

Global attention facilitates the planning, but not execution of goal-directed reaches

J. Daniel McCarthy

Department of Cognitive,
Linguistic & Psychological Sciences, Brown University,
Providence, RI, USA



Joo-Hyun Song

Department of Cognitive,
Linguistic & Psychological Sciences and Brown Institute
for Brain Science, Brown University, Providence, RI, USA



In daily life, humans interact with multiple objects in complex environments. A large body of literature demonstrates that target selection is biased toward recently attended features, such that reaches are faster and trajectory curvature is reduced when target features (i.e., color) are repeated (priming of pop-out). In the real world, however, objects are comprised of several features—some of which may be more suitable for action than others. When fetching a mug from the cupboard, for example, attention not only has to be allocated to the object, but also the handle. To date, no study has investigated the impact of hierarchical feature organization on target selection for action. Here, we employed a color-odddity search task in which targets were Pac-men (i.e., a circle with a triangle cut out) oriented to be either consistent or inconsistent with the percept of a global Kanizsa triangle. We found that reaches were initiated faster when a task-irrelevant illusory figure was present independent of color repetition. Additionally, consistent with priming of pop-out, both reach planning and execution were facilitated when local target colors were repeated, regardless of whether a global figure was present. We also demonstrated that figures defined by illusory, but not real contours, afforded an early target selection benefit. In sum, these findings suggest that when local targets are perceptually grouped to form an illusory surface, attention quickly spreads across the global figure and facilitates the early stage of reach planning, but not execution. In contrast, local color priming is evident throughout goal-directed reaching.

Introduction

Our visual world is complex, and multiple objects compete for limited attentional resources. Successful interaction with the environment often requires selecting a single object among several possibilities. For instance, when fetching a book off the shelf, one has to ignore the wealth of available options and select appropriate actions to be executed toward the desired title. Moreover, objects are commonly comprised of several features that can be described at various levels of hierarchical organization (e.g., a bookcase has shelves, and each shelf contains several books). Thus, picking up a suitcase, for example, not only entails allocating attention towards the global object, but also identifying relevant features that are suitable for interaction (i.e., the handle).

It is suggested that attentional guidance operates in a global-to-local fashion, such that the gist of a visual scene is perceived more rapidly compared to its local features (Hegde, 2008; Hochstein & Ahissar, 2002; Navon, 1977; Rauschenberger & Yantis, 2001; Rensink & Enns, 1995). For instance, when entering a room, we can readily recognize that we are in a kitchen, but it takes slightly longer to identify the counter and locate a bowl sitting among many other items. This notion of global precedence is elegantly demonstrated by several perceptual phenomena. Navon letters (Navon, 1977) illustrate that a large letter comprised of smaller letters is more easily identified than the individual letters themselves. Additionally, Kanizsa figures (Kanizsa, 1955, 1979) demonstrate that perceptually salient, global shapes can be generated via the local arrangement of “Pac-men” inducers (i.e., a circle with a triangle matching the color of the background cut out),

Citation: McCarthy, J. D., & Song, J.-H. (2016). Global attention facilitates the planning, but not execution of goal-directed reaches. *Journal of Vision*, 16(9):7, 1–16, doi:10.1167/16.9.7.

doi: 10.1167/16.9.7

Received January 22, 2016; published July 28, 2016

ISSN 1534-7362



and the modal completion processes (for review see Albert, 2007) underlying these percepts facilitate the spread of attention across the global illusory surface (Davis & Driver, 1997, 1998; Driver, Davis, Russell, Turatto, & Freeman, 2001). Notably, it has been reported that Kanizsa figures can be detected without focal attention during visual search (Davis & Driver, 1994) and are detected more efficiently than local configurations in which the Pac-men are rotated outward such that no global surface is present (Conci, Müller, & Elliott, 2007). Electrophysiological evidence also supports this search asymmetry: Global Kanizsa figures showed enhanced sensory processing and earlier attentional selection compared to local targets (Conci, Töllner, Leszczynski, & Müller, 2011). Taken together, these results demonstrate that global attention operates early and is followed by the analysis of local elements. To date, however, this search strategy has only been investigated at the perceptual level. How might this global-to-local stream of processing impact the selection of local targets during visually guided reaching?

Several studies have investigated target selection in humans using visually guided reaching tasks in which a local target is defined by a unique color among uniformly colored distractors (e.g., Moher & Song, 2013; Song & Nakayama, 2006, 2007b, 2008). For example, Song and Nakayama (2006, 2008) demonstrated that target selection is biased toward recently attended features. Specifically, the time to initiate a reach toward a target is faster when the target and distractor colors are repeated—a phenomenon called “priming of pop-out” (PoP; e.g., Maljkovic & Nakayama, 1994). Moreover, reach duration and curvature are also reduced when colors are repeated (Song & Nakayama, 2006, 2008). Interestingly, recent work (Erb, Moher, Sobel, & Song, 2016) suggests that initiation latency reflects a response threshold adjustment related to motor inhibition, whereas movement time and curvature reflect the relative activation of competing motor responses. Specifically, when multiple competing response options are available, the registered conflict leads to a temporary suppression of motor output to avoid responding in error. This delay allows time for a later control process to intervene and resolve conflict between the coactive responses to support effective response selection (Erb et al., 2016; Shenav, Botvinick, & Cohen, 2013). According to this interpretation, PoP both facilitates early pop-out of the target as indexed by faster initiation latency and also improves the efficiency of reaches by resolving local color competition between the potential targets.

Importantly, in a visual search task requiring participants to search for an odd-colored target among homogeneous color distractors and perform a fine detailed target discrimination (i.e., which side of the target is cut off), Bravo and Nakayama (1992) observed

that reaction times via a keypress decreased as the number of distractors increased when the color of the target and distractors reversed unpredictably; however, reaction time remained constant when the target and distractors maintained their color across trials. Therefore, Bravo and Nakayama (1992) proposed that when target colors are unpredictable, this discrimination requires global-to-local process of attentional allocation: broadly distributed (global) attention to detect the target, and narrowly focused (local) attention to discriminate the target. The global process becomes easier when more distractors are present and perceptual grouping is strong, resulting in more efficient target selection (Nakayama, Joseph, & Parasuraman, 1998). Importantly, this perceptual grouping benefit is observed in both reaching (Song & Nakayama, 2006; Song, Takahashi, & McPeck, 2008) and eye movement tasks (McPeck, Maljkovic, & Nakayama, 1999) even when no discrimination is required, suggesting that goal-directed action requires both globally distributed and locally focused attention.

In the present study, we conducted a series of experiments designed to examine possible influences of global and local attentional deployment on target selection for action. Participants performed a visually guided reaching task in which they searched for a uniquely colored target among distractors and pointed to its location. We exploited perceptual grouping via illusory contour formation so that individual targets could be perceived as part of a greater whole and compared search in these displays to those in which no grouping occurred. We note that our use of illusory contours provides an alternative to previous work (Bravo & Nakayama, 1992; McPeck et al., 1999; Song & Nakayama, 2006; Song et al., 2008) that allows us to investigate the role of perceptual grouping without manipulating the number of distractors, and in turn the number of possible response options in a display. In Experiment 1, Pac-men targets were oriented to be either consistent or inconsistent with a global Kanizsa triangle (Kanizsa, 1955, 1979; see Figure 1). Because illusory contours have been shown to improve early attentional selection (Conci et al., 2011), we reasoned that the presence of a task-irrelevant global figure would lower the initial response threshold (Erb et al., 2016) and expedite reach planning but would not impact the later stage of reach execution. Alternatively, however, it could be the case that the presence of an illusory contour impacts goal-directed reaching more generally, similar to the perceptual grouping effects demonstrated in Song and Nakayama (2006) and Song et al. (2008). Moreover, consistent with PoP (e.g., Maljkovic & Nakayama, 1994), we expected that local color priming would be reflected throughout the target selection process (Song & Nakayama, 2006, 2008). In Experiment 2, we manipulated the target display

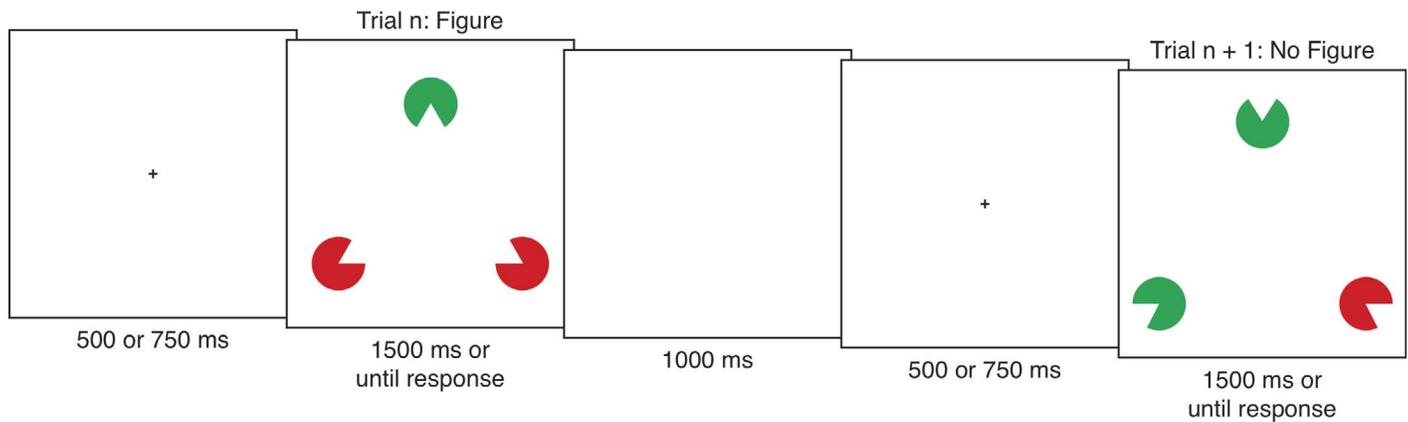


Figure 1. A sample sequence of trials from Experiment 1. Participants pointed to the uniquely colored target. On Figure (grouped) trials, the Pac-men targets were oriented to be consistent with the percept of three circles occluded by triangle that matched the color of the background. On nonfigure (ungrouped) trials, the Pac-men targets were rotated 180° outward according to their center of gravity (see Methods) so that no illusory triangle was present in the display.

configuration across trials to determine if the early attentional influence of illusory contours is invariant to changes in the global figure orientation. Lastly, Experiment 3 investigated if modal and amodal grouping processes arising from visual interpolation (for review see Albert, 2007) affect target selection in a similar fashion, as well as how they compare to when a real figure was present. Taken together, our results suggest that when targets are grouped to form a Kanizsa figure, attention quickly spreads across the illusory surface and facilitates reach planning, but not execution. In contrast, local color priming generally improves the efficiency of goal-directed reaching.

Experiment 1: Perceptual grouping via illusory contours facilitates planning of goal-directed reaches

This experiment was designed to determine how target grouping through illusory contour formation impacts goal-directed reaching. We used a color-oddity search task (Song & Nakayama, 2006, 2008) in which local targets were Pac-men oriented to be either consistent or inconsistent with a global Kanizsa triangle (Kanizsa, 1955, 1979; see Figure 1). Participants made visually guided reaches toward odd-colored targets that were perceptually grouped (Figure trials) or ungrouped (No Figure trials). Consistent with the finding that illusory contours drive early attentional selection (Conci et al., 2011), we reasoned that the presence of a task-irrelevant global figure would impact the early stage of target selection (i.e., movement planning) and reduce the initial response threshold (Erb et al., 2016). Specifically, the time to initiate a reach

should be faster when an illusory figure is present compared to when there is no figure in the display, independent of target color. It is also possible, however, that the presence of a global figure impacts goal-directed reaching more generally, similar to the perceptual grouping benefits demonstrated in Song and Nakayama (2006). Moreover, as predicted by PoP, we hypothesized that local color priming should be evident throughout the selection process: In addition to reducing initiation latency, repeating target colors should also decrease movement time and curvature regardless of whether or not an illusory figure is present.

Methods

Participants

Eighteen Brown University students (six female, mean age = 21.3 years) participated in a session lasting approximately 1 hr and received course credit or monetary compensation. All participants were right-handed, reported normal or corrected-to-normal color vision, and were naive to the aims of the experiment. The protocol was approved by the Brown University Institutional Review Board. All procedures reported in this manuscript followed the guidelines of the Declaration of Helsinki.

Apparatus

Stimuli were projected from a ViewSonic PJD6221 Projector (ViewSonic Co., Walnut, CA) at a rate of 60 Hz from behind a Plexiglas display (21.5 in., 1280 × 1024) that was mounted upright on a table perpendicular to the participant's line of vision. Participants were seated in a chair at a viewing distance of ~57 cm from

the display. The stimulus computer was a 2.3 GHz Dell OptiPlex 780 (Dell Inc., Round Rock, TX) with an NVIDIA GeForce 8500GT (NVIDIA Co., Santa Clara, CA) graphics processor (256 MB of DDR2 SDRAM). Three-dimensional (3-D) hand position was recorded using a Polhemus Liberty 240/8 (Polhemus, Colchester, VT) electromagnetic position and orientation recording system at a rate of ~ 160 Hz with a measuring error of 3-mm root mean square. A position sensor was attached near the tip of each participant's index finger using a Velcro strap. Participants placed their index finger on a Styrofoam block adhered to the table 27 cm in front of the display along the z -dimension (i.e., the axis between the participant and the screen) and was aligned with the bottom of the display along the x -dimension (i.e., the axis between the left and right sides of the screen). Stimuli were created and presented with the Psychophysics Toolbox (Brainard, 1997) for MATLAB (Mathworks Inc., Natick, MA).

Stimuli and procedures

All stimuli were presented on a white background. Each trial began with a central fixation cross ($1/3^\circ$ visual angle). During each trial, three Pac-men style targets (radius = 2° visual angle) appeared on the screen. This number of targets was chosen to maximize competition for selection in a pop-out task (e.g., Bravo & Nakayama, 1992; Song & Nakayama, 2006). The three Pac-men were equally spaced and placed at 4, 8, and 12 o'clock on an imaginary circle surrounding fixation with a radius of 8.85° and an interim distance of 14.7° . These measures were calculated as the distance between the centers of gravity for the Pac-man targets, derived from the following equation:

$$\left[\frac{2r(\sin(\pi/2))}{(3\pi/2)} \right]$$

The targets were either green (International Commission on Illumination chromaticity coordinates: $x = 0.321$, $y = 0.598$) or red (International Commission on Illumination chromaticity coordinates: $x = 0.648$, $y = 0.331$) and were equated for luminance (~ 27.5 cd/m²). On each trial, one Pac-man appeared in the randomly selected target color and the remaining Pac-men were rendered in the other color. The target Pac-man was randomly selected from one of the three locations described above and the distractor Pac-men were placed in the remaining two locations. On Figure trials, the Pac-men were rotated inward to be consistent with the percept of three circles occluded by a triangle whose color matched the background; this configuration generated the percept of an equilateral illusory triangle with a side length of 13.85° defined by the inducing Pac-

men with a support ratio of ~ 0.3 (the ratio of the physically specified contour provided by the Pac-men to the total edge length of the triangle; Shipley & Kellman, 1992). On No Figure trials, the Pac-men were rotated outward 180° according to their center of gravity (described above) so that no illusory triangle was present and the centroids of the Pac-men were in the same location in both conditions. The trial order was randomly determined for both target color (red or green) and configuration (Figure or No Figure) within each block.

The reach tracker was calibrated at the beginning of each session by instructing participants to touch nine equally spaced points on the screen. Following calibration, participants were instructed to keep their finger in the starting position until the target stimuli appeared and to touch the uniquely colored target on every trial. Each trial began with a central fixation cross that was visible for either 500 or 750 ms (randomly determined on each trial). The timer was reset if any finger movements occurred during the fixation period to discourage participants from moving their hand before the target stimuli appeared. Thus, the fixation cross always remained on the screen until 500 or 750 ms elapsed with their finger at the starting position, after which the fixation cross was removed and three targets appeared. If the participant did not touch one of the three targets within 1500 ms, the trial was counted as incorrect and participants heard a tone to indicate they responded too slowly. The targets remained on the screen for an additional 200 ms following participants' final response to encourage them to rest briefly on the target. This resulted in more consistent deceleration at the end of reach movements so that maximum and minimum speed thresholds could be used to effectively to analyze movement trajectories. Participants received auditory feedback after each trial during the 1000 ms intertrial interval to indicate whether they responded correctly (high-pitched beep) or incorrectly (low-pitch beep).

The experiment began with 24 practice trials, followed by 10 blocks of 60 trials each. Due to tracker issues and time constraints of the study, however, two of the participants only completed eight blocks and one participant only completed nine blocks. Participants were given an opportunity to rest between each block. The total session lasted approximately 1 hr.

Data analysis

Responses were counted as correct if the participant's finger came within 0.5 cm of the display on the z -dimension and simultaneously 2 cm of the target on the x - and y -dimensions within the 1500-ms time limit. Responses were counted as incorrect if this threshold

was exceeded for any nontarget or the participant did not pass the reaching threshold during the time limit.

Reach data was analyzed offline using custom scripts in MATLAB (Mathworks Inc., Natick, MA). Three-dimensional speed scalars were created for each trial using a differentiation procedure in MATLAB. These scalars were then submitted to a Butterworth filter (second order, 10 Hz high cutoff). *Movement onset* was defined as the first time point in each trial after stimulus onset at which the speed of hand movements exceeded 10 cm/s. *Resultant speed* was calculated as the distance traveled in 3-D space (i.e., the square root of the sum of the squared distance traveled along the x -, y -, and z -axes) at each sample divided by the time elapsed since the previous sample. *Movement offset* was defined as the first subsequent measurement in each trial when resultant speed fell below 10 cm/s. Each trial was individually inspected (Song & Nakayama, 2006, 2007a, 2008); for trials in which the default threshold clearly missed part of the movement or included a considerable movement back toward the starting point, thresholds were adjusted manually to more appropriate levels for that trial. *Initiation latency* was defined as the time elapsed between stimulus onset and movement onset. *Movement time* was defined as the time elapsed between movement onset and movement offset.

Trajectories for calculating movement curvature were measured in two-dimensional xy space by calculating a straight line from the start to the end point of the movement and measuring the perpendicular deviation of the actual movement from a line at each sample throughout the movement. *Curvature* was defined as the maximum point of deviation (in centimeters, unsigned) divided by the length of the line (in centimeters) from the point of movement onset to the point of movement offset (e.g., Desmurget, Jordan, Prablanc, & Jeannerod, 1997; Song & Nakayama, 2006). Throughout the rest of the manuscript, we use centimeters as the measurement scale for reporting curvature; we note, however, that the value is reported following a normalization procedure and therefore does not reflect the absolute value in centimeters of the deviation.

Statistical analyses

Only correct trials were included in the analysis. In addition, trials in which no movements were initiated, a significant number of samples were dropped from the recording, or participants did not select a target within the 1500-ms time limit were removed from the analysis.

To evaluate global and local attentional influences on target selection, we compared how the global display configuration (Figure vs. No Figure) and local target color (repeated vs. switched) impacted three measures of goal-directed action: initiation latency,

movement time, and reach curvature. For each measure, the mean values for each participant were calculated and submitted to a 2 (configuration: Figure vs. No Figure) \times 2 (target color repetition: repeated vs. switched) repeated-measures analysis of variance (ANOVA).

Results

Overall, target selection accuracy was very high ($M = 99.63\%$, $SEM = 0.10\%$) and an average of 0.78 % of trials ($SEM = 0.30\%$) were excluded based on the criteria listed above. Thus, the final analysis was conducted on an average of 98.86% of the total trials.

Consistent with the notion of illusory contours driving early attentional selection, reaches were initiated more rapidly in the Figure (342 ± 2 ms)¹ compared to the No Figure (348 ± 2 ms) condition, $F[1, 17] = 24.63$, $p < 0.001$, $\eta^2 = 0.59$ (Figure 2, top). Importantly, the presence of a figure had no impact on movement time or curvature (both $ps > 0.2$), suggesting that global attentional influences had faded by the time of movement onset. Moreover, repeating local target colors led to reduced initiation latency (Repeat: 343 ± 2 ms, Switch: 349 ± 2 ms, $F[1, 17] = 7.80$, $p = 0.013$, $\eta^2 = 0.31$), as well as movement time (Repeat: 430 ± 2 ms, Switch: 440 ± 2 ms, $F[1, 17] = 57.02$, $p < 0.001$, $\eta^2 = 0.77$) and curvature (Repeat: 0.08 ± 0.003 , Switch: 0.116 ± 0.003 ms, $F[1, 17] = 26.94$, $p < 0.001$, $\eta^2 = 0.61$), consistent with previous studies on PoP (Figure 2). The interaction was not observed for any of the three measures (all $ps > 0.6$). In sum, the results replicate the basic PoP effect showing that color priming impacted both early and late stages of goal-directed reaching (Song & Nakayama, 2006, 2008), whereas the influence of the global illusory figure was restricted to the early stage of movement planning.

Experiment 2: Shape invariant facilitation of reach planning by illusory contours

As shown in Figure 3, closer inspection of the data from Experiment 1 revealed that initiation latency decreased as Figure trials were successively repeated (linear contrast: $F[1, 17] = 4.90$, $p = 0.04$, $\eta^2 = 0.22$). Here, we investigated whether this observed benefit of global figure repetition is limited to the exact same figure being repeated as in Experiment 1. Would priming still occur if the orientation of the figure switched across trials?

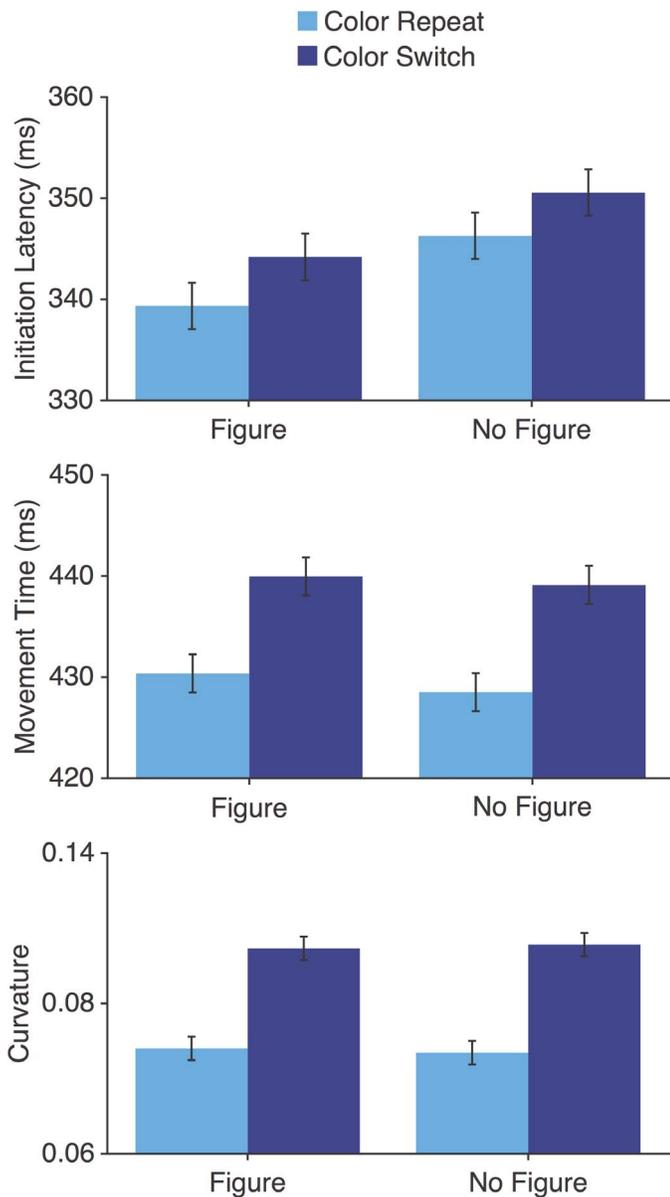


Figure 2. Results of Experiment 1. Reaches were initiated faster for Figure trials compared to No Figure trials (top). Color priming was observed for all three measures. Error bars represent 95% confidence intervals for the within-subject design (Loftus & Masson, 1994).

Research on visual priming suggests that objects can be identified more efficiently after prior exposure despite changes in position and rotation (e.g., Biederman & Cooper, 1991, 2009; Knowlton, McAuliffe, Coelho, & Hummel, 2009), but it is unclear if figures generated through illusory contour formation like those used here would demonstrate similar benefits of shape invariance. To address this question, we ran an experiment in which the orientation of the target display could flip along the horizontal axis across trials (Figure 4). We predicted that if the effect of global figure priming is shape invariant, we should observe no

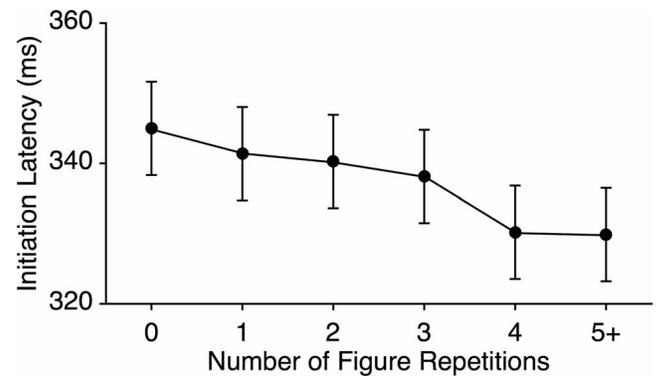


Figure 3. Effects of Figure repetition in Experiment 1. The line with circles illustrates the initiation latencies for repeated Figure presentations averaged across subjects. Error bars represent 95% confidence intervals for the within-subjects design (Loftus & Masson, 1994).

difference in initiation latency between trials in which the orientation of the figure changed compared to trials in which it did not, independent of target color. Alternatively, if priming is dependent on the global figure being exactly the same, we would expect longer initiation latencies when the orientation of the target display switched across trials relative to when no change occurred.

Methods

Participants

Eighteen Brown University students (14 female, mean age = 19 years) participated in a session lasting approximately 1 hr and received course credit or monetary compensation. All participants were right-handed, reported normal or corrected-to-normal color

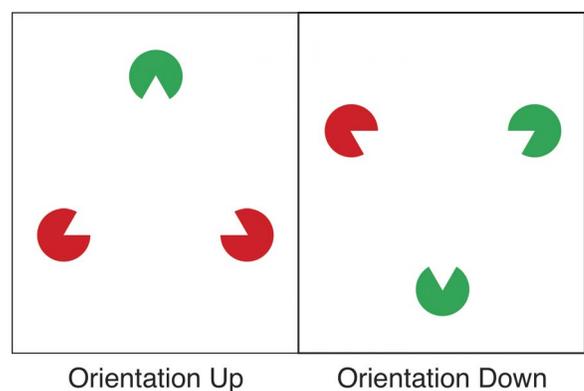


Figure 4. Stimuli used in the second experiment. An illusory triangle was always present and could be oriented upward (left) or downward (right).

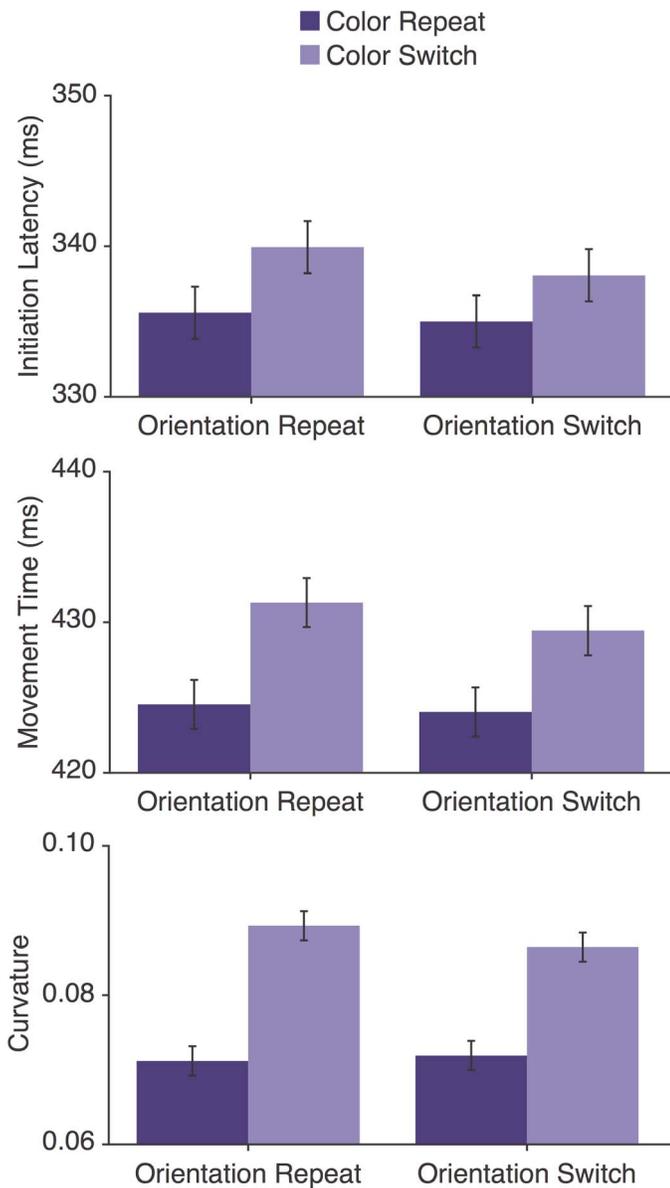


Figure 5. Results of Experiment 2. Changing the orientation of the global Figure across trials had no impact on initiation latency (top), movement time (middle), or curvature (bottom). Color priming was observed for all three measures. Error bars represent 95% confidence intervals for the within-subjects design (Loftus & Masson, 1994).

vision, and were naive to the aims of the experiment. The protocol was approved by the Brown University Institutional Review Board. All procedures reported in this manuscript followed the guidelines of the Declaration of Helsinki.

Stimuli and procedures

The stimuli and procedures were the same as those used in Experiment 1 with the following exceptions:

An illusory triangle was present at all times, but the targets were positioned to be consistent with the percept of either an upward or downward pointing triangle (Figure 4). Thus, on a given trial, the three Pac-men were equally spaced and placed at 4, 8, and 12 o'clock or at 2, 6, and 10 o'clock on an imaginary circle.

Statistical analyses

Again, only correct and visually inspected trials were included in the analysis. We conducted 2×2 repeated-measures ANOVA with factors of global orientation (repeat vs. switch) and target color (repeat vs. switch) to test the hypothesis that similar to object priming (e.g., Biederman & Cooper, 1991, 2009; Knowlton et al., 2009), early global figure priming is invariant to shape.

Results

Target selection accuracy was very high ($M = 99.54\%$, $SEM = 0.18\%$) and an average of 1.24% of trials ($SEM = 0.30\%$) were removed based on the exclusion criteria described earlier. The final analysis was conducted on an average of 98.3% of the total trials. As shown in Figure 4 (top), initiation latency did not differ between trials in which the orientation of the figure repeated compared to when it switched, $F[1, 17] = 1.16$, $n.s.$, consistent with the hypothesis that early global figure priming is shape invariant. In addition, Figure 5 illustrates that no main effect of global orientation was observed for movement time (middle), $F[1, 17] = 2.22$, $n.s.$, or curvature (bottom), $F[1, 17] = 0.70$, $n.s.$ Color priming was observed for all three measures, replicating the basic finding of PoP: initiation latency (Repeat: 335 ± 2 ms, Switch: 339 ± 2 ms, $F[1, 17] = 12.15$, $p = 0.003$, $\eta^2 = 0.42$); movement time (Repeat: 424 ± 2 ms, Switch: 430 ± 2 ms, $F[1, 17] = 40.48$, $p < 0.001$, $\eta^2 = 0.70$); curvature (Repeat: 0.072 ± 0.002 , Switch: 0.088 ± 0.002 , $F[1, 17] = 30.80$, $p < 0.001$, $\eta^2 = 0.64$). No significant interactions were observed for any of the three measures (all $ps > 0.09$). Therefore, the data replicate the basic finding of PoP and support the hypothesis that figure priming is shape invariant.

Experiment 3: Global figures defined by illusory, but not real contours, facilitate reach planning

In this experiment, we sought to determine if other perceptual grouping processes resulting in figure

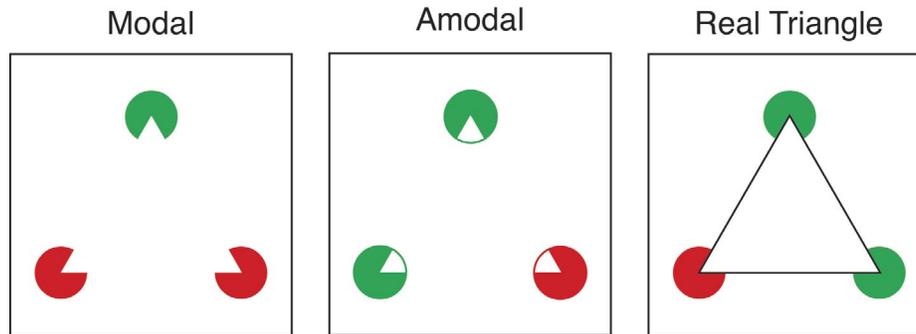


Figure 6. Stimuli used in the third experiment. Pac-men targets give rise to the percept of a modally completed triangle (left). Pac-men surrounded by a circle support the percept of an amodally completed triangle behind three circular apertures (middle). A triangle defined by a real contour occludes three circular targets (right).

percepts, as well as real figures, afford early global attentional benefits in a similar manner to the Kanizsa display used in the first two experiments. Kanizsa figures represent the case of *modal* completion (Michotte & Burke, 1951; Michotte, 1963): An illusory surface matching the color of the background is perceived in front of the Pac-men inducers. *Amodal* completion (Michotte & Burke, 1951; Michotte, 1963) illustrates another case of perceptual grouping in which a partly occluded object is perceived to lie below the inducing stimuli. It has been proposed that similar mechanisms underlie these two processes (Grossberg & Mingolla, 1985; Kalar, Garrigan, Wickens, Hilger, & Kellman, 2010; Kellman, 2003; Kellman & Shipley, 1991; Murray, Foxe, Javitt, & Foxe, 2004; Sugita, 1999; von der Heydt, Peterhans, & Baumgartner, 1984; Zhou, Friedman, & von der Heydt, 2000), although there is some controversy (e.g., Anderson, 2007; Anderson, Singh, & Fleming, 2002; Singh, 2004; Spehar & Halim, 2015). Moreover, there is some evidence that similar neural mechanisms underlie the processing of real contours as well as illusory contours generated through modal completion (Lee & Nguyen, 2001; Peterhans & von der Heydt, 1991; Vogels & Orban, 1987; von der Heydt et al., 1984). Given these proposed similarities, it raises the possibility that the observed effects related to global attention in the present manuscript are simply a result of a figure being present in the display. Accordingly, here we ask: When it comes to early global priming in target selection, are all figures created equal?

To address this question, we modified the color-odddity search task to include modally and amodally completed figures, as well as figures defined by real contours (Figure 6). We examined whether modal and amodal completion—both of which rely on perceptual grouping to form figure percepts—similarly facilitate the early stages of target selection, as well as how they may or may not differ from real figures with explicit contour information.

Methods

Participants

Eighteen Brown University students (15 female, mean age = 22 years) participated in a session lasting approximately 1 hr and received course credit or monetary compensation. All participants were right-handed, reported normal or corrected-to-normal color vision, and were naive to the aims of the experiment. The protocol was approved by the Brown University Institutional Review Board. All procedures reported in this manuscript followed the guidelines of the Declaration of Helsinki.

Stimuli and Procedures

The stimuli and procedures are identical to those of Experiment 1 with the exception that three target display configurations were used: Pac-men targets inducing a modally completed triangle (Figure 6, left), Pac-men targets surrounded by a circle giving rise to the percept of an amodally completed triangle viewed through three apertures (Figure 6, middle), and three circular targets occluded by a triangle (Figure 6, right). The circles surrounding the inducers in the amodal condition and the border of the triangle in the real contour condition both subtended 0.07° visual angle. Lastly, based on the observation that early global priming increased with successive figure presentations, only one stimulus configuration was shown throughout each block. We reasoned that because introducing an additional condition would not allow for several repetitions of the same configuration, potential differences between the three stimulus displays may not be as readily apparent using mixed blocks. Thus, each condition was shown for four blocks of 50 trials each resulting in 12 total blocks and 600 total trials. The block order was randomly determined for each participant.

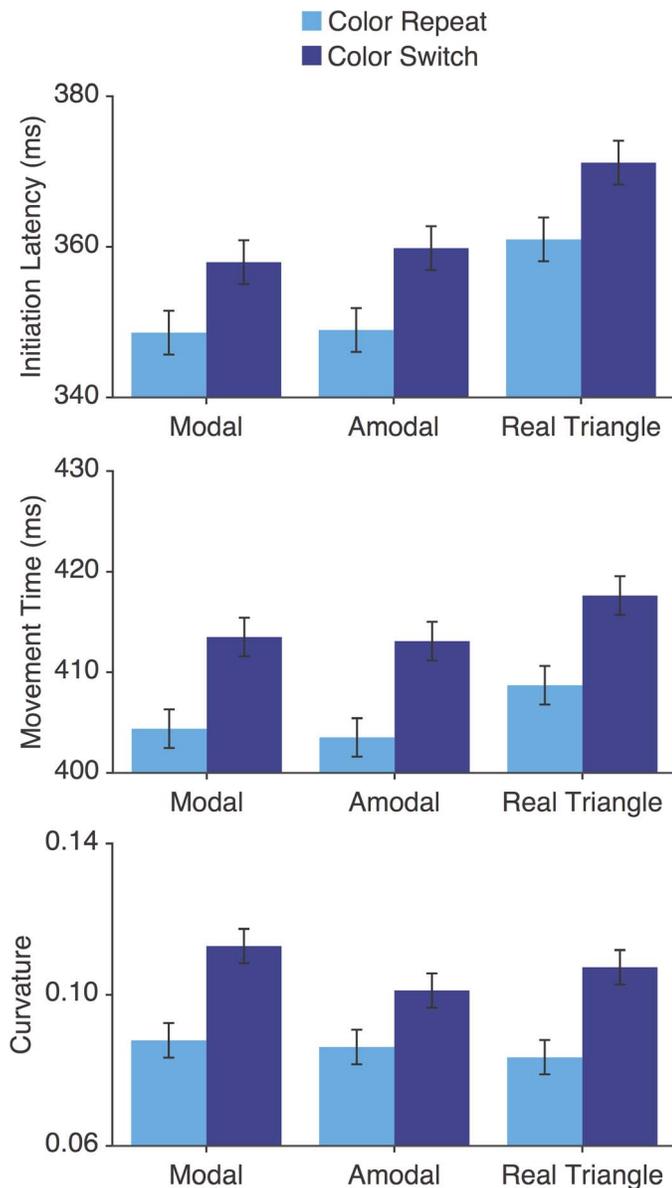


Figure 7. Results of Experiment 3. Reaches were initiated faster for modal and amodal trials compared to real triangle trials, and a main effect of target color was observed (top). Color priming was also observed for movement time (middle) and curvature (bottom). Error bars represent 95% confidence intervals for the within-subject design (Loftus & Masson, 1994).

Statistical analyses

Only correct and visually inspected trials were included in the analysis. To determine if attentional selection benefits differ between figures arising from perceptual grouping and those defined by real contours, we conducted 3×2 repeated-measures ANOVA with factors of configuration (modal vs. amodal vs. real triangle) and target color (repeat vs. switch).

Results

The mean accuracy across subjects was 99.35% ($SEM = 0.21\%$) and an average of 0.92% of trials ($SEM = 0.23\%$) were dropped based on the exclusion criteria. This resulted in an average of 98.43% of trials being included in the analysis. As shown in Figure 7, the main effect of configuration was observed for initiation latency; however, because Mauchly's test of sphericity was violated, $X^2[2] = 10.3$, $p = 0.006$, degrees of freedom were corrected using Greenhouse–Geisser estimates of sphericity ($\epsilon = 0.68$). Importantly, the Greenhouse–Geisser corrected main effect of configuration was also significant, $F[2, 34] = 4.13$, $p = 0.043$, $\eta^2 = 0.20$. Follow-up paired t tests revealed that initiation latency was faster to the modal configuration relative to the display containing a real triangle (Modal: 353 ± 3 ms, Real Triangle: 366 ± 3 ms, $t[17] = -2.20$, $p = 0.042$). Additionally, initiation latencies were faster in the amodal condition (355 ± 3 ms) compared to the display containing a real triangle, and this trend approached significance, $t[17] = -2.08$, $p = 0.053$. Moreover, initiation latencies in the modal and amodal conditions did not significantly differ, $t[17] = -0.39$, $n.s.$ Thus, figures arising from modal completion afford a more robust early global attentional benefit compared to figures with explicitly defined contours; however, the benefit from amodal completion is relatively unstable. The main effect of configuration was not significant for movement duration, $F[2, 34] = 0.81$, $n.s.$, or curvature, $F[2, 34] = 2.08$, $n.s.$, again suggesting that global attention facilitates only the early stage of goal-directed action. As expected, color priming was observed all three measures (all p s < 0.001 , all η^2 s > 0.5): initiation latency (Repeat: 353 ± 3 ms, Switch: 363 ± 3 ms); movement time (Repeat: 406 ± 2 ms, Switch: 415 ± 2 ms); curvature (Repeat: 0.085 ± 0.005 , Switch: 0.105 ± 0.005). No significant interactions were observed (all p s > 0.08). Taken together, the data suggest that modal completion processes supporting perceptual grouping facilitate reach planning, whereas figures with real contours do not; however, the data did not provide strong evidence in favor of a difference between the amodal and real triangle conditions. Additionally, color priming was evident in all measures, consistent with the basic finding of PoP.

Discussion

We investigated how visually guided reaching is impacted when the targets to be selected are perceptually grouped as part of a greater whole. Experiment 1 demonstrated that the presence of a global Kanizsa figure reduced the time to plan a movement (initiation

latency), but did not impact movement execution (movement time and curvature). Furthermore, both movement planning and execution were more efficient when target colors were repeated, replicating the classic PoP effect (Song & Nakayama, 2006, 2008). Experiment 2 also replicated PoP and suggested that early global priming is invariant with respect to the shape of the global figure. Lastly, Experiment 3 demonstrated that reach planning was facilitated by modal completion, but not figures defined by real contours. Importantly, in all three experiments, effects related to the global illusory figure were constrained to the early stage of reach planning, suggesting that the perceptual grouping of potential reach targets via illusory contours does not influence reach execution. We now discuss the primary conclusions that can be drawn from the results.

Illusory contours promote the spread of early global attention and facilitate reach planning

The results of Experiment 1 are consistent with research demonstrating that Kanizsa figures are detected early and efficiently in visual search (Conci et al., 2007; Conci et al., 2011; Davis & Driver, 1994; Rauschenberger & Yantis, 2001; Senkowski, Rottger, Grimm, Foxe, & Herrmann, 2005). For example, global Kanizsa squares are detected more easily in visual search compared to locally grouped elements that do not give rise to global surface percepts (Conci et al., 2007). Moreover, increasing the number of distractors in such search displays had little impact on reaction times, suggesting that Kanizsa figures pop out during visual search (Davis & Driver, 1994; Senkowski et al., 2005). Senkowski et al. (2005) also found an enhanced N2pc component (a marker of attentional orienting; Eimer, 1996; Luck & Hillyard, 1994) contralateral to the target in search displays containing a Kanizsa figure, further demonstrating early attentional selection. Moreover, in a related electroencephalogram (EEG) study, searching for local rather than global targets elicited smaller amplitudes in early sensory components P1 and N1 and delayed the N2pc by ~70 ms (Conci et al., 2011) consistent with the notion of early global precedence.

We note, however, there are some that argue Kanizsa figures do not trigger attentional guidance in visual search. For instance, using misaligned Pac-men as distractors instead of outward facing inducers to eliminate subjective figure percepts, Grabowecky and Treisman (1989) showed that reaction times increased with set size. Thus, they concluded that search was serial and required attention. Moreover, Gurnsey, Poirier, and Gascon (1996) argued that the results of

Davis and Driver's (1994) experiments demonstrating parallel search for Kanizsa figures among outward facing inducer displays may not have resulted from subjective contours per se, but rather differences in outline and closure between the target and distractors. Building off this criticism, as well as Gurnsey, Humphrey, and Kapitan's (1992) finding of efficient parallel search for subjective contours induced by line ends, Li, Cave, and Wolfe (2008) examined visual search for Kanizsa targets differing in orientation or shape from other Kanizsa distractors. They compared search slopes to conditions containing line drawings and found that real, but not illusory contours, produced flatter search slopes with the addition of distractors. Thus, the authors concluded that illusory figures do not guide attentional deployment.

Though these results may appear to stand in contrast to our findings, there are several important differences in the design of our study. First, in the previous research discussed above, the search target was always a global figure. Instead, the figure in our study was task-irrelevant and the targets were the inducers themselves. To our knowledge, ours is the first study to investigate search for individual inducing components of a grouped Kanizsa configuration using visually guided reaching. Nonetheless, we find that the presence of an illusory figure facilitates reach planning. Importantly, this reduced initiation latency does not induce a tradeoff in the later stage of movement planning (i.e., slower and more curved movements) as has been demonstrated in previous work investigating PoP (Song & Nakayama, 2008). Second, Li et al. (2008) demonstrated that search for real contours was more efficient compared to illusory contours. In our study, however, we find that the presence of an illusory figure expedites the early stages of target selection, whereas figures defined by real contours do not. We discuss this discrepancy with the conclusions of Experiment 3 in more detail below. Finally, the distracting stimuli in Li et al. (2008) induce competition at the global level. Because there was only a single global figure in our design, we would not expect to see such interference. Instead, we suggest our observed early benefit may be a result of attentional spreading across the illusory surface. Specifically, previous research indicates that in the case of modal completion, the presence of a potential visual surface leads to the attraction of attention across that surface to include the inducing information (Davis & Driver, 1997; Driver et al., 2001). Accordingly, it may be the case that when a Kanizsa figure is present, the global spreading of attention to the potential target locations is facilitated, allowing for faster deployment of focal attention to the target.

Priming of early global attention is invariant to the shape of the illusory figure

Experiment 2 was designed to determine if early global priming by Kanizsa figures is shape invariant. This idea was inspired by the visual priming literature demonstrating that object identification is more efficient after prior exposure even when the prime is presented in a different location or is rotated relative to the test object (e.g., Biederman & Cooper, 1991, 2009; Knowlton et al., 2009). For example, Knowlton et al. (2009) showed that objects were identified faster when the same image was previously shown in a sequence of images several seconds before. Importantly, there was no difference in the magnitude of priming for inverted and rotated objects compared to identical images. In addition, identification time was superior compared to words or object category exemplars. Our initial reasoning was that the sequential figure priming effect (i.e., successively faster initiation latency with repeated Kanizsa figure presentations) might also be invariant to inversion due to the global illusory object percept. Specifically, no costs to initiation latency would be observed when the orientation of the figure was inverted across trials. We observed that this was indeed the case: Early global priming appears to be invariant to the orientation of the illusory figure.

Global figures defined by illusory, but not real contours, afford an early selection advantage during goal-directed reaching

The results of Experiment 3 suggest that figures arising from modal completion facilitate reach planning during target selection, whereas real figures do not. Specifically, initiation latencies were slower in real figure blocks relative to modal blocks. This pattern of data was similar for the amodal and real figure conditions but much weaker. Thus, while it has been argued that the perception of modally and amodally completed contours arise due to the same boundary interpolation processes (Grossberg & Mingolla, 1985; Kalar et al., 2010; Kellman & Shipley, 1991) and similar neural mechanisms (Lee & Nguyen, 2001; Peterhans & von der Heydt, 1989; Sugita, 1999; von der Heydt et al., 1984; Zhou et al., 2000), our results suggest that in the case of goal-directed reaching, modal completion affords a superior benefit compared to amodal completion.

Why might this be the case? After all, EEG research indicates that both modal (Conci et al., 2011; Senkowski et al., 2005) and amodal (Kasai & Takeya, 2012) completion cause attention to spread over the interpolated region; importantly, however, the latter study only compared objects connected by amodal

completion to those connected by an explicit contour and did not investigate modal completion. Moreover, in contrast to results from intracranial recordings in nonhuman primates (e.g., Lee & Nguyen, 2001; von der Heydt & Peterhans, 1989), recent EEG work in humans suggests that amodal completion is a more effortful process compared to modal completion (Brodeur, Lepore, & Debruille, 2006; Murray et al., 2004). Thus, while amodal completion also supports perceptual grouping, this increased processing difficulty may explain why the selection benefits observed here were less robust compared to those afforded by modal completion.

Such a discrepancy has also been demonstrated in perceptual tasks in which participants responded via a keypress. Davis and Driver (1998) demonstrated that attention spreads for modally, but not amodally completed regions. Specifically, their display contained an oval that could be perceived to be in front of (modal completion) or behind (amodal completion) a central bar. Participants identified a target letter that could appear either on the central bar or in the surrounding region. Interestingly, in the modal condition, cueing the outer shape (i.e., briefly changing the width of the oval) facilitated target detection not only in the outer regions, but in the center as well; however, this was not the case when the oval was amodally completed behind the central bar. They concluded that perceptual filling-in attracted attention to both the modally completed surface and the inducers. Accordingly, this early spread of attention across the modal, but not amodal display, may explain the differences we observed here.

Our finding that illusory, but not real contours, facilitate the early stage of goal directed reaching also appears to stand in contrast to previous research indicating the opposite pattern of results (Li et al., 2008). Specifically, Li et al. (2008) concluded that Kanizsa figures do not guide attentional deployment, as visual search was found to be less efficient compared to figures with real contours. Additionally, contrary to our findings, past research demonstrates that reporting the location of a figure defined by real contours in an array of similar elements is slightly more efficient than illusory figures, and far superior to amodally completed figures (Gegenfurtner, Brown, & Rieger, 1997). Importantly, however, the task in these two experiments required finding a global figure among other figures or similar elements; instead, we required participants to select a local inducer as their target. Thus, these discrepancies may be explained due to differences in the task demands.

We interpret our findings as a benefit of perceptual grouping: Because modal completion (and possibly amodal completion to a lesser extent) requires the grouping of local elements to form figure precepts, it

facilitates the spread of early global attention across the illusory surface. Indeed, EEG studies have demonstrated that illusory contours evoke a larger N1 amplitude (Pegna, Khateb, Murray, Landis, & Michel, 2002) and increased gamma activity over visual cortex compared to real contours (Tallon-Baudry, Bertrand, Delpuech, & Pernier, 1996; Tallon-Baudry, Bertrand, Wienbruch, Ross, & Pantev, 1997), which has been interpreted as evidence for perceptual filling in or feature binding. Importantly, superior feature discrimination has been demonstrated when features belong to the same, rather than different, objects (Duncan, 1984), and it is suggested that this is due to attention being able to shift more effectively within than between objects (e.g., Egly, Driver, & Rafal, 1994; Fiebelkorn, Saalman, & Kastner, 2013).

Furthermore, literature on object-based attention (for reviews see Chen, 2012; Driver & Baylis, 1998; Scholl, 2001) suggests that the spread of attention is constrained to the boundaries of the attended object. Critically, in the case of modal completion, attention not only spreads across the illusory surface, but also to the inducing elements (Davis & Driver, 1997, 1998; Driver et al., 2001). In contrast, in the real figure condition, all of the contour information is explicitly provided. Thus, according to object-based theories, attention should only spread to the boundaries of the figure itself resulting in the percept of an object segmented from the background elements. As a result, this segmentation introduces increased figure-ground competition (for review see Wagemans et al., 2012) that takes time to resolve before attention can be allocated to the occluded (i.e., amodally completed) targets. Interestingly, search for occluded targets has been shown to be less efficient compared to unoccluded targets during visual search (Davis & Driver, 1998; He & Nakayama, 1992; Rensink & Enns, 1998). Thus, we suggest that similar to these findings showing impaired selection in keypress tasks, the presence of a real triangle introduces global figure precedence and occludes the local targets, leading to slower early selection compared to when targets can be perceptually grouped via modal completion.

Why reach planning but not execution?

Unlike the findings of Song and Nakayama (2006, 2008) that showed perceptual grouping of distractors impacts both early and late stages goal-directed action, we find that perceptual grouping via modal completion impacts only reach planning. Critically, however, the perceptual grouping in Song and Nakayama (2006) was achieved by increasing the number of distractors, and in turn the number of response options in the display.

In our study, the number of potential target locations was held constant and with the exception of Experiment 2, target location did not vary. Thus, there was far less uncertainty regarding the potential target location on a given trial. Because of this consistency, one might expect that any influence of the global display would only impact very early stages of the decision process with local color competition being the prominent source of interference.

Recent work also indicates that reach planning and execution embody different aspects of decision-making. Specifically, initiation latency is thought to reflect a response threshold adjustment process related to the inhibition of motor output, whereas movement time and curvature reflect an ongoing monitoring process representing the coactivation of competing responses throughout a trial (Erb et al., 2016). According to the model proposed by Shenhav et al. (2013), conflict registered between the competing target options during reach planning should lead to a temporary suppression of the motor response until adequate information is acquired to reach a threshold for deciding to move. This adjustment allows additional time for a controlled response selection process to be recruited and resolve conflict between the coactive responses during reach execution to support efficient target selection. Thus, the early spreading of attention via modal completion of the potential targets might impact the initial response threshold by speeding up the rate of information accumulation and/or raising the initial baseline of available evidence, both of which could reduce the time needed to reach a decision to move. The monitoring process, however, is evident throughout both stages of target selection reflecting local color competition between the target and distractors.

On a related note, goal-directed reaching has also been suggested to rely on multiple frames of reference. Specifically, an action-centered framework is thought to be involved during the early stage of response planning to resolve the general (i.e., global) locations of targets and distractors, whereas an environment-centered framework emerges later during execution to aid in the finer discrimination of the specific (i.e., local) target location (Keulen, Adam, Fischer, Kuipers, & Jolles, 2002). Importantly, it is suggested that this latter, environment-centered framework is not exclusive to the execution phase and may also play a role in reach planning. This notion is in line with our suggestion that the spread of attention via modal completion facilitates early global orienting in the action-centered framework and reduces the duration of reach planning. In turn, this might lead to earlier recruitment of the environment-centered framework consistent with the additive influence of local color priming in both early and late stages of goal-directed reaching.

Conclusions

We demonstrate that a global-to-local cascade of attentional guidance impacts target selection. The presence of an illusory figure reduced the time to initiate reaches but had no impact on reach execution. Moreover, consistent with PoP, repeating the local target color facilitated both early and late stages of goal-directed reaching. In addition, repeated figure presentations successively reduced the time to initiate reaches and changing the global orientation of the figure did not mitigate this priming effect. Lastly, we found that Kanizsa figures, but not those defined by real contours, afforded an early global benefit. We propose this difference might be due to the early spreading of attention across the illusory surface that leads to perceptual grouping, rather than segmentation of the display elements, allowing for local attention to be more efficiently allocated to the target. Taken together, these results demonstrate that illusory contours facilitate reach planning through the spread of early global attention, but do not impact the later stage of reach execution. In contrast, local color competition impacts target selection throughout the continuous decision process. Collectively, these results suggest the multiple attentional mechanisms underlie our ability to plan and execute appropriate actions, enabling us to efficiently select suitable object features for interaction in daily life.

Keywords: visually guided reaching, global–local attention, perceptual grouping, perceptual organization

Acknowledgments

This work was supported by a Social, Behavioral, and Economic Sciences Postdoctoral Research Fellowship (SPRF) awarded by the National Science Foundation (1514246) to J. D. M. as well as an Institutional Development Award (IDeA) from the National Institute of General Medical Sciences of the National Institutes of Health (P20GM103645) and a grant from the Rhode Island Foundation (20144132) awarded to J.-H. S. The authors would also like to thank the reviewers for their helpful comments and Jennifer Flaherty for her contributions to this project.

Commercial relationships: none.
Corresponding author: J. Daniel McCarthy.
Email: dan_mccarthy@brown.edu.
Address: Department of Cognitive, Linguistic & Psychological Sciences, Brown University, Providence, RI, USA.

Footnote

¹ Reported error terms reflect 95% confidence intervals for the within-subjects design (Loftus & Masson, 1994).

References

- Albert, M. K. (2007). Mechanisms of modal and amodal interpolation. *Psychological Review*, *114*(2), 455–469.
- Anderson, B. L. (2007). The demise of the identity hypothesis and the insufficiency and nonnecessity of contour relatability in predicting object interpolation: Comment on Kellman, Garrigan, and Shipley (2005). *Psychological Review*, *114*(2), 470–487.
- Anderson, B. L., Singh, M., & Fleming, R. W. (2002). The interpolation of object and surface structure. *Cognitive Psychology*, *44*(2), 148–190.
- Biederman, I., & Cooper, E. E. (1991). Evidence for complete translational and reflectional invariance in visual object priming. *Perception*, *20*(5), 585–593.
- Biederman, I., & Cooper, E. E. (2009). Translational and reflectional priming invariance: A retrospective. *Perception*, *38*(6), 809–817.
- Brainard, D. H. (1997). The Psychophysics Toolbox. *Spatial Vision*, *10*(4), 433–436.
- Bravo, M. J., & Nakayama, K. (1992). The role of attention in different visual-search tasks. *Perception & Psychophysics*, *51*(5), 465–472.
- Brodeur, M., Lepore, F., & Debruille, J. B. (2006). The effect of interpolation and perceptual difficulty on the visual potentials evoked by illusory figures. *Brain Research*, *1068*(1), 143–150.
- Chen, Z. (2012). Object-based attention: A tutorial review. *Attention, Perception & Psychophysics*, *74*(5), 784–802.
- Conci, M., Müller, H. J., & Elliott, M. A. (2007). The contrasting impact of global and local object attributes on Kanizsa figure detection. *Perception & Psychophysics*, *69*(8), 1278–1294.
- 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.
- Davis, G., & Driver, J. (1994). Parallel detection of Kanizsa subjective figures in the human visual system. *Nature*, *371*(6500), 791–793.
- Davis, G., & Driver, J. (1997). A functional role for

- illusory colour spreading in the control of focused visual attention. *Perception*, 26(11), 1397–1411.
- Davis, G., & Driver, J. (1998). Kanizsa subjective figures can act as occluding surfaces at parallel stages of visual search. *Journal of Experimental Psychology: Human Perception & Performance*, 24(1), 169–184.
- Desmurget, M., Jordan, M., Prablanc, C., & Jeannerod, M. (1997). Constrained and unconstrained movements involve different control strategies. *Journal of Neurophysiology*, 77(3), 1644–1650.
- Driver, J., & Baylis, G. C. (1998). Attention and visual object segmentation. In R. Parasuraman (Ed.), *The attentive brain* (pp. 299–325). Cambridge, MA: MIT Press.
- Driver, J., Davis, G., Russell, C., Turatto, M., & Freeman, E. (2001). Segmentation, attention and phenomenal visual objects. *Cognition*, 80(1–2), 61–95.
- Duncan, J. (1984). Selective attention and the organization of visual information. *Journal of Experimental Psychology: General*, 113(4), 501–517.
- Egly, R., Driver, J., & Rafal, R. D. (1994). Shifting visual attention between objects and locations: Evidence from normal and parietal lesion subjects. *Journal of Experimental Psychology: General*, 123(2), 161–177.
- Eimer, M. (1996). The N2pc component as an indicator of attentional selectivity. *Electroencephalography & Clinical Neurophysiology*, 99(3), 225–234.
- Erb, C. D., Moher, J., Sobel, D. M., & Song, J. H. (2016). Reach tracking reveals dissociable processes underlying cognitive control. *Cognition*, 152, 114–126.
- Fiebelkorn, I. C., Saalman, Y. B., & Kastner, S. (2013). Rhythmic sampling within and between objects despite sustained attention at a cued location. *Current Biology*, 23(24), 2553–2558.
- Gegenfurtner, K. R., Brown, J. E., & Rieger, J. (1997). Interpolation processes in the perception of real and illusory contours. *Perception*, 26(11), 1445–1458.
- Grabowecky, M., & Treisman, A. (1989). Attention and fixation in subjective contour perception. *Investigative Ophthalmology & Visual Science*, 30(Suppl.), 457.
- Grossberg, S., & Mingolla, E. (1985). Neural dynamics of form perception: Boundary completion, illusory figures, and neon color spreading. *Psychological Review*, 92(2), 173.
- Gurnsey, R., Humphrey, G. K., & Kapitan, P. (1992). Parallel discrimination of subjective contours defined by offset gratings. *Perception & Psychophysics*, 52(3), 263–276.
- Gurnsey, R., Poirier, F. J. A. M., & Gascon, E. (1996). There is no evidence that Kanizsa-type subjective contours can be detected in parallel. *Perception*, 25(7), 861–874.
- He, Z. J., & Nakayama, K. (1992). Surfaces versus features in visual search. *Nature*, 359(6392), 231–233.
- Hegde, J. (2008). Time course of visual perception: coarse-to-fine processing and beyond. *Progress in Neurobiology*, 84(4), 405–439.
- Hochstein, S., & Ahissar, M. (2002). View from the top: Hierarchies and reverse hierarchies in the visual system. *Neuron*, 36(5), 791–804.
- Kalar, D. J., Garrigan, P., Wickens, T. D., Hilger, J. D., & Kellman, P. J. (2010). A unified model of illusory and occluded contour interpolation. *Vision Research*, 50(3), 284–299.
- Kanizsa, G. (1955). Margini quasi-percettivi in campi con stimolazione omogenea [Translation: Quasi-perceptual margins in homogeneously stimulated fields]. In S. Petry & G. F. Meyer (Eds.), *The perception of illusory contours* (pp. 40–49). New York: Springer.
- Kanizsa, G. (1979). *Organization in vision: Essays on gestalt perception*. New York: Praeger.
- Kasai, T., & Takeya, R. (2012). Time course of spatial and feature selective attention for partly-occluded objects. *Neuropsychologia*, 50(9), 2281–2289.
- Kellman, P. J. (2003). Interpolation processes in the visual perception of objects. *Neural Networks*, 16(5–6), 915–923.
- Kellman, P. J., & Shipley, T. F. (1991). A theory of visual interpolation in object perception. *Cognitive Psychology*, 23(2), 141–221.
- Keulen, R. F., Adam, J. J., Fischer, M. H., Kuipers, H., & Jolles, J. (2002). Selective reaching: Evidence for multiple frames of reference. *Journal of Experimental Psychology: Human Perception & Performance*, 28(3), 515–526.
- Knowlton, B. J., McAuliffe, S. P., Coelho, C. J., & Hummel, J. E. (2009). Visual priming of inverted and rotated objects. *Journal of Experimental Psychology: Learning, Memory & Cognition*, 35(4), 837–848.
- Lee, T. S., & Nguyen, M. (2001). Dynamics of subjective contour formation in the early visual cortex. *Proceedings of the National Academy of Sciences*, 98(4), 1907–1911.
- Li, X. S., Cave, K. R., & Wolfe, J. M. (2008). Kanizsa-type subjective contours do not guide attentional

- deployment in visual search but fine termination contours do. *Perception & Psychophysics*, 70(3), 477–488.
- Loftus, G. R., & Masson, M. E. J. (1994). Using confidence-intervals in within-subject designs. *Psychonomic Bulletin & Review*, 1(4), 476–490.
- Luck, S. J., & Hillyard, S. A. (1994). Spatial filtering during visual search: Evidence from human electrophysiology. *Journal of Experimental Psychology: Human Perception & Performance*, 20(5), 1000–1014.
- Maljkovic, V., & Nakayama, K. (1994). Priming of pop-out: I. Role of features. *Memory & Cognition*, 22(6), 657–672.
- McPeck, R. M., Maljkovic, V., & Nakayama, K. (1999). Saccades require focal attention and are facilitated by a short-term memory system. *Vision Research*, 39(8), 1555–1566.
- Michotte, A., & Burke, L. (1951). Une nouvelle énigme de la psychologie de la perception: le “donnée amodal” dans l’expérience sensorielle [Translation: A new enigma in the psychology of perception: amodal data in sensory experience] (pp. 179–180). Actes du 13^{ème} Congrès Internationale de Psychologie, Stockholm, Sweden.
- Michotte, A. (1963). *The perception of causality*. London: Methuen. Translation from Michotte, 1954 by T. R. Miles & E. Miles.
- Moher, J., & Song, J. H. (2013). Context-dependent sequential effects of target selection for action. *Journal of Vision*, 13(8):10, 1–13, doi:10.1167/13.8.10. [PubMed] [Article]
- Murray, M. M., Foxe, D. M., Javitt, D. C., & Foxe, J. J. (2004). Setting boundaries: Brain dynamics of modal and amodal illusory shape completion in humans. *The Journal of Neuroscience*, 24(31), 6898–6903.
- Nakayama, K., Joseph, J. S., & Parasuraman, R. (1998). Attention, pattern recognition and popout in visual search. In R. Parasuraman (Ed.), *The attentive brain*. Cambridge, MA: MIT Press.
- Navon, D. (1977). Forest before trees: The precedence of global features in visual perception. *Cognitive Psychology*, 9(3), 353–383.
- Pegna, A. J., Khateb, A., Murray, M. M., Landis, T., & Michel, C. M. (2002). Neural processing of illusory and real contours revealed by high-density ERP mapping. *Neuroreport*, 13(7), 965–968.
- Peterhans, E., & von der Heydt, R. (1989). Mechanisms of contour perception in monkey visual cortex. II. Contours bridging gaps. *The Journal of Neuroscience*, 9(5), 1749–1763.
- Peterhans, E., & von der Heydt, R. (1991). Subjective contours—Bridging the gap between psychophysics and physiology. *Trends in Neuroscience*, 14(3), 112–119.
- Rauschenberger, R., & Yantis, S. (2001). Attentional capture by globally defined objects. *Perception & Psychophysics*, 63(7), 1250–1261.
- Rensink, R. A., & Enns, J. T. (1995). Preemption effects in visual search: Evidence for low-level grouping. *Psychological Review*, 102(1), 101–130.
- Rensink, R. A., & Enns, J. T. (1998). Early completion of occluded objects. *Vision Research*, 38(15–16), 2489–2505.
- Scholl, B. J. (2001). Objects and attention: The state of the art. *Cognition*, 80(1–2), 1–46.
- Senkowski, D., Rottger, S., Grimm, S., Foxe, J. J., & Herrmann, C. S. (2005). Kanizsa subjective figures capture visual spatial attention: Evidence from electrophysiological and behavioral data. *Neuropsychologia*, 43(6), 872–886.
- Shenhav, A., Botvinick, M. M., & Cohen, J. D. (2013). The expected value of control: An integrative theory of anterior cingulate cortex function. *Neuron*, 79(2), 217–240.
- Shipley, T. F., & Kellman, P. J. (1992). Strength of visual interpolation depends on the ratio of physically specified to total edge length. *Perception & Psychophysics*, 52(1), 97–106.
- Singh, M. (2004). Modal and amodal completion generate different shapes. *Psychological Science*, 15(7), 454–459.
- Song, J. H., & Nakayama, K. (2006). Role of focal attention on latencies and trajectories of visually guided manual pointing. *Journal of Vision*, 6(9):11, 982–995, doi:10.1167/6.9.11. [PubMed] [Article]
- Song, J. H., & Nakayama, K. (2007a). Automatic adjustment of visuomotor readiness. *Journal of Vision*, 7(5):2, 1–9, doi:10.1167/7.5.2. [PubMed] [Article]
- Song, J. H., & Nakayama, K. (2007b). Fixation offset facilitates saccades and manual reaching for single but not multiple target displays. *Experimental Brain Research*, 177(2), 223–232.
- Song, J. H., & Nakayama, K. (2008). Target selection in visual search as revealed by movement trajectories. *Vision Research*, 48(7), 853–861.
- Song, J. H., Takahashi, N., & McPeck, R. M. (2008). Target selection for visually guided reaching in macaque. *Journal of Neurophysiology*, 99(1), 14–24.
- Spehar, B., & Halim, V. A. (2015). Created unequal: Temporal dynamics of modal and amodal bound-

- ary interpolation. *Vision Research*, e-pub ahead of print, doi:10.1016/j.visres.2015.10.006.
- Sugita, Y. (1999). Grouping of image fragments in primary visual cortex. *Nature*, *401*(6750), 269–272.
- Tallon-Baudry, C., Bertrand, O., Delpuech, C., & Pernier, J. (1996). Stimulus specificity of phase-locked and non-phase-locked 40 Hz visual responses in human. *Journal of Neuroscience*, *16*(13), 4240–4249.
- Tallon-Baudry, C., Bertrand, O., Wienbruch, C., Ross, B., & Pantev, C. (1997). Combined EEG and MEG recordings of visual 40 Hz responses to illusory triangles in human. *Neuroreport*, *8*(5), 1103–1107.
- Vogels, R., & Orban, G. A. (1987). Illusory contour orientation discrimination. *Vision Research*, *27*(3), 453–467.
- von der Heydt, R., & Peterhans, E. (1989). Mechanisms of contour perception in monkey visual cortex. I. Lines of pattern discontinuity. *The Journal of Neuroscience*, *9*(5), 1731–1748.
- von der Heydt, R., Peterhans, E., & Baumgartner, G. (1984). Illusory contours and cortical neuron responses. *Science*, *224*(4654), 1260–1262.
- Wagemans, J., Elder, J. H., Kubovy, M., Palmer, S. E., Peterson, M. A., Singh, M., & von der Heydt, R. (2012). A century of Gestalt psychology in visual perception: I. Perceptual grouping and figure - ground organization. *Psychonomic Bulletin & Review*, *138*(6), 1172–1217.
- Zhou, H., Friedman, H. S., & von der Heydt, R. (2000). Coding of border ownership in monkey visual cortex. *The Journal of Neuroscience*, *20*(17), 6594–6611.