal lobe)	R	40	61	−49	25	587
Simple effects						
Inattention condition						
Supramarginal gyrus (parietal lobe)	R	40	60	−49	29	1,488
Middle frontal gyrus (frontal lobe)	R	46	39	36	19	1,238
Inferior occipital gyrus (occipital lobe)	L	18	−30	−88	−8	1,630
Inferior parietal lobe (parietal lobe)	L	40	−24	−43	52	2,991
Divided-attention condition						
Bilateral lingual gyrus (occipital lobe)	L/R	17	3	−88	7	20,505
Medial frontal gyrus (frontal lobe)	R	32	6	14	40	2,878

Note. The number of voxels refers to the size of the cluster following application of the cluster-level statistical threshold estimator.

(Anderson et al., 2000). Activation in the parahippocampal gyrus in response to inattention trials compared with divided-attention trials may also be involved in mechanisms related to encoding (Kensinger et al., 2003). While these results related to perceptual grouping and attention are supported by previous research, this study further extends these findings by providing a direct comparison of perceptual grouping mechanisms under varying levels of attention. Results indicated that the right supramarginal gyrus is involved in perceptual grouping specifically under conditions of inattention. Together, the results of this study replicate previous behavioral studies in which the Ponzo illusion was elicited under conditions of inattention (Carther-Krone et al., 2016; Moore & Egeth, 1997) and extend them to include the underlying neural mechanisms. Given that much of the visual world at any moment is not represented in conscious perception, these findings provide crucial information about how we make sense of visual scenes in the real world.

Grouped Versus Ungrouped Stimuli

When pattern matrix trials were contrasted with random matrix trials across attentional conditions, our analysis revealed activations in the inferior parietal cortex, medial frontal

gyrus, inferior occipital gyrus, and cingulate gyrus. This is consistent with previous research demonstrating that the early visual cortex (Ross et al., 2000) as well as inferior parietal cortex and prefrontal cortex (Seymour et al., 2008) are involved in attending to grouped versus ungrouped stimuli. Neuroimaging studies point to the inferior parietal cortex as an important region underlying perceptual grouping, namely in integrating local features into a global percept, which is supported by studies showing that damage to the inferior parietal cortex leads to difficulties integrating local elements into a global whole (Huberle & Karnath, 2006; Karnath et al., 2000). In addition to the inferior parietal cortex, activation was also found in the frontal region of the cortex, which has been commonly implicated with visual processes succeeding local feature integration, such as perceiving and recognizing objects (Logethetis, 1998). Activation in the early visual cortex of the occipital lobe has been shown to be involved in maintaining sensitivity to the contrasts and spatial organization of cues involved in perceptual grouping (Ross et al., 2000) and is important in extracting bottom-up information required to perceive the grouped stimuli. Finally, activation in the cingulate gyrus has been shown to be involved in encoding and retrieving information (Anderson et al., 2000), which is likely activated in response to instructing participants to recall information about the background in divided-attention conditions. Together these findings demonstrate that the inferior parietal, middle frontal, and early occipital and cingulate regions are involved in gestalt perception in general. This is supported by previous research and provides evidence that grouping mechanisms were successfully activated using our stimulus involving a visual illusion.

Divided-Attention Versus Inattention Conditions

When divided-attention trials were contrasted with inattention trials, our analysis showed activation in the bilateral frontal, temporal, and cingulate gyrus. This is consistent with previous research demonstrating that the frontal and temporal regions of the brain are recruited as the cognitive load required to perform a task increases (Fink et al., 1996; Herath et al., 2001; Johnson & Zatorre, 2006), as well as the importance of the cingulate cortex in encoding and retrieving (Anderson et al., 2000). Previous research has shown cingulate and prefrontal cortex activation in response to a linguistic dual task paradigm (Benedict et al., 1998), and prefrontal activation has been shown to be involved in top-down attentional control (Corbetta & Shulman, 2002). Prior research has also shown that the cingulate cortex is activated in response to increased task difficulty in a working memory task, while the prefrontal cortex responds to increased working memory load (Barch et al., 1997). Because participants in this study had to perform the line discrimination task while attending to the background in the divided-attention condition, activation in the cingulate cortex likely represents an increase in task difficulty compared with the inattention trials, while prefrontal activation likely represents an increase in working memory load and executive functioning (Loose et al., 2003).

Increased activation was also found bilaterally in the superior temporal gyrus at the region of the temporoparietal junction (TPJ). While this region has been implicated in detection of salient distractors and cognitive control more generally (Chang et al., 2013; Geng & Mangun, 2011), more specifically this region appears to be robustly activated in response to detecting behaviorally relevant stimuli (Corbetta et al., 2008; Serences et al., 2005). As a result, the TPJ is a possible brain region responsible for the integration of top-down and bottom-up processes. In the current study, the divided-attention condition required increased cognitive control compared with the inattention condition due to the increased task demands, with participants tasked to detect behaviorally relevant stimuli

(i.e., the background patterns) while carrying out the line discrimination task. Although participants were instructed to perform the line discrimination task while attending to the background dot patterns, because these patterns did not occur on every trial, it is possible that the random occurrence of these patterns provided enough saliency to capture attention in a bottom-up fashion initially, bringing patterns into awareness for later recollection. This would suggest that TPJ has a role in integrating bottom-up and top-down attentional processes.

When inattention trials were contrasted with divided-attention trials, activation was only found in the left parahippocampal gyrus. While it is unclear how this region may be specifically involved in inattention per se, this region has been shown in prior research to be involved in the successful encoding of stimuli in a relatively easy divided-attention task when compared with a more cognitively demanding divided-attention task (Kensinger et al., 2003). While further research is necessary to uncover the extent to which activation in this region is specific to implicit grouping, this activation nonetheless suggests that encoding occurs to some extent, likely involving the horizontal lines to which attention is pointed in the inattention condition.

Brain Activity Related to the Interaction Between Grouping and Attention

Activation in the right supramarginal gyrus of the parietal lobe was characterized by a significant interaction between grouping and attention. Our interpretation of this interaction was guided by a simple effects analysis examining brain regions activated for pattern compared with random matrix trials at each attentional condition separately, demonstrating significant activation of the right supramarginal gyrus for pattern matrix trials compared with random matrix trials in the inattention condition.

While parietal activation was found generally in response to grouped stimuli, the distinct region activated in response to inattention suggests the importance of this region in perceptual grouping even before attentional mechanisms are recruited. The region of the supramarginal gyrus is located in the inferior parietal cortex, which has been established as important in forming object representations, a process important in grouping perceptual information together. Because inattention trials required participants to indicate the longer of the two horizontal lines while implicitly grouping the background stimuli together to form the illusion, and divided-attention trials required participants to indicate the longer of the two lines while explicitly attending to the background stimuli, this would suggest that activation in the parietal lobe in the inattention condition is involved in implicitly grouping the black dots together to form the illusory percept. This is supported by previous research showing differing activation in the inferior parietal lobe in response to grouped shapes compared with ungrouped shapes when observers report being unaware of the groupings (Xu & Chun, 2007).

While activation in the inferior parietal lobe in response to perceptual grouping and the ability to group visual information under conditions of inattention has been previously and well established as separate entities, the importance of this finding is that it shows the inferior parietal lobe as a region responsible for perceptual grouping even when participants are not able to explicitly report on the grouped information. Prior studies tend to focus on low-level brain regions such as the early visual cortex as areas implicated in implicit grouping, and findings from this study suggest that processing in higher regions are modulating grouping effects even when attention is not specifically directed at them.

Possible Limitations

A possible concern that should be acknowledged in the divided-attention runs is the difference in instructions for this study compared with similar studies that have used this paradigm in the past. While previous studies of inattention probe participants about the irrelevant background stimuli and then ask them to continue performing the same task again, with the assumption being that drawing their attention to the background will lead to a division of attention from that point forward, in this study, we explicitly asked participants to attend to the irrelevant stimuli while performing the discrimination trials after we had probed them about the background following the inattention trials. This difference in task instruction may result in a limitation of the generalizability of results in the divided-attention runs but was modified to ensure that participants were really motivated to divide their attention. Another modification of this study from prior similar studies is the presentation of the background illusion with the lines always converging toward the top of the screen, which allowed us to query participants about the background over the whole block of trials as opposed to a single trial. While it is possible that this may have introduced a response bias, a prior version of this experiment (Carther-Krone et al., 2016) where participants were shown the illusion with the lines converging toward the top and bottom of the screen showed that participants accurately identified the perceived longer line as that at the converging end, whether the lines converged toward the top or bottom of the screen, supporting our claim that participants are in fact influenced by the Ponzo illusion.

In referring to the divided-attention condition, it should also be acknowledged that while increased task are most likely driving activation found in the frontal lobe, the manipulation of the attentional condition may be confounded by eye movements. Because participants are instructed to attend to the background as well as the horizontal lines, increased eye movement may be more likely in the divided-attention condition, which may also explain the frontal activation in this attentional condition. Future research involving eye tracking is suggested to remove eye movement as a potential confound in these types of studies.

A final concern involves the inclusion of all participants in our study. Of the 22 participants in this study, 11 participants noted seeing the pattern when probed following the inattention trials. However, of these 11 participants, only 6 were able to accurately identify the pattern. Because consciously perceiving the pattern based on awareness measures involves explicitly stating the pattern was seen as well as accurately identifying it, our sample included six participants who fit this criterion. While removing these participants may be viewed as the optimal solution to ensuring a more representative *inattention* condition, we would argue that this is not the case because exclusion procedures suffer from regression-to-the-mean effects (Shanks, 2017). As such we have chosen to include all the participants in our analysis to avoid this statistical error, as well as to strengthen the power of our sample. However, at the request of one of the reviewers, we also ran the analysis with the exclusion of those participants who reported seeing the pattern at the query stage and found similar results.[1] Namely, many of the regions of interest discussed in this study were the same whether or not all participants were included. As such, we have full confidence that our findings represent the question asked in this study.

Conclusion

In summary, the present findings suggest that the right supramarginal gyrus is an important region for implicit perceptual grouping. While previous research has demonstrated this region to be responsible for object representation, most research has focused on grouping

under conditions of divided attention or selective attention, often using multiple sensory modalities to support their claims. Of the research that examines grouping under conditions of inattention, findings tend to be limited to low-level brain regions, demonstrating involvement of early visual cortex in grouping information when attentional processes are limited. Here, we not only examined perceptual grouping under two varying conditions of attention, but we provided a direct comparison between regions activated in response to grouped versus ungrouped stimuli in each attentional condition. Our findings converge with previous studies showing similar regions of activation for both perceptual grouping and divided attention in general, emphasizing that the stimuli used in our study was able to replicate previous findings. This provided the support required to perform the direct comparison, which indicated the importance of the right supramarginal gyrus in grouping under conditions of inattention. This demonstrates that even under conditions of inattention, more complex visual processing is occurring. Future research involving multiple types of Gestalt processing under varying conditions of attention will serve to strengthen this finding. However, our current findings clearly demonstrate that visual information below the level of explicit awareness can influence perception of the visual world and that the neural mechanisms driving perception are modulated by attentional allocation.

Declaration of Conflicting Interests

Funding

ORCID iDs

Tiffany A. Carther-Krone 🆔 https://orcid.org/0000-0002-6665-9727
Jonathan J. Marotta 🆔 https://orcid.org/0000-0001-6635-4694

Note

1. Analysis of only the participants who were able to consciously perceive the pattern based on awareness measures following the inattention block ($N = 16$) showed similar activations to those in Table 1. Activation was no longer found in in the left frontal, temporal, and bilateral cingulate gyrus for inattention versus divided-attention trials or right frontal gyrus for perceptual grouping in inattention trials.

References

Anderson, N. D., Iidaka, T., Cabeza, R., Kapur, S., McIntosh, A. R., & Craik, F. I. (2000). The effects of divided attention on encoding-and retrieval-related brain activity: A PET study of younger and older adults. *Journal of Cognitive Neuroscience*, *12*, 775–792.

Barch, D. M., Braver, T. S., Nystrom, L. E., Forman, S. D., Noll, D. C., & Cohen, J. D. (1997). Dissociating working memory from task difficulty in human prefrontal cortex. *Neuropsychologia*, *35*, 1373–1380.

Benedict, R. H., Lockwood, A. H., Shucard, J. L., Shucard, D. W., Wack, D., & Murphy, B. W. (1998). Functional neuroimaging of attention in the auditory modality. *Neuroreport*, *9*, 121–126.

Carther-Krone, T. A., Shomstein, S., & Marotta, J. J. (2016). Looking without perceiving: Impaired preattentive perceptual grouping in autism spectrum disorder. *PLoS One*, *11*, e0158566. https://doi.org/10.1371/journal.pone.0158566

Chang, C. F., Hsu, T. Y., Tseng, P., Liang, W. K., Tzeng, O. J., Hung, D. L., & Juan, C. H. (2013). Right temporoparietal junction and attentional reorienting. *Human Brain Mapping*, *34*, 869–877.

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

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

Driver, J., Davis, G., Russell, C., Turatto, M., & Freeman, E. (2001). Segmentation, attention and phenomenal visual objects. *Cognition*, *80*, 61–95. https://doi.org/10.1016/S0010-0277(00)00151-7

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

Forman, S. D., Cohen, J. D., Fitzgerald, M., Eddy, W. F., Mintun, M. A., & Noll, D. C. (1995). Improved assessment of significant activation in functional magnetic resonance imaging (fMRI): Use of a cluster-size threshold. *Magnetic Resonance in Medicine*, *33*, 636–647. https://doi.org/10.1002/mrm.1910330508

Geng, J. J., & Mangun, G. R. (2011). Right temporoparietal junction activation by a salient contextual cue facilitates target discrimination. *Neuroimage*, *54*, 594–601.

Goebel, R., Esposito, F., & Formisano, E. (2006). Analysis of functional image analysis contest (FIAC) data with brainvoyager QX: From single-subject to cortically aligned group general linear model analysis and self-organizing group independent component analysis. *Human Brain Mapping*, *27*, 392–401. https://doi.org/10.1002/hbm.20249

Han, S., Jiang, Y., Mao, L., Humphreys, G. W., & Gu, H. (2005). Attentional modulation of perceptual grouping in human visual cortex: Functional MRI studies. *Human Brain Mapping*, *25*, 424–432. https://doi.org/10.1002/hbm.20119

Han, S., Jiang, Y., Mao, L., Humphreys, G. W., & Qin, J. (2005). Attentional modulation of perceptual grouping in human visual cortex: ERP studies. *Human Brain Mapping*, *26*, 199–209. https://doi.org/10.1002/hbm.20157

Han, S., Song, Y., Ding, Y., Yund, E. W., & Woods, D. L. (2001). Neural substrates for visual perceptual grouping in humans. *Psychophysiology*, *38*, 926–935. https://doi.org/10.1111/1469-8986.3860926

He, D., Mo, C., Wang, Y., & Fang, F. (2015). Position shifts of fMRI-based population receptive fields in human visual cortex induced by Ponzo illusion. *Experimental Brain Research*, *233*, 3535–3541. https://doi.org/10.1007/s00221-015-4425-3

Herath, P., Klingberg, T., Young, J., Amunts, K., & Roland, P. (2001). Neural correlates of dual task interference can be dissociated from those of divided attention: An fMRI study. *Cerebral Cortex*, *11*, 796–805.

Huberle, E., & Karnath, H. O. (2006). Global shape recognition is modulated by the spatial distance of local elements – Evidence from simultanagnosia. *Neuropsychologia*, *44*, 905–911. https://doi.org/10.1016/j.neuropsychologia.2005.08.013

Johnson, J. A., & Zatorre, R. J. (2006). Neural substrates for dividing and focusing attention between simultaneous auditory and visual events. *Neuroimage*, *31*, 1673–1681.

Karnath, H., Ferber, S., Rorden, C., & Driver, J. (2000). The fate of global information in dorsal simultanagnosia. *Neurocase*, *6*, 295–306. https://doi.org/10.1080/13554790008402778

Kastner, S., De Weerd, P., Desimone, R., & Ungerleider, L. G. (1998). Mechanisms of directed attention in the human extrastriate cortex as revealed by functional MRI. *Science*, *282*, 108–111. https://doi.org/10.1126/science.282.5386.108

Kensinger, E. A., Clarke, R. J., & Corkin, S. (2003). What neural correlates underline successful encoding and retrieval? A functional magnetic resonance imaging study using a divided attention paradigm. *Journal of Neuroscience*, *23*, 2407–2415.

Kimchi, R., & Peterson, M. A. (2008). Fig-ground segmentation can occur without attention. *Psychological Science*, *19*, 660–668. https://doi.org/10.1111/j.1467-9280.2008.02140.x

Kimchi, R., & Razpurker-Apfeld, I. (2004). Perceptual grouping and attention: Not all groupings are equal. *Psychonomic Bulletin & Review*, *11*, 687–696. https://doi.org/10.3758/BF03196621

Kok, P., Bains, L. J., van Mourik, T., Norris, D. G., & de Lange, F. P. (2016). Selective activation of the deep layers of the human primary visual cortex by top-down feedback. *Current Biology*, *26*, 371–376. https://doi.org/10.1016/j.cub.2015.12.038

Lamy, D., Segal, H., & Ruderman, L. (2006). Grouping does not require attention. *Perception & Psychophysics*, *68*, 17–31. https://doi.org/10.3758/BF03193652

Lo, S. Y., & Yeh, S. L. (2011). Independence between implicit and explicit processing as revealed by the Simon effect. *Consciousness and Cognition*, *20*, 523–533. https://doi.org/10.1016/j.concog.2010.11.007

Logethetis, N. (1998). Object vision and visual awareness. *Current Opinion in Neurobiology*, *8*, 536–544.

Loose, R., Kaufmann, C., Auer, D. P., & Lange, K. W. (2003). Human prefrontal and sensory cortical activity during divided attention tasks. *Human Brain Mapping*, *18*, 249–259.

Mikellidou, K., Gouws, A. D., Clawson, H., Thompson, P., Morland, A. B., & Keefe, B. D. (2016). An orientation dependent size illusion is underpinned by processing in the extrastriate visual area, LO1. *Iperception*, *7*, 2041669516667628. https://doi.org/10.1177/2041669516667628

Moore, C. M., & Egeth, H. (1997). Perception without attention: Evidence of grouping under conditions of inattention. *Journal of Experimental Psychology: Human Perception and Performance*, *23*, 339–352. https://doi.org/10.1037/0096-1523.23.2.339

Müller, D., Winkler, I., Roeber, U., Schaffer, S., Czigler, I., & Schröger, E. (2010). Visual object representations can be formed outside the focus of voluntary attention: Evidence from event-related brain potentials. *Journal of Cognitive Neuroscience*, *22*, 1179–1188. https://doi.org/10.1162/jocn.2009.21271

Ponzo, M. (1910). Intorno ad alcune illusioni nel campo delle sensazioni tattili, sull'illusione di Aristotele efenomeni analoghi [On some tactile illusions, Aristotle's illusion, and similar phenomena]. *Archiv Für Die Gesamte Psychologie*, *16*, 307–345.

Prieto, A., Mayas, J., & Ballesteros, S. (2014). Time course of grouping by proximity and similarity in a haptic speeded orientation task. *LNCS, Haptics: Neuroscience, Devices, Modeling, and Applications*, *8618*, 379–385. https://doi.org/10.1007/978-3-662-44193-0_47

Reynolds, J. H., Chelazzi, L., & Desimone, R. (1999). Competitive mechanisms subserve attention in macaque areas V2 and V4. *Journal of Neuroscience*, *19*, 1736–1753. https://doi.org/10.1523/JNEUROSCI.19-05-01736.1999

Ross, W. D., Grossberg, S., & Mingolla, E. (2000). Visual cortical mechanisms of perceptual grouping: Interacting layers, networks, columns, and maps. *Neural Networks*, *13*, 571–588. https://doi.org/10.1016/S0893-6080(00)00040-X

Russell, C., & Driver, J. (2005). New indirect measures of "inattentive" visual grouping in a change-detection task. *Perception & Psychophysics*, *67*, 606–623. https://doi.org/10.3758/BF03193518

Salo, E., Salmela, V., Salmi, J., Numminen, J., & Alho, K. (2017). Brain activity associated with selective attention, divided attention and distraction. *Brain Research*, *1664*, 25–36. https://doi.org/10.1016/j.brainres.2017.03.021

Santangelo, V., Fagioli, S., & Macaluso, E. (2010). The costs of monitoring simultaneously two sensory modalities decrease when dividing attention in space. *Neuroimage*, *49*, 2717–2727. https://doi.org/10.1016/j.neuroimage.2009.10.061

Selles, R. W., Michielsen, M. E., Bussmann, J. B., Stam, H. J., Hurkmans, H. L., Heijnen, I., . . . Ribbers, G. M. (2014). Effects of a mirror-induced visual illusion on a reaching task in stroke patients: Implications for mirror therapy training. *Neurorehabilitation and Neural Repair*, *28*, 652–659. https://doi.org/10.1177/1545968314521005

Serences, J. T., Shomstein, S., Leber, A. B., Golay, X., Egeth, H. E., & Yantis, S. (2005). Coordination of voluntary and stimulus-driven attentional control in human cortex. *Psychological Science*, *16*, 114–122.

Seymour, K., Karnath, H. O., & Himmelbach, M. (2008). Perceptual grouping in the human brain: Common processing of different cues. *Neuroreport*, *19*, 1769–1772. https://doi.org/10.1097/WNR.0b013e328318ed82

Shanks, D. R. (2017). Regressive research: The pitfalls of post hoc data selection in the study of unconscious mental processes. *Psychonomic Bulletin & Review*, *24*, 752–775.

Shomstein, S., Kimchi, R., Hammer, M., & Behrmann, M. (2010). Perceptual grouping operates independently of attentional selection: Evidence from hemispatial neglect. *Attention, Perception, & Psychophysics*, *72*, 607–618. https://doi.org/10.3758/APP.72.3.607

Talairach, J., & Tournoux, P. (1988). *Co-planar stereotaxic atlas of the human brain*. Thieme.

Vidal, J. R., Chaumon, M., O'Regan, J. K., & Tallon-Baudry, C. (2006). Visual grouping and the focusing of attention induce gamma-band oscillations at different frequencies in human magneto-encephalogram signals. *Journal of Cognitive Neuroscience*, *18*, 1850–1862. https://doi.org/10.1162/jocn.2006.18.11.1850

Vuilleumier, P., & Landis, T. (1998). Illusory contours and spatial neglect. *Neuroreport*, *9*, 2481–2484. https://doi.org/10.1097/00001756-199808030-00010

Vuilleumier, P., Valenza, N., & Landis, T. (2001). Explicit and implicit perception of illusory contours in unilateral spatial neglect: Behavioural and anatomical correlates of preattentive grouping mechanisms. *Neuropsychologia*, *39*, 597–610. https://doi.org/10.1016/S0028-3932(00)00148-2

Wertheimer, M. (1923). Untersuchungen zur Lehre von der Gestalt II. *Psycholosgische Forschung*, *4*, 301–350. https://doi.org/10.1007/BF00410640

Xu, Y., & Chun, M. M. (2007). Visual grouping in human parietal cortex. *Proceedings of the National Academy of Sciences of the United States of America*, *104*, 18766–18771. https://doi.org/10.1073/pnas.0705618104