



Functional involvement of subcortical structures in global-local processing

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ABSTRACT

The present study examined the involvement of subcortical structures in the processing of global and local information. To this end, we used a stereoscope to present hierarchical stimuli (global shapes composed of local elements) in a dichoptic or a monocular fashion, such that global and local information was either presented to the same eye (same-eye condition) or segregated between the eyes (different-eyes condition). In Experiment 1, the typical global advantage and global-to-local interference were observed for the same-eye presentation condition. On the other hand, no indication of a global advantage or of global-to-local interference emerged in the different-eyes presentation condition. In Experiment 2 we replicated these results, ruling out a possible alternative explanation that the pattern of results observed for the different-eyes presentation condition resulted merely from segregation of the stimulus between the eyes. Rather, the experiment demonstrated that the global-to-local interference was eliminated only when global and local information was segregated between the eyes. Taken together, these findings suggest that processing the global aspect of hierarchical stimuli involves subcortical regions indexed by monocular portions of the visual system.

The topic of how the global structure and the local details of a visual scene are processed has been extensively studied using the global-local task (Navon, 1977; for reviews see Kimchi, 1992, 2015; Navon, 2003). In this task, participants are presented with hierarchical stimuli in which larger figures are constructed by appropriate arrangement of smaller figures (first introduced by Asch, 1962 and later by Kinchla, 1974, 1977). Participants are then requested to identify the larger (global) figure or the smaller (local) figures in separate blocks of trials. An example of hierarchical stimuli is a set of large letters constructed from the same set of small letters having either the same identity or a different identity as the large letters.

The typical results observed when this global-local task is performed include a global advantage—faster identification of the global than the local letter—and global-to-local interference—irrelevant global conflicting information interferes with identification of the local letter, but not vice versa (Navon, 1977). It should be noted that several variables can moderate these effects or even reverse them, such as the overall size of the hierarchical stimulus, the number and relative size of the local elements, spatial uncertainty, and exposure duration (see Kimchi, 1992, 2015, for reviews). Nonetheless, all else being equal, global superiority as reflected in relative speed of processing and/or asymmetric interference is observed up to the limits of visibility and visual acuity.

1. Neural substrates of global and local processing

Evidence of relative hemispheric specialization for global and local processing of hierarchical visual stimuli has been found in imaging studies, in research with patients who suffer from temporal parietal lesions, and in studies that presented hierarchical visual stimuli to different visual fields to healthy adults (e.g., Fink et al., 1997; Kimchi & Merhav, 1991; Martinez et al., 1997; Robertson et al., 1988; Robertson & Lamb, 1991). Findings from these studies indicate that the right hemisphere (right lingual gyrus) is more proficient in processing global information, while the left hemisphere (left inferior occipital cortex) exhibits more effective involvement in locally directed attention. According to Fink et al. (1997), these hemispheric differences reach level V2 of the visual cortex.

Recent studies have demonstrated that neural processing of global-local information, including differential hemispheric proficiency, can be modulated by changes in task properties. For example, Han et al. (2002) found that the asymmetric pattern of results is weakened under unilateral presentation. Additionally, researchers have demonstrated that certain variables, among them the number of stimuli, the modality of presentation (unilateral or bilateral) and the grouping principle of the local elements that determines the global shape (whether elements are grouped based on shape similarity or proximity), modulate neural

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substrate activation in global-local processing of compound stimuli (e.g., Han et al., 2004; Mao et al., 2006).

Research concerning the neural substrate of global-local processing in humans has focused on cortical regions and mechanisms. Yet, studies on global-local processing in non-human species, including pigeons (e.g., Cavoto & Cook, 2001), honeybees (Avargues-Weber et al., 2015), fish (Truppa et al., 2010), and domestic chicks (Chiandetti et al., 2014), suggest the possible involvement of subcortical structures in this processing. For example, Truppa et al. (2010) found that fish (redtail splitfins) that were presented with hierarchical stimuli exhibited a global preference. Since fish lack neocortex-like cells, their performance on the global-local task depends on other, non-cortical, lower structures of the brain (e.g., optic tectum). It is possible to assume that during the course of evolution, these lower subcortical structures have remained involved in global-local processing in primates as well.

Some information regarding subcortical involvement in global-local processing in humans can be derived from a study conducted on Huntington's disease patients (Roman et al., 1998). In this study, incongruent hierarchical stimuli presented to the patients yielded longer reaction time (RT) across global and local tasks relative to an age-matched control group. Since it is well known that Huntington's disease is a subcortical degenerative disorder, those results may point to the involvement of subcortical regions in the processing of global-local information.

Subcortical involvement in global-local processing may also be implied by the relationship between spatial frequency analysis and global and local information in hierarchical stimuli. For example, Shulman and colleagues (Shulman et al., 1986; Shulman & Wilson, 1987) showed that participants were faster at detecting high-frequency gratings following detection of a target at the local level of a hierarchical stimulus, and were faster at detecting low-frequency gratings following detection of a target at the global level. It has thus been suggested that the global advantage arises from the faster processing of low spatial frequencies compared to high spatial frequencies (e.g., Badcock et al., 1990; Han et al., 2002; Hughes et al., 1990; Shulman et al., 1986; Shulman & Wilson, 1987). Low spatial frequency is also associated with magnocellular subcortical initial processing, which enables us to detect stimuli at the periphery of our visual field (Johnson, 2005; Schiller et al., 1979). We note that although the differential rates of processing low and high spatial frequencies may play a role in global and local perception, it cannot account for several findings, such as the effects of meaningfulness and goodness of form on the global/local advantage (e.g., Poirel et al., 2006; Sebrechts & Fragala, 1985) and the global advantage in the perception of Kanizsa illusory figures (Conci et al., 2011). Yet, to the extent that low spatial frequency is involved in global processing, the fact that low spatial frequency is associated with low levels of the visual system may suggest subcortical involvement in global processing. In addition, several studies suggest the involvement of low levels of the visual system in the processing of facial (global) configurations (Gabay, Burlingham, & Behrmann, 2014; Gabay, Nestor, et al., 2014).

2. The current study

This study aims to explore whether subcortical structures play a functional role in the processing of global and local aspects of a visual stimulus.

The involvement of subcortical structures in cognitive processes may be examined by manipulating the eye-of-origin of the visual stimulus in order to isolate monocular versus binocular neural channels (e.g., Batson et al., 2011; Gabay, Nestor, et al., 2014; Karni & Sagi, 1991). This technique is based on the fact that visual input is monocularly segregated through the lateral geniculate nucleus and up to the input layers of the primary visual cortex (V1) (Horton et al., 1990; Menon et al., 1997). Binocular representations, on the other hand, take place mostly in extrastriate visual areas (Bi et al., 2011) (see Fig. 1). Note that observers are not explicitly aware of the eye of origin of the stimuli they perceive (Blake & Cormack, 1979; Kimchi et al., 1995; Schwarzkopf et al., 2010).

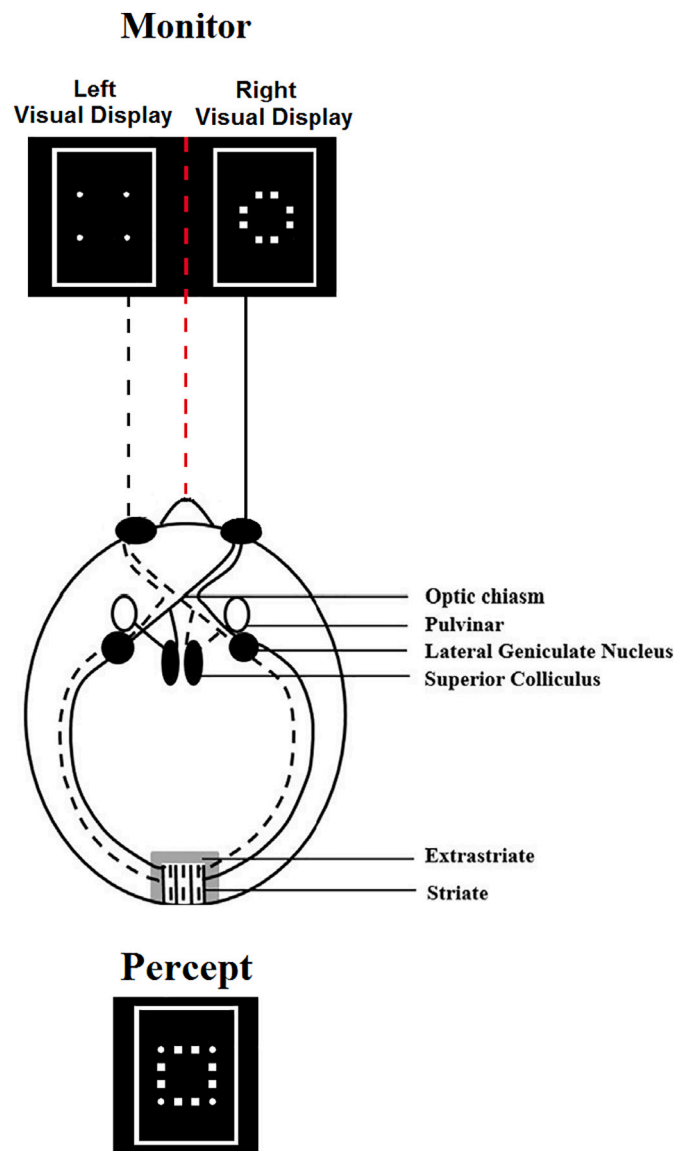


Fig. 1. A schematic depiction of the experimental apparatus and visual pathways from the eyes to the brain (shown in axial plane). The stereoscope provided visual information that could either be segregated between the eyes or presented as a whole to the same eye. The visual information first passes through monocularly segregated subcortical regions (left eye, dashed lines; right eye, solid lines) and is then projected to the pulvinar, LGN, and superior colliculus en route to the striate and then the binocular extrastriate regions.

Across two experiments, we used eye-of-origin manipulation to segregate the visual display so that each eye would receive different visual information. When the stimulus is segregated between the eyes, different monocular channels are presented with different aspects of the stimulus. In contrast, when the stimulus is presented to a single eye, a single monocular channel is presented with the stimulus in a unitary fashion. Segregation of different aspects of a stimulus between the eyes should hamper the ability of subcortical structures to process the visual stimulus as a whole, but should have no effect on cortical processing (since the percept remains intact). Presenting a stimulus to one eye, however, should not influence the processing of subcortical (or cortical) structures. In the first experiment, global and local information of hierarchical stimuli was either segregated between the eyes or presented as a whole to a single eye. We reasoned that if global-local processing involves monocular levels of the visual system, the typical effects associated with processing hierarchical stimuli (i.e., global

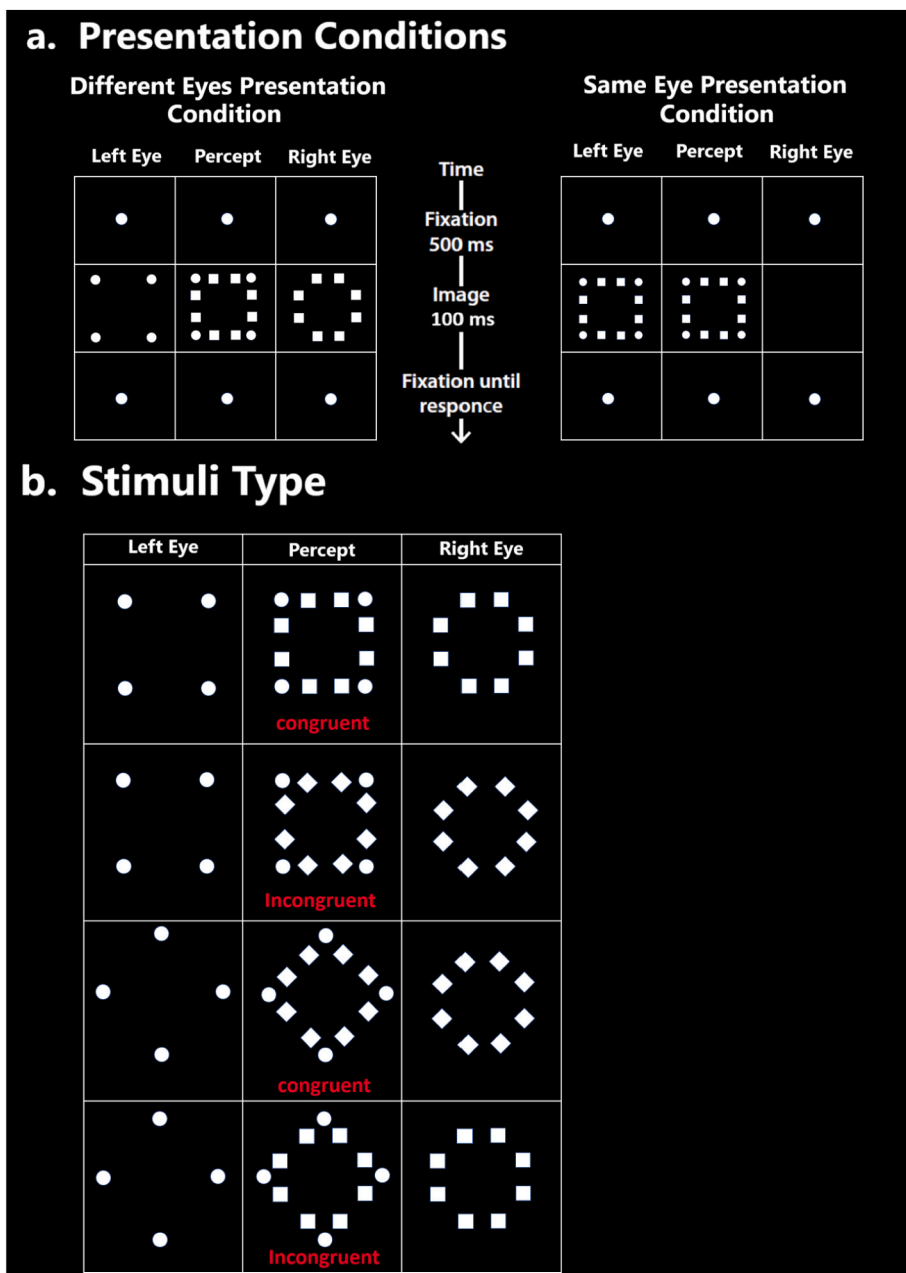


Fig. 2. (a) Presentation conditions and sequence of events in a trial in Experiment 1. Same-Eye Presentation: the hierarchical stimulus is presented as a whole to one eye; the example depicts a global square made up of local squares presented to the left eye. Different-Eyes Presentation: the global and local aspects of the hierarchical stimulus are segregated between the eyes. The example depicts local squares arranged in a task-irrelevant circle presented to the right eye, and four task-irrelevant circles that serve as placeholders forming the vertices of a global square presented to the left eye. (b) Stimuli used in Experiment 1. The stimuli in the right and left eye columns represent the visual stimuli presented to each of the eyes in the different-eyes presentation condition. In the same-eye presentation condition, the stimuli portrayed in the percept column were presented to a single eye. For both presentation conditions, stimuli are global squares or diamonds made of local squares or diamonds and circles. Local task-relevant elements can be congruent or incongruent with the global configuration.

advantage and global-to-local interference) will be stronger when both global and local aspects are presented to the same eye compared to different eyes. To foreshadow the results, typical global advantage and global-to-local interference were observed when both global and local aspects were presented to the same eye, but neither effect was observed when these aspects were presented to different eyes. In the second experiment we replicated these results, providing evidence that the disappearance of the global-to-local interference in the different-eyes condition was not merely a consequence of segregating the visual input between the eyes, but rather of segregating the global and the local information between different monocular channels.

3. Experiment 1

Experiment 1 was designed to explore the involvement of sub-cortical structures in global-local processing, as indicated by the behavioral effects observed in a typical global-local task. Participants were presented with hierarchical stimuli and performed the classical

global and local tasks in separate blocks. The hierarchical stimuli comprised task-relevant local elements (either squares or diamonds) and task-irrelevant local circles that served as placeholders, forming the vertices of the global configuration (either square or diamond; see Fig. 2). The local elements and global configuration were either congruent (e.g., a global square made of local squares) or incongruent (e.g., a global diamond made of local squares).

For each task (global and local), two presentation conditions were used. In the different-eyes presentation condition, the global and local aspects of the hierarchical stimulus were segregated between the eyes. One eye was presented with the task-relevant local elements arranged in a task-irrelevant circular arrangement. Simultaneously, the other eye was presented only with the placeholders—the task-irrelevant small circles—that formed the task-relevant global configuration. In the same-eye presentation condition, the hierarchical stimulus was presented as a whole to a single eye. It is important to note that in both conditions the percept was an intact hierarchical stimulus (see Fig. 2).

Table 1
Accuracy rate for each condition in Experiment 1.

Different-eyes presentation condition				Same-eye presentation condition			
Global task		Local task		Global task		Local task	
IC ^a	CN	IC	CN	IC	CN	IC	CN
0.95	0.95	0.96	0.97	0.97	0.96	0.96	0.97

^a IC = Incongruent; CN = Congruent.

The typical pattern of results observed with the global-local task—global advantage and global-to-local interference—is expected for the same-eye presentation condition. Reduced effects for the different-eyes presentation condition would imply the involvement of monocular (subcortical) structures in global-local processing.

4. Method

4.1. Participants

Since no previous studies employed stereoscopic presentation to study global-local processing in a similar fashion, we used a relatively large sample size. Thirty-six participants consented to take part in this experiment. All of them had normal or corrected-to-normal vision and were compensated with payment or course credit. The protocol was approved by the Institutional Review Board of the University of Haifa.

4.2. Stimuli

Stimuli consisted of 12 white local elements against a black background. Eight of them consisted of squares or diamonds (0.8° height and width) and the remaining four, which formed the vertices of the global configuration, consisted of circles (0.57° in diameter). The location at which the squares or diamonds appeared remained constant throughout the experiment. Their location was determined by creating a global square (with local diamonds or local squares), followed by the removal of the vertices, leaving 8 elements. A distance of 2° was set between each two adjacent squares/diamonds located on the sides of the global configuration. The location of the circles, which served as the vertices of the global shape, was manipulated in order to create a global configuration of a square or a diamond. When the location of the vertices formed a global square, vertices on each side of the configuration were 6° apart. This distance remained the same for the global configuration of the diamond, wherein the vertices' of the global configuration were rotated by 45°.

4.3. Procedure

Each eye was presented with a white rectangular frame (15.34° height, 11.42° width) in which the visual display appeared. Each trial began with presentation of a fixation dot (0.57° diameter) to both eyes for 500 ms, followed by a 100-ms presentation of the target stimulus. Then the fixation dot reappeared and stayed on the screen until the participant responded (see Fig. 2a). Half of the participants were instructed to respond to squares by pressing the leftmost button of a response box with their left index finger and to diamonds by pressing the rightmost button with their right index finger, and the other half were given the opposite response mapping. A correct response was followed by 1000 ms of black screen until the beginning of the next trial, while an incorrect response was followed by the word “error” (in Hebrew) colored in red for 1000 ms, after which the next trial began.

For the global task, participants were instructed to identify the global configuration (square or diamond), while for the local task they were instructed to identify the local elements (squares or diamonds). The two tasks were administered in separate blocks, and their order was

counterbalanced between participants. For each task, the trials were divided equally and randomly between the same-eye and the different-eyes presentation conditions. In the same-eye presentation condition, the compound stimuli were presented to a single eye, while the other eye was presented only with the rectangular frame. In the different-eyes presentation condition, one eye was presented with the circle placeholders that formed the global configuration and the other eye was presented with the local shapes (Fig. 2a).

On half of the trials, the global configuration and the local elements were the same shape (congruent stimuli), while on the other half the global configuration and the local elements were different shapes (incongruent stimuli; see Fig. 2b). In each presentation condition, the visual stimuli were presented with equal frequency to each eye. Across the experimental trials, all the combinations of task (global, local), presentation condition (same eye, different eyes), and congruency (congruent, incongruent) were presented with equal frequency. After completing 16 practice trials, each participant performed 320 experimental trials.

5. Results and discussion

We excluded five participants from the analysis: two who had accuracy rates below 80%, and three due to difficulties in stereoscope calibration.

Trials on which participants responded incorrectly to the target were excluded from the reaction time (RT) analyses (4% of trials). In addition, trials in which RTs were shorter or longer than 2 SD from the mean of each participant in each experimental condition were also excluded from the analyses (less than 5% of trials).

Table 1 shows the accuracy rates as a function of task and congruency for each presentation condition. Accuracy was high (mean = 0.96), and there was no indication of speed-accuracy tradeoff. Therefore, accuracy is not discussed further.

Fig. 3 depicts RTs as a function of task and congruency for each presentation condition. The RT data were submitted to a three-way repeated-measures ANOVA (task: global, local X congruency: congruent incongruent X presentation condition: same-eye, different-eyes). The analysis revealed a significant effect of congruency [$F(1,31) = 31.25$, $MSE = 902$, $p < .01$, $\eta^2 = 0.5$], indicating shorter RTs for congruent compared to incongruent stimuli, and a significant two-way interaction between task and presentation condition [$F(1,31) = 7.99$, $MSE = 9580$, $p < .01$, $\eta^2 = 0.2$]. Most importantly, the three-way interaction between task, presentation condition, and congruency was significant [$F(1,31) = 4.98$, $MSE = 947$, $p < .05$, $\eta^2 = 0.14$].

Following this interaction, we analyzed the data for each presentation condition separately. A significant effect of task emerged for the same-eye presentation condition [$F(1,31) = 5.62$, $MSE = 10,197$, $p < .05$, $\eta^2 = 0.15$]: RTs for the global task were shorter than for the local task, indicating a global advantage. The effect of congruency was also significant [$F(1,31) = 30.45$, $MSE = 454$, $p < .05$, $\eta^2 = 0.49$] and did not interact with task [$F < 1$]: RTs for congruent trials were shorter than for incongruent trials for both the global and the local tasks, suggesting symmetrical interference between the global and the local levels. For the different-eyes presentation condition, the effect of task was not significant [$F < 1$]. The significant effect of congruency [$F(1,31) = 11.48$, $MSE = 1252$, $p < .05$, $\eta^2 = 0.27$] was qualified by a significant two-way interaction between task and congruency [$F(1,31) = 5.81$, $MSE = 1097$, $p < .05$, $\eta^2 = 0.16$]. Follow-up analysis demonstrated a significant effect of congruency for the global task [$F(1,31) = 15.48$, $MSE = 1289.10$, $p < .01$, $\eta^2 = 0.33$], but not for the local task [$F < 1$], hence indicating only local-to-global interference.

Different patterns of results were observed for the two presentation conditions. The results for the same-eye presentation condition revealed a global advantage, a finding observed in many studies using global-local tasks. In addition, the results revealed symmetrical interference between the global and the local levels, namely, global-to-local as well

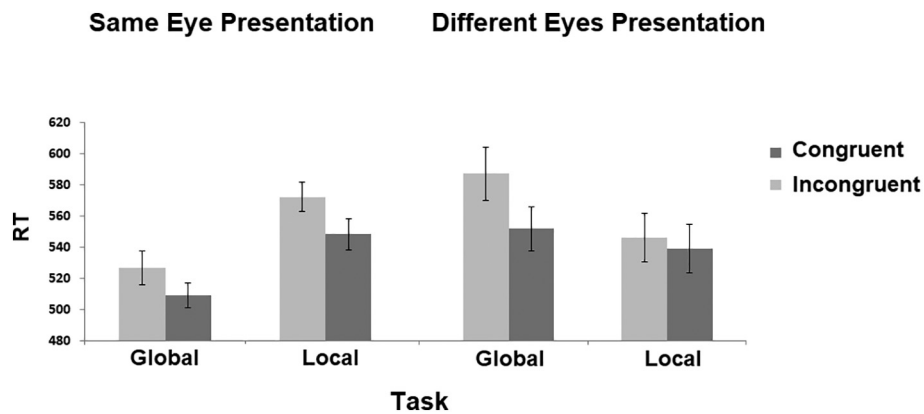


Fig. 3. Mean RT (in ms) as a function of task, and congruency, for each presentation condition in Experiment 1.

as local-to-global interference. Although this is not the typical pattern of results, several studies did obtain symmetrical interference (e.g., Boer & Keuss, 1982; Kinchla & Wolfe, 1979; Pomerantz, 1983). On the other hand, when the global and local aspects of the stimuli were segregated between the eyes, only local-to-global interference was statistically significant, with no indication of global advantage or global-to-local interference. The finding that both global advantage and global-to-local interference were present only for the same-eye presentation condition but not for the different-eyes presentation condition implies a clear monocular involvement in global processing. Hence, global processing involves subcortical mechanisms, as indexed by monocular portions of the visual system.

In contrast to the global-to-local interference that was observed only in the same-eye presentation condition, local-to-global interference was observed both in the same-eye and in the different-eyes presentation conditions. This finding indicates that local-to-global interference is not hampered by segregation of the stimulus into different monocular channels and may suggest that local-to-global interference relies mainly on cortical substrates.

6. Experiment 2

The results of Experiment 1 demonstrated both a global advantage and global-to-local interference in the same-eye presentation condition. In contrast, there was no indication of such effects when local information and global information were presented to different eyes. These results suggest the involvement of subcortical structures in global processing.

It is possible, however, that the absence of global-to-local interference in the different-eyes presentation condition is merely the consequence of segregating the visual input between the eyes and not the result of specific segregation of global and local information. Thus, in the current experiment we sought to replicate the pattern of results observed in Experiment 1 and strengthen the conclusions regarding the involvement of subcortical structures in global processing by ruling out this alternative explanation. Namely, we sought to provide evidence showing that the absence of global-to-local interference for the different-eyes presentation condition was not due to an effect of segregation per se, but rather due to the segregation of global and local information between the eyes, thus implying subcortical involvement in global processing. To this end, we divided the different-eyes presentation into two conditions. In the control condition, the stimulus was segregated between the eyes such that one eye was presented with the local elements arranged according to the global configuration of the stimulus, while the other eye was presented with circular placeholders used just to complete the perceptual stimulus. In the experimental condition, which was similar to the different-eyes presentation condition in Experiment 1, the stimulus was segregated between the eyes

such that one eye was presented with the local elements and the other eye was presented with circle placeholders forming the global configuration of the stimulus (see Fig. 4). Thus, although the stimulus was segregated between the eyes in both conditions, only in the experimental condition was the global and local information segregated between the eyes. If global-to-local interference is influenced by the segregation of global and local information between the eyes, then such interference should emerge only in the control condition. If the absence of global-to-local interference results from segregation per se, then no global-to-local interference is expected in either the control or the experimental conditions.

7. Method

7.1. Participants

Sample size was estimated using G*Power software (Faul et al., 2007). The power of the study was estimated using the effect size of the interaction between task and congruency for the different eyes condition from Experiment 1. Our calculation showed that with 20 participants the level of power for detecting differences in congruency was > 90%. 28 participants were recruited to take part in this experiment. All had normal or corrected-to-normal vision and none had participated in Experiment 1. Participants were compensated with payment or course credits. The protocol was approved by the Institutional Review Board of University of Haifa.

7.2. Stimuli

Stimuli were composed of eight white geometrical figures presented against a black background. As in the first experiment, the white geometrical elements were either squares (0.8°), circles (0.57°) or diamonds (tilted squares), forming a global configuration of diamonds or squares. When the local elements were arranged in the shape of a global square, vertices on each side of the configuration were 6° apart. The global configuration of the diamond was identical to that of the square, except that it was rotated by 45° .

In contrast to Experiment 1, in which only the task-irrelevant circles served as the vertices of the global configuration, diamonds, squares and circles could all be used as vertices of the global shape (see Fig. 4). For the different-eyes presentation trials in the control condition, the task-relevant local elements were arranged in the same global configuration as the global configuration of the binocular percept, while the task-irrelevant circles merely completed the percept (i.e. the square/diamond elements were used as vertices). Similar to the different-eyes presentation condition in Experiment 1, in the experimental condition the task-irrelevant circles were placeholders and used as vertices of the global configuration. Unlike in Experiment 1, however, the local

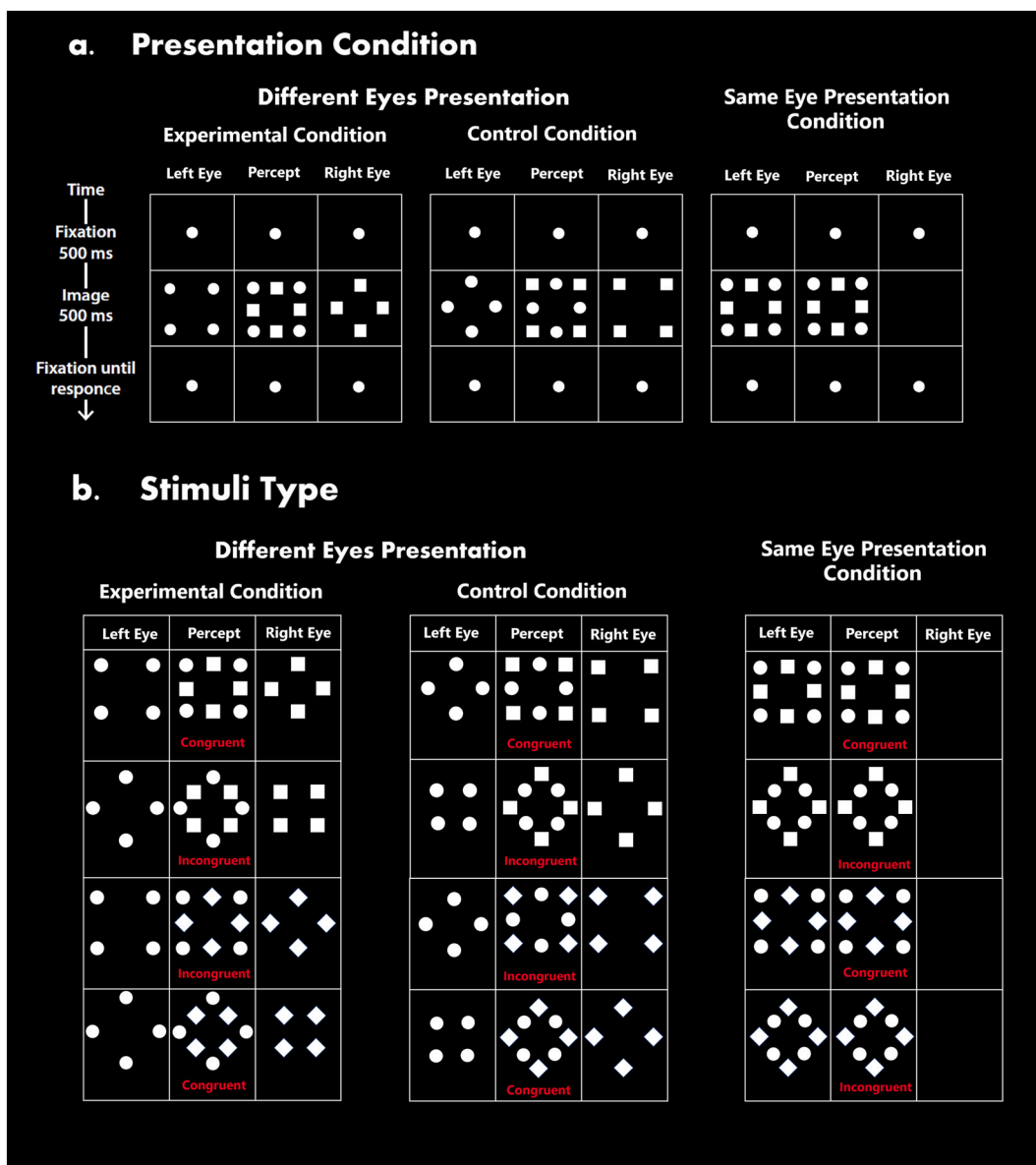


Fig. 4. (a) Presentation conditions and sequence of events on each trial in Experiment 2. Same-Eye presentation: the hierarchical stimulus is presented as a whole to one eye; the example depicts a global square made up of local squares presented to the left eye. Different-Eyes presentation – experimental condition: the global and local aspects of the stimuli are segregated between the eyes. The example depicts local squares arranged in a diamond presented to the right eye, and four task-irrelevant circles presented to the left eye that serve as placeholders forming the vertices of a global square. Different-Eyes presentation – control condition: the global and local aspects of the stimuli are presented to the same eye. The example depicts local squares forming the vertices of a global square presented to the right eye, and four task-irrelevant circles presented to the left eye that are used to complete the perceptual stimulus. (b) Stimuli used in Experiment 2. For all presentation conditions, the stimuli are global squares or diamonds made of local squares or diamonds and circles. Local task-relevant elements can be congruent or incongruent with the global configuration. The percept column portrays the stimulus as it is perceived by binocular structures. In the experimental condition one eye (right eye in the example) was presented with the local elements and the other eye (left eye) was presented with circle placeholders forming the global configuration of the stimulus. In the control condition, one eye (right eye in the example) was presented with the local elements arranged in the global configuration of the stimulus, while the other eye (left eye in the example) was presented with circular placeholders used just to complete the perceptual stimulus. In the same-eye presentation condition, one eye (right eye in the example) was presented only with white rectangular frame, while the other eye (left eye in the example) was presented with the entire configuration.

elements were arranged in a task-relevant configuration that was different from the global configuration of the binocular percept.

7.3. Procedure

Each eye was shown a white rectangular frame (15.94° height, 11.42° width) in which the visual display was presented. A fixation dot (0.57° in diameter) marking the beginning of a trial was presented to both eyes for 500 ms, followed by the stimuli that appeared for 100 ms and was then replaced with a fixation dot until the participant

responded. A correct response was followed by 1000 ms of black screen until the beginning of the next trial. An incorrect response was followed by the word “error” in Hebrew colored in red (the word was presented for 1000 ms, after which the next trial began).

Trials were divided equally between same-eye and different-eyes presentations. For both presentation conditions, on half of the trials the elements placed at the vertices were squares/diamonds, while circles were used as vertices on the other half of the trials. The different-eyes presentation trials were divided equally between the experimental condition and the control condition. In the experimental condition, one

Table 2
Accuracy rate for each condition in Experiment 2.

Different-eyes presentation control condition				Different-eyes presentation experimental condition				Same-eye presentation			
Global		Local		Global		Local		Global		Local	
IC ^a	CN	IC	CN	IC	CN	IC	CN	IC	CN	IC	CN
0.94	0.94	0.94	0.94	0.91	0.95	0.94	0.96	0.94	0.96	0.94	0.94

^a IC = Incongruent; CN = Congruent.

eye was presented with the local elements arranged in a task-relevant configuration (but different from the configuration of the percept) and the other eye was presented with the circular placeholders, creating the global configuration of the percept. In the control condition, one eye was presented with the local elements arranged in the same global configuration as the percept, while the other eye was presented with the task-irrelevant circles, which were used only to complete the perceptual stimulus. The global configuration was either congruent or incongruent with its local features (e.g., a global square consisting of squares and circles is congruent, while a global square consisting of diamonds and circles is incongruent). The visual stimuli were presented with equal frequency to each eye (in all three presentation conditions).

After completing 16 practice trials, each participant performed 640 experimental trials in two blocks, one with a global task and the other with a local task. Trials were divided equally between the same-eye presentation condition and the different-eyes presentation condition.

Half of the participants were instructed to respond to squares by pressing the leftmost button of a response box with their left index finger and to diamonds by pressing the rightmost button with their right index finger. The other half of the participants were asked to press the rightmost button in response to squares and the leftmost button in response to diamonds.

8. Results and discussion

We excluded three participants from the analysis whose accuracy rates were below 80%.

In all RT analyses, we excluded trials in which participants responded incorrectly to the target (6% of all trials). In addition, trials in which RT was shorter or longer than 2 SD (as calculated for every participant at every experimental condition) were also excluded from the analyses (less than 4%).

Table 2 shows the accuracy rates as a function of task and congruency for each presentation condition. Accuracy was high (mean = 0.94), and there was no indication of speed-accuracy tradeoff. Therefore, accuracy is not discussed further.

Fig. 5 depicts the mean RTs as a function of presentation condition (same-eye, different-eyes experimental, different-eyes control), task

(global, local) and congruency (congruent, incongruent). The RT data were submitted to a three-way repeated measures ANOVA (Presentation condition X Task X Congruency). The analysis showed a main effect of task [$F(1,24) = 12.28$, $MSE = 8575$, $p < .01$, $\eta^2 = 0.33$], revealing shorter RTs in the global task than in the local task, replicating the global advantage effect observed in Experiment 1. The main effect of congruency was also significant [$F(1,24) = 26.82$, $MSE = 887$, $p < .01$, $\eta^2 = 0.52$]. There was no main effect of presentation condition [$F < 1$]. Most importantly, the three-way interaction between presentation condition, task and congruency was significant [$F(2,48) = 7.83$, $MSE = 493$, $p < .01$, $\eta^2 = 0.24$].

We further analyzed this interaction by examining the three presentation conditions separately. For the same-eye presentation condition, significant main effects of task and congruency were observed [$F(1,24) = 13.31$, $MSE = 2954$, $p < .01$, $\eta^2 = 0.35$, $F(1,24) = 8.49$, $MSE = 924$, $p < .01$, $\eta^2 = 0.26$; respectively]. The two way interaction between task and congruency was also significant [$F(1,24) = 5.6$, $MSE = 660$, $p < .01$, $\eta^2 = 0.19$]. Follow-up analyses that examined the congruency effect for each task separately demonstrated a significant global-to-local interference [$F(1,24) = 23$, $MSE = 485$, $p < .001$, $\eta^2 = 0.48$], and a non-significant local-to-global interference [$F < 1$]. For the different-eyes presentation control condition, significant main effects of task and congruency were observed [$F(1,24) = 12.4$, $MSE = 35,200$, $p < .01$, $\eta^2 = 0.34$, $F(1,24) = 13.1$, $MSE = 1013$, $p < .01$, $\eta^2 = 1.2$; respectively]. The two way interaction was not significant [$F(1,24) = 1.06$, $MSE = 427$, $p = .31$]. There was a significant local-to-global interference [$F(1,24) = 7.18$, $MSE = 614$, $p < .05$, $\eta^2 = 0.23$] and a significant global to local interference [$F(1,24) = 11.28$, $MSE = 824$, $p < .001$, $\eta^2 = 0.31$]. Finally, significant main effects of task and congruency were observed for the different-eyes presentation experimental condition [$F(1,24) = 6.5$, $MSE = 3139$, $p < .05$, $\eta^2 = 0.21$, $F(1,24) = 6.3$, $MSE = 631$, $p < .05$, $\eta^2 = 0.19$; respectively]. The two-way interaction was also significant [$F(1,24) = 7$, $MSE = 522$, $p < .05$, $\eta^2 = 0.22$]. Follow-up analyses that examined the congruency effect for each task separately demonstrated a significant local-to-global interference [$F(1,24) = 12.6$, $MSE = 612$, $p < .01$, $\eta^2 = 0.34$], and most importantly, a non-significant global to local interference [$F < 1$].

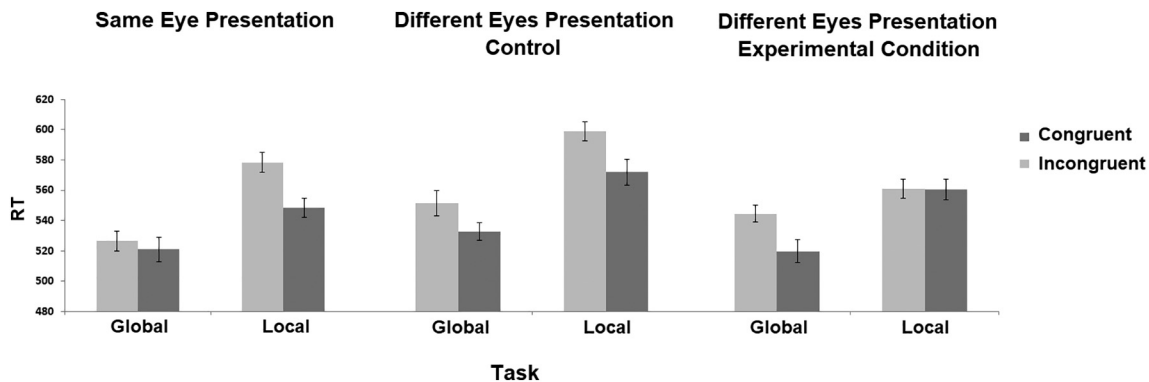


Fig. 5. Mean RT (in ms) as a function of task and congruency, for each presentation condition in Experiment 2.

Although the two-way interaction between presentation condition and task was not significant [$F(2,48) = 2.17$, $MSE = 710$, $p = .12$], we sought to examine whether the modulation of global advantage, observed in Experiment 1, was replicated. First, we compared average global advantage (i.e., difference in RTs between the global task and the local task) in the same-eye presentation condition and the different-eyes presentation control condition, to the global advantage in the different-eyes presentation experimental condition. The results were marginally significant [$F(1,24) = 3.5$, $MSE = 812$, $p = .07$, $\eta p^2 = 0.12$], indicating a pattern of reduced global advantage in the experimental condition compared with the other two conditions. The comparison between global advantage for same-eye presentation condition and different-eyes presentation control condition, was not significant [$F < 1$].

Similar to the results of Experiment 1, these results indicate that global-to-local interference was modulated depending on whether the global and the local information was presented to the same eye or segregated between the eyes. When the visual input was segregated between the eyes but the global and local aspects of the stimulus were presented to the same eye (i.e., different-eyes presentation – control condition), global-to-local interference was observed. This interference was similar to the interference observed in the same-eye presentation condition, in which there was no segregation between the eyes whatsoever. In a clear contrast, when the global and local aspects of the stimulus were segregated between the eyes (i.e., different-eyes presentation – experimental condition), no global-to-local interference emerged. Additionally, the global advantage effect was reduced in the experimental condition, compared to the averaged global advantage effect of the control condition and the same-eye presentation condition. Thus, although global advantage was not abolished, as it was for the different-eyes presentation condition in Experiment 1, the pattern of modulation of global advantage for the experimental condition was replicated. These findings suggest that the pattern of results observed for the different-eyes presentation condition in Experiment 1 was indeed a consequence of segregating the global and local information between the eyes, thus strengthening the notion that monocular structures are involved in global processing.

9. General discussion

This study aimed at examining the possible involvement of subcortical mechanisms in global and local processing.

We examined the involvement of monocular neural channels in the processing of hierarchical stimuli by manipulating the visual information presented to each eye separately and segregating the global and local information between the eyes. If global-local processing is influenced by segregation of the visual input between the eyes, it is possible to deduce the functional involvement of subcortical structures in this cognitive process (Batson et al., 2011; Karni & Sagi, 1991).

In Experiment 1, our stimulus was presented either as a whole to the same eye or segregated between the eyes, such that one eye was presented with the global configuration (square or a diamond) while the other eye was presented with the local elements (small squares or diamonds). In the same-eye presentation condition, both a global advantage (i.e., shorter RT for the global than the local task) and global-to-local interference (i.e., incongruent global information interfered with responses to the local elements) were observed. In contrast, under the different-eyes presentation condition, there was no global advantage and no global-to-local interference. In Experiment 2, we examined whether the results for the different-eyes presentation condition in Experiment 1 were indeed a consequence of segregating the global and local information between different monocular channels rather than a consequence of segregating the visual input per se. To this end, we introduced two conditions for different-eyes presentation. In both conditions the stimulus was segregated between the eyes. However, in the different-eyes presentation control condition, the global and local

information was presented to the same eye, while the irrelevant circles that were merely used to complete the perceptual stimulus, were presented to the other eye. In contrast, in the different-eyes presentation experimental condition, the global and local aspects of the stimulus were segregated between the eyes. The results show global-to-local interference for the control condition, but not for the experimental condition. Thus, the results of Experiment 1 were replicated, and the potential alternative account of the results as a consequence of segregation per se of visual input between the eyes was ruled out.

In both experiments, segregating the global and local information between the eyes influenced also the global advantage effect. This was more pronounced in the first experiment, possibly due to differences in stimuli characteristics, but was also evident in the pattern of results obtained in Experiment 2. Taken together, these findings suggest that processing the global aspect of hierarchical stimuli involves subcortical regions.

It should be noted that a control experiment was conducted in order to validate the experimental procedure,¹ indicating that in the different eyes presentation conditions, an integrated consistent percept of the image was created and that there was no rivalry between adjacent information presented to different eyes (for details see Supplementary material 1).

Our findings suggesting that monocular portions of the visual system are involved in global processing may not be surprising from an evolutionary perspective. In order to adapt to the environment successfully, most living organisms must be able to perceive global information (e.g., identify specific configurations) to some extent, since even species that possess only a rudimentary neural system should be able to identify predators and dissociate them from conspecifics. The literature on face perception has demonstrated that even wasps and honeybees rely on global configurations in order to discriminate kin from non-kin (Dyer et al., 2005; Sheehan & Tibbetts, 2011; Tibbetts, 2002). Additionally, researchers have also suggested that the sensitivity of human newborns and even fetuses to specific global configural information is guided by subcortical mechanisms (Johnson et al., 1991; Johnson & Morton, 1991; Reid et al., 2017). In light of these findings, it is possible to assume that subcortical structures have the ability to process global information. In accordance with this explanation, Gabay, Burlingham, and Behrmann (2014) found evidence implicating low-level monocular structures in the processing of facial configurations in human adults.

Nevertheless, most imaging studies seem to have neglected the involvement of subcortical mechanisms in global processing and instead focus on cortical functions (e.g., Fink et al., 1997; Han et al., 2004; Martinez et al., 1997). For instance, human face perception (which relies mostly on global/holistic processing) is suggested to be guided by the cortical face processing network (Avidan & Behrmann, 2009; Ishai, 2008). Similarly, most models of visual processing also emphasize the involvement of cortical structures. For example, Hochstein and Ahissar (2002) suggested the “reverse hierarchy” theory, in which a single hierarchical processing path can be traced in a “forward” and “backward” fashion. According to this theory, conscious perception begins at the top of the hierarchy with global information, whereas the reverse hierarchy track followed in order to consciously identify local elements. The reverse hierarchy theory refers only to cortical structures (V1 onwards). If we were to extend this theoretical perspective to include lower visual areas as well, we might plausibly assume that this perspective would predict local (implicit) processing at the bottom of the hierarchy (subcortical areas), followed by conscious global perception at the top of the hierarchy (cortical areas). Yet this explanation is inconsistent with the pattern of results found in the current study pointing to low-level subcortical involvement in global processing.

¹ One of the reviewers raised the possibility of binocular rivalry as an alternative explanation for our results.

It should be noted, however, that subcortical involvement in global processing does not necessarily imply that global information is represented when the stimulus is suppressed from awareness. Examining the role of visual awareness in the perceptual organization of hierarchical stimuli, Sabary et al. (2020) demonstrated that local elements are represented in the absence of awareness, whereas visual awareness appears to be essential for the grouping of the local elements into a global shape.

It should be further noted that evidence regarding subcortical involvement in global processing does not contradict cortical contribution to such processing (Conci et al., 2011). It is plausible that cortical and subcortical mechanisms make their own unique contributions to the process. For instance, it is possible that the higher binocular level is involved in conscious perception of global information, while lower monocular levels are involved in rapid implicit global processing. This account can explain global advantage in higher-level functions, such as visual working memory (Nie et al., 2017). A theoretical model suggesting the existence of two processing paths that differentiate low spatial frequency from high spatial frequency information may concur with this notion (Bar et al., 2006). According to Bar et al. (2006), low spatial frequency (global) information reaches frontal cortical areas rapidly via magnocellular pathways, unlike high spatial frequency information (local and global), which continues to be processed in a bottom-up fashion. The two processing pathways facilitate one another and contribute to the formation of an explicit integrative percept. According to this explanation, it is possible that monocular portions of the visual system are involved in the bottom-up pathway (which includes both global and local information).

An integration between the evolutionary perspective and the theory of two processing pathways may suggest the involvement of the superior colliculus in the subcortical processing of global information. The role of subcortical areas and possibly the superior colliculus in global processing can be derived from studies with fish that lack neocortex-like cells and only possess a retino-tectal visual pathway. In a study conducted on redtail splitfins, Truppa et al. (2010) found a preference for global configuration in global-local processing, similar to that found in humans.

In conclusion, our study examined subcortical involvement in global-local processing. Since most studies have focused on the role of cortical structures in global-local processing, our study offers innovative and intriguing results. The results of the two experiments reported here support the notion that monocular structures of the visual system are involved in global processing. Further research based on these findings can establish a broader understanding of the interplay between cortical and subcortical structures in global-local processing.

CRedit authorship contribution statement

Margarita Soloveichick: Conceptualization, Methodology, Formal analysis, Investigation, Writing - Original Draft, Visualization.

Ruth Kimchi: Conceptualization, Methodology, Writing - Review & Editing, Supervision.

Shai Gabay: Conceptualization, Methodology, Formal analysis, Methodology, Writing - Review & Editing, Supervision, Funding acquisition.

Declaration of competing interest

None.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.cognition.2020.104476>.

References

- Asch, S. E. (1962). A problem in the theory of associations. *Psychologische Beiträge*, 6, 553–563.
- Avargues-Weber, A., Dyer, A. G., Ferrah, N., & Giurfa, M. (2015). The forest or the trees: Preference for global over local image processing is reversed by prior experience in honeybees. *Proceedings of the Royal Society B: Biological Sciences*, 282(1799), 20142384.
- Avidan, G., & Behrmann, M. (2009). Functional MRI reveals compromised neural integrity of the face processing network in congenital prosopagnosia. *Current Biology*, 19(13), 1146–1150.
- Badcock, J. C., Whitworth, F. A., Badcock, D. R., & Lovegrove, W. J. (1990). Low-frequency filtering and the processing of local—Global stimuli. *Perception*, 19(5), 617–629.
- Bar, M., Kassam, K. S., Ghuman, A. S., Boshyan, J., Schmid, A. M., Dale, A. M., ... Halgren, E. (2006). Top-down facilitation of visual recognition. *Proceedings of the National Academy of Sciences*, 103(2), 449–454.
- Batson, M. A., Beer, A. L., Seitz, A. R., & Watanabe, T. (2011). Spatial shifts of audio-visual interactions by perceptual learning are specific to the trained orientation and eye. *Seeing and Perceiving*, 24, 579–594.
- Bi, H., Zhang, B., Tao, X., Harwerth, R. S., Smith, E. L., III, & Chino, Y. M. (2011). Neuronal responses in visual area V2 (V2) of macaque monkeys with strabismic amblyopia. *Cerebral Cortex*, 21(9), 2033–2045.
- Blake, R., & Cormack, R. H. (1979). On utricular discrimination. *Perception & Psychophysics*, 26(1), 53–68.
- Boer, L. C., & Keuss, P. J. G. (1982). Global precedence as a postperceptual effect: An analysis of speed-accuracy tradeoff functions. *Perception & Psychophysics*, 31, 358–366.
- Cavoto, K. K., & Cook, R. G. (2001). Cognitive precedence for local information in hierarchical stimulus processing by pigeons. *Journal of Experimental Psychology: Animal Behavior Processes*, 27(1), 3–16.
- Chiandetti, C., Pecchia, T., Patt, F., & Vallortigara, G. (2014). Visual hierarchical processing and lateralization of cognitive functions through domestic chicks' eyes. *PLoS One*, 9(1), Article e84435.
- Conci, M., Töllner, T., Leszczynski, M., & Müller, H. J. (2011). The time-course of global and local attentional guidance in Kanizsa-figure detection. *Neuropsychologia*, 49(9), 2456–2464.
- Dyer, A. G., Neumeyer, C., & Chittka, L. (2005). Honeybee (*Apis mellifera*) vision can discriminate between and recognize images of human faces. *Journal of Experimental Biology*, 208(24), 4709–4714.
- Faul, F., Erdfelder, E., Lang, A. G., & Buchner, A. (2007). G* Power 3: A flexible statistical power analysis program for the social, behavioral, and biomedical sciences. *Behavior Research Methods*, 39(2), 175–191.
- Fink, G. R., Halligan, P. W., Marshall, J. C., Frith, C. D., Frackowiak, R. S. J., & Dolan, R. J. (1997). Neural mechanisms involved in the processing of global and local aspects of hierarchically organized visual stimuli. *Brain*, 120, 1779–1791.
- Gabay, S., Burlingham, C., & Behrmann, M. (2014). The nature of face representations in subcortical regions. *Neuropsychologia*, 59, 35–46.
- Gabay, S., Nestor, A., Dundas, E., & Behrmann, M. (2014). Monocular advantage for face perception implicates subcortical mechanisms in adult humans. *Journal of Cognitive Neuroscience*, 26(5), 927–937.
- Han, S., Jiang, Y., & Gu, H. (2004). Neural substrates differentiating global/local processing of bilateral visual inputs. *Human Brain Mapping*, 22(4), 321–328.
- 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.
- Hochstein, S., & Ahissar, M. (2002). View from the top: Hierarchies and reverse hierarchies in the visual system. *Neuron*, 36(5), 791–804.
- Horton, J. C., Dagi, L. R., McCrane, E. P., & de Monasterio, F. M. (1990). Arrangement of ocular dominance columns in human visual cortex. *Archives of Ophthalmology*, 108, 1025–1031.
- Hughes, H. C., Fendrich, R., & Reuter-Lorenz, P. A. (1990). Global versus local processing in the absence of low spatial frequencies. *Journal of Cognitive Neuroscience*, 2(3), 272–282.
- Ishai, A. (2008). Let's face it: It's a cortical network. *Neuroimage*, 40(2), 415–419.
- Johnson, M. H. (2005). Subcortical face processing. *Nature Reviews Neuroscience*, 6(10), 766–774.
- Johnson, M. H., Dziurawiec, S., Ellis, H., & Morton, J. (1991). Newborns' preferential tracking of face-like stimuli and its subsequent decline. *Cognition*, 40(1–2), 1–19.
- Johnson, M. H., & Morton, J. (1991). *Biology and cognitive development: The case of face recognition*. Oxford, UK: Blackwell.
- Karni, A., & Sagi, D. (1991). Where practice makes perfect in texture discrimination: Evidence for primary visual cortex plasticity. *Proceedings of the National Academy of Sciences*, 88, 4966–4970.
- Kimchi, R. (1992). Primacy of wholistic processing and global/local paradigm: A critical review. *Psychological Bulletin*, 112(1), 24–38.
- Kimchi, R. (2015). The perception of hierarchical structure. In J. Wagemans (Ed.), *Oxford handbook of perceptual organization* (pp. 129–149). Oxford: Oxford University Press.
- Kimchi, R., & Merhav, I. (1991). Hemispheric processing of global form, local form, and texture. *Acta Psychologica*, 76(2), 133–147.
- Kimchi, R., Trainin, O., & Gopher, D. (1995). Can attention be directed voluntarily to an eye? *Acta Psychologica*, 89, 229–238.
- Kinchla, R. A. (1974). Detecting target elements in multi-element arrays: A confusability model. *Perception & Psychophysics*, 15, 149–158.
- Kinchla, R. A. (1977). The role of structural redundancy in the perception of visual

- targets. *Perception & Psychophysics*, 22, 19–30.
- Kinchla, R. A., & Wolfe, J. M. (1979). The order of visual processing: “Top-down,” “bottom-up,” or “middle-out”. *Perception & Psychophysics*, 25, 225–231.
- Mao, L., Zhang, X., Chen, J., Gu, H., & Han, S. (2006). Neural substrates of global perception are modulated by local element grouping. *Chinese Science Bulletin*, 51(3), 298–303.
- 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.
- Menon, R. S., Ogawa, S., Strupp, J. P., & Ugurbil, K. (1997). Ocular dominance in human V1 demonstrated by functional magnetic resonance imaging. *Journal of Neurophysiology*, 77, 2780–2787.
- Navon, D. (1977). Forest before trees: The precedence of global features in visual perception. *Cognitive Psychology*, 9, 353–383.
- Navon, D. (2003). What does a compound letter tell the psychologist's mind? *Acta Psychologica*, 114(3), 273–309.
- Nie, Q. Y., Müller, H. J., & Conci, M. (2017). Hierarchical organization in visual working memory: From global ensemble to individual object structure. *Cognition*, 159, 85–96.
- Poirel, N., Pineau, A., & Mellet, E. (2006). Implicit identification of irrelevant local objects interacts with global/local processing of hierarchical stimuli. *Acta Psychologica*, 122(3), 321–336.
- Pomerantz, J. R. (1983). Global and local precedence: Selective attention in form and motion perception. *Journal of Experimental Psychology: General*, 112, 516–540.
- Reid, V. M., Dunn, K., Young, R. J., Amu, J., Donovan, T., & Reissland, N. (2017). The human fetus preferentially engages with face-like visual stimuli. *Current Biology*, 27(12), 1825–1828.
- Robertson, L. C., & Lamb, M. R. (1991). Neuropsychological contributions to theories of part/whole organization. *Cognitive Psychology*, 23, 299–330.
- Robertson, L. C., Lamb, M. R., & Knight, R. T. (1988). Effects of lesions of temporal-parietal junction on perceptual and attentional processing in humans. *The Journal of Neuroscience*, 8(10), 3757–3769.
- Roman, M. J., Delis, D. C., Filoteo, V. J., Demadura, T. L., Paulsen, J., Swerdlow, N. R., ... Shults, C. (1998). Is there a “subcortical” profile of attentional dysfunction? A comparison of patients with Huntington's and Parkinson's diseases on a global-local focused attention task. *Journal of Clinical and Experimental Neuropsychology*, 20(6), 873–884.
- Sabary, S., Devyatko, D., & Kimchi, R. (2020). The role of visual awareness in processing of global structure: Evidence from the perceptual organization of hierarchical patterns. *Cognition*, 205, 104442.
- Schiller, P. H., Malpeli, J. G., & Schein, S. J. (1979). Composition of geniculostriate input to superior colliculus of the rhesus monkey. *Journal of Neurophysiology*, 42, 1124–1133.
- Schwarzkopf, D. S., Schindler, A., & Rees, G. (2010). Knowing with which eye we see: Utricular discrimination and eye-specific signals in human visual cortex. *PLoS One*, 5, Article e13775.
- Sebrechts, M. M., & Fragala, J. J. (1985). Variation on parts and wholes: Information precedence vs. global precedence. *Proceedings of the seventh annual conference of the Cognitive Science Society* (pp. 11–18).
- Sheehan, M. J., & Tibbetts, E. A. (2011). Specialized face learning is associated with individual recognition in paper wasps. *Science*, 334(6060), 1272–1275.
- Shulman, G. L., Sullivan, M. A., Gish, K., & Sakoda, W. J. (1986). The role of spatial-frequency channels in the perception of local and global structure. *Perception*, 15(3), 259–273.
- Shulman, G. L., & Wilson, J. (1987). Spatial frequency and selective attention to local and global information. *Perception*, 16(1), 89–101.
- Tibbetts, E. A. (2002). Visual signals of individual identity in the wasp *Polistes fuscatus*. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 269(1499), 1423–1428.
- Truppa, V., Sovrano, V. A., Spinozzi, G., & Bisazza, A. (2010). Processing of visual hierarchical stimuli by fish (*Xenotoca eiseni*). *Behavioural Brain Research*, 207(1), 51–60.