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Connecting the Dots: Object Connectedness Deceives Perception but Not Movement Planning

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Abstract

The perceptual system parses complex scenes into discrete objects. Parsing is also required for planning visually guided movements when more than one potential target is present. To examine whether visual perception and motor planning use the same or different parsing strategies, we used the connectedness illusion, in which observers typically report seeing fewer targets if pairs of targets are connected by short lines. We found that despite this illusion, when observers are asked to make speeded reaches toward targets in such displays, their reaches are unaffected by the presence of the connecting lines. Instead, their movement plans, as revealed by their movement trajectories, are influenced by the number of potential targets irrespective of whether connecting lines are present or not. This suggests that scene parsing for perception depends on mechanisms that are distinct from those that allow observers to plan rapid and efficient target-directed movements in situations with multiple potential targets.

Keywords

perception, action, scene parsing, reaching movements, movement planning, two visual streams, motor processes

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Vision plays a significant role in everyday life, allowing people to perceive their surroundings and to guide their actions with respect to the objects in the environment. It has been proposed that the processing of incoming visual information takes place along two separate but interacting streams, each arising from primary visual cortex (Goodale & Milner, 1992). According to this proposal, the ventral stream—projecting to the inferotemporal cortex—is responsible for the detailed perceptual representation of the objects in one's surroundings, whereas the dorsal stream—projecting to posterior parietal areas—provides the metrics for flexible moment-to-moment programming and control of visually guided actions, such as reaching and grasping.

Understanding one's surroundings for the purposes of perception and action, however, requires more than simply identifying and acting on objects in isolation. In reality, the visual world presents observers with cluttered and complex visual scenes that the visual system must parse and segment into discrete and meaningful objects. This process is clearly critical for perceiving objects (for relevant theories of perceptual parsing—particularly within the realm of numerical cognition—see, e.g., Allik & Tuulmets, 1991; Dehaene & Changeux, 1993), but is arguably just as important for successfully planning and executing visually guided actions directed at those objects. Historically, explanations of the two-visual-streams account have posited that the ventral stream plays the central role in scene parsing. It remains unclear, however,

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whether the ventral stream also parses visual arrays into objects for action, or whether this component of action planning is an extension of the dorsal stream's role in the visual control of action.

It has recently been shown that estimations of numerosity can be affected by the degree of apparent connectedness between adjacent objects in an array (Franconeri, Bemis, & Alvarez, 2009; He, Zhang, Zhou, & Chen, 2009). For example, when small circles within an array are connected by single lines to make pairs, observers underestimate the total number of objects in the display, despite being told to ignore any lines and focus only on the circles. In other words, connectedness disrupts the perceptual system's ability to effectively segment the display into discrete objects. Although the effect of connectedness is stronger with larger set sizes and a greater percentage of connected pairs, the illusion still persists in displays with as few as 6 to 10 objects and in displays with a single connected pair.

We tested whether scene segmentation for an action task involving rapid reaching would show the same sensitivity to connectedness as perception or would escape the effects of this illusion. The action task required subjects to initiate a speeded arm movement toward a display with multiple potential targets before one of the targets was cued for action (Chapman et al., 2010a, 2010b; Gallivan et al., 2011; Wood et al., 2011). Using this paradigm, we previously showed that when there were equal numbers of potential targets on the two sides of a display, participants aimed their initial trajectories toward a midpoint between the two sides. Furthermore, when the distribution of potential targets on the two sides was not equal (but each potential target had an equal probability of becoming the goal target), initial trajectories were biased toward the side of the display that contained a greater number of potential targets. This behavior maximizes the chances of success on the task because movements are directed toward the most probable location of the eventual goal, so that the "cost" of correcting movements in-flight is minimized (for a more thorough discussion, see Chapman et al., 2010a, 2010b; Gallivan et al., 2011; Wood et al., 2011). Because it provides a behavioral readout of rapid comparisons of target numerosity for motor planning, this paradigm is ideal for measuring object segmentation in action.

In the present study, we found that, despite a robust effect of the connectedness illusion on perception, there was no evidence of an effect of object connectedness on movement planning. Instead, participants planned and executed rapid reaches that reflected the true number of potential targets presented. This suggests that scene segmentation for perception and for action (specifically, movement planning) must rely on fundamentally different computations.

Method

Participants

A total of 30 participants (mean age = 22.5 years; 18 females, 12 males) were recruited from the undergraduate student population at The University of Western Ontario to take part in both a perceptual and a rapid-reaching task. All participants were right-handed, as determined by the Edinburgh handedness questionnaire (Oldfield, 1971), and had normal or corrected-to-normal vision. Informed consent was obtained in accordance with procedures approved by the university's Psychology Review Ethics Board. Seven participants were excluded from analysis because they failed to meet the timing constraints for performance on the tasks (for a description of the removal procedures, see Supplemental Analytical Procedures in the Supplemental Material available online). All participants received monetary compensation for their participation.

Apparatus and stimuli

Participants were seated comfortably at a table for the duration of the experiment. Target displays were presented on a 32-in. touch screen (NEC MultiSync LCD4020) and were controlled using custom MATLAB software (Version 6.5) and the Psychtoolbox (Version 2; Brainard, 1997; Pelli, 1997). For the perceptual task, voice onset was recorded using a microphone placed in front of the participant, and the participant's response was recorded by the experimenter. For the reaching task, trajectories were recorded (at 150 Hz) via an OPTOTRAK motion-tracking system (Northern Digital Inc., Waterloo, Ontario, Canada) using two infrared emitting diode (IRED) markers placed on the index finger of the right hand (one on the tip and the other directly behind it). Marker wires were held in place with a wristband to allow for unrestricted movement of the arm. There were also three stationary IREDs placed on the touch screen.

Target displays consisted of groups of two, four, or six small circles (1-cm radius, unfilled black circles on a white background), one group to the left and one to the right of fixation. We use the term *target configuration* to refer to the numbers of circles (potential targets) on the two sides in a given display. Neighboring circles on each side either were connected by a small line (1 cm) in sets of two or were disconnected. Disconnected circles had half of a connection line (0.5 cm) at one of the possible connection locations. The circles on each side of space were either all connected in pairs or all disconnected. Therefore, there were four levels of *connectedness*: circles on the left connected and those on the right disconnected, circles on the right connected and those on the left disconnected, circles on both sides connected, and circles on both sides disconnected (see

Fig. 1a). Some combinations of target configuration and connectedness were not included either because it was impossible to connect the circles with 1-cm lines or because the comparison between the left and right sides of the displays would not generate a reliable underestimation (see Supplemental Experimental Procedures and Fig. S3 in the Supplemental Material for further details concerning the stimuli and apparatus).

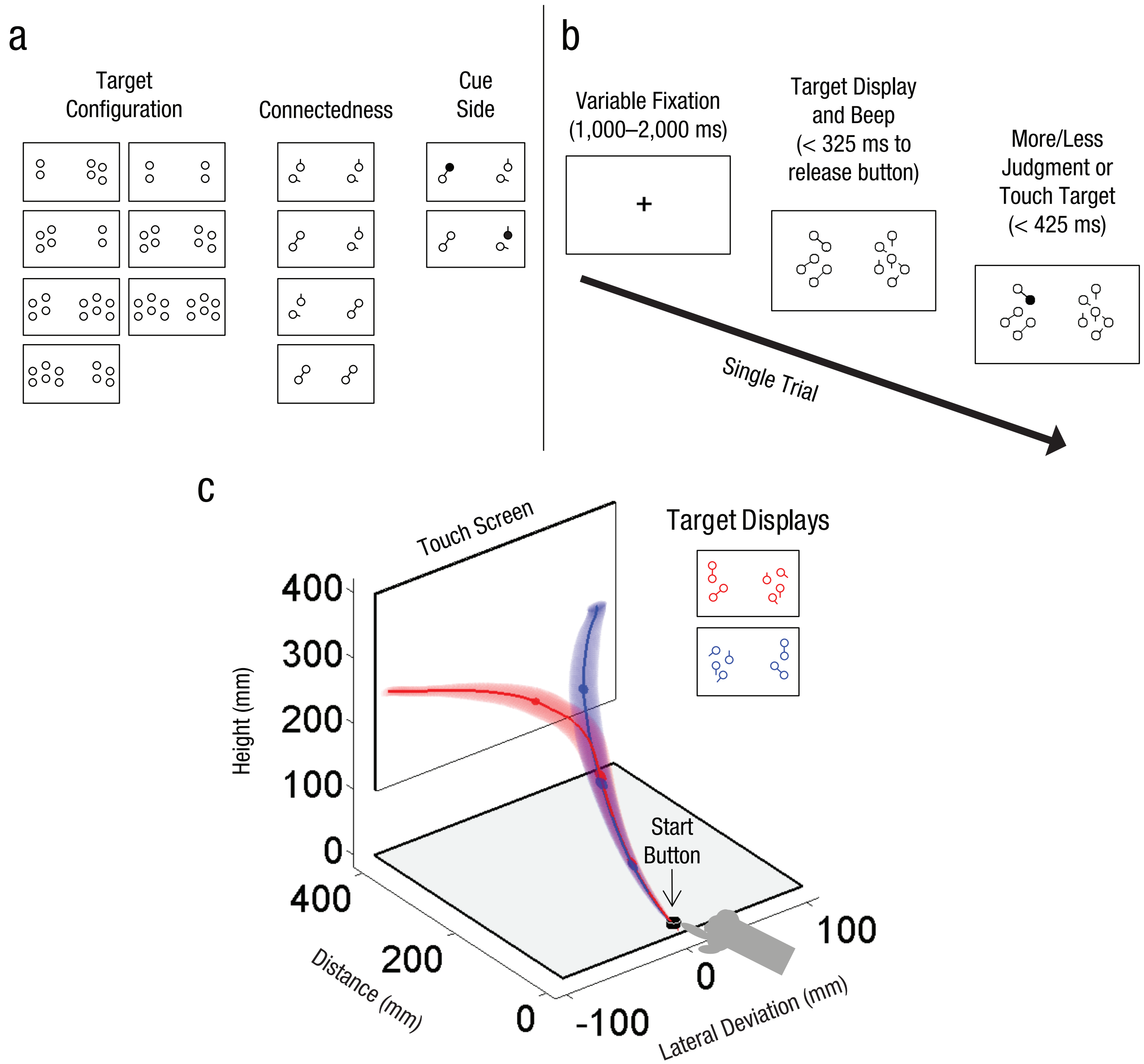

Fig. 1. Illustration of trial types, the trial sequence, and the general experimental setup. Trial types were defined by the combination of three factors (a): *target configuration*, the number of potential targets on each side of the display (seven levels); *connectedness*, whether circles on each side were connected or disconnected (four levels); and *cue side*, whether the filled-in goal target was on the left or right side. For both tasks, participants began each trial by fixating a cross for a variable time interval (1,000–2,000 ms) while holding their right index finger on the start button (b). The target display then replaced the fixation screen and was accompanied by an audio cue signaling participants to release the start button (within 325 ms). Upon release of the start button, one of the circles on the screen filled in black, and participants either indicated if the side with this target had a greater or smaller number of circles than the other side (perceptual task) or reached to touch the location of this target (reaching task). Responses were required within 425 ms. The three-dimensional view of the experimental setup (c; x = lateral deviation, y = reach distance, z = reach height) shows reach trajectories (color-coded) for two example target displays (at right), averaged across all participants. Data analysis was conducted on the lateral deviation. The displays are not drawn to scale.

Procedure

On the basis of work by Song and Nakayama (2008, 2009), we developed a rapid-reaching paradigm that requires participants to rapidly initiate a response before a goal target has been cued. We used the same displays for the perceptual task. Each trial began with the participant viewing a black fixation cross (centered on the touch screen) for a variable delay (1,000–2,000) while holding the right index finger on a start button (Fig. 1b). The fixation screen was then replaced by one of the possible target displays. At the same time, an audio cue (beep) signaled participants to release the start button within 325 ms. Immediately following release of the button, one of the targets in the display (the goal target) filled in black. Each potential target had an equal probability of filling in. The participant then had 425 ms to complete the task. In the perceptual task, the participant was required to indicate verbally if the side of the display on which the black circle appeared contained a greater number of circles ("more") or a smaller number of circles ("less") than the opposite side. For the reaching task, the participant had to rapidly reach toward the touch screen and put his or her fingertip on the cued target location. The goal target appeared an equal number of times on the two sides of the display, to control for the effects of any side bias (Chapman et al., 2010b). Crucially, participants were told to ignore all lines and focus only on the circles.

At the end of each trial, the touch screen displayed feedback indicating the participant's performance on that trial: "Too Early" (if the start button was released before 100 ms had elapsed), "Timed Out" (if the start button was not released within 325 ms), "Too Slow" (if the response—verbal onset for the perceptual task, touching the screen for the reaching task—was not given within 425 ms of releasing the start button), or "Good" (if the verbal response was given in the correct amount of time or the screen was touched within a 6-cm × 6-cm invisible box centered on the target circle within the correct amount of time). For the reaching task only, "Miss" was displayed if the participant touched the screen outside the 6-cm × 6-cm box. Trials deemed too early or timed out were aborted, and a target display did not appear on the screen. Participants were given the opportunity to learn and practice both tasks before data acquisition began. The perceptual task included a total of 280 trials divided into seven blocks, with five repetitions of each trial type (combination of target configuration, connectedness, and cue side) randomly distributed across the entire experiment. The reaching task included 680 trials divided into 17 blocks, with at least five repetitions of each trial type across the entire experiment.

Data analysis

Responses in the perceptual task were analyzed using a 7 (target configuration) × 4 (connectedness) × 2 (cue side) repeated measures analysis of variance (ANOVA; see Fig. 1a for a schematic example of the factors) on the number of "less" responses. Because each trial type occurred five times, the significance levels for the "more" responses could be inferred from the results of the ANOVA carried out on the "less" responses. We applied Greenhouse-Geisser corrections to the ANOVAs for which sphericity of the data could not be assumed (specifically, for the interaction between target configuration and connectedness, as well as for additional analyses included in the Supplemental Material). We applied Bonferroni corrections to all post hoc analyses to correct for multiple comparisons.

For analysis of performance in the rapid-reaching task, we used functional data-analysis techniques to fit mathematical functions and to spatially normalize the reach trajectories. We then used a functional ANOVA (Ramsay & Silverman, 2005) to evaluate trajectory differences between all conditions of interest in the lateral (x) dimension (see Fig. 1c). Functional ANOVA gives a functional F statistic that shows not only if, but also where and to what magnitude, a functionally defined measure differs across trial types. For further details on the analysis of the rapid-reaching task, see Supplemental Analytical Procedures in the Supplemental Material.

Results

In the perceptual task, participants indicated if the side of the display on which the goal target appeared had a greater or smaller number of circles than the other side. A repeated measures ANOVA revealed main effects for both connectedness, $F(3, 66) = 304.73$, $p < .001$, $\eta^2 = .44$, and target configuration, $F(6, 132) = 134.79$, $p < .001$, $\eta^2 = .14$. There was also a significant interaction between connectedness and target configuration, $F(8.36, 183.91) = 13.51$, $p < .001$, $\eta^2 = .19$, reflecting the fact that the connectedness illusion resulted in underestimation of the true number of targets in the array. Post hoc analyses revealed that when the number of circles was equal on the two sides of the display, the presence of connections on one side resulted in underestimation of the number of targets on that side (ps < .01). Similarly, for trials with unequal numbers of circles on the two sides, the presence of connections on the side with more circles resulted in underestimation of the number of circles on that side; in other words, participants treated these trials similarly to the way they treated baseline trials (i.e., trials on which the circles were connected on both sides of the display or disconnected on both sides of the display) in which the number of circles was equal on the two sides (*p*s < .01). Data from selected comparisons are shown in bar graphs in Figures 2 and 3, as well as in Figures S1 and S2 in the Supplemental Material. Post hoc results for all comparisons can be found in Table S1 in the Supplemental Material.

The analysis also revealed no effect of cue side ($p >$ .05), suggesting that the side on which the cue (and thus the reference for the response) was presented was not a factor in how participants responded. In summary, then, connectedness had a strong and reliable effect on perceptual estimations of numerosity; that is, the perceptual system was unable to overcome the effects of the illusion and effectively parse the individual objects—even though participants were given explicit instructions to concentrate on the objects and to ignore the connecting lines. (See Additional Data and Analyses in the Supplemental Material for an analysis of the timing measures for the perceptual task.)

In sharp contrast to the responses that participants made in the perceptual task, the initial trajectories of their movements in the rapid-reaching task, which reflect movement planning, were not influenced by the presence of the connecting lines. In other words, their reaching movements were completely unaffected by the connectedness illusion.

We established that this was the case by using functional ANOVAs to compare the trajectories across different target configurations and levels of connectedness. In Figures 2 and 3, we use significance bars to indicate the regions in which significant differences were found between the compared trajectories; the intensity of the shading at each specific point denotes the magnitude of the difference at that point (as captured by the *p* value of the comparison). The absence of a significance bar indicates the lack of any significant differences between trajectories from the start point to the goal target.

The effects of the different target configurations and levels of connectedness on reach trajectories are best seen by viewing the movements in their entirety (see Figs. 2 and 3). When the number of circles was equal on the two sides of the display, reaches extended down the middle and were corrected after the goal location was revealed. When the numbers on the two sides were not equal, however, reaches were biased toward the side where there was a greater number of circles. These effects can be seen in the plots for baseline trials in the top and bottom rows of Figures 2 and 3. The figures also show, however, that the presence of connectedness on only one side of the display had absolutely no effect on trajectories (middle rows in Figs. 2 and 3). That is, despite the presence of connections on the left or right side, participants behaved as they did on baseline trials, and their trajectories were influenced only by the actual number of potential targets. (See Figs. S1 and S2 in the Supplemental Material for results when the goal target was on the right side of the display.)

Although we have shown results only for those displays that correspond to the arrays we employed in previous studies (Chapman et al., 2010a, 2010b; Gallivan et al., 2011; Wood et al., 2011), it is important to note that object connectedness also had no effect on reaches on trials with larger numbers of potential targets. In summary, despite a robust effect of object connectedness on perceptual comparisons, participants were able to rapidly plan and execute strategic reaches on the basis of the true number of potential targets, even when the displays included connections. This suggests that the computations underlying object segmentation in rapid action planning are quite different from those responsible for the parsing of visual scenes in perception. For analysis of kinematic measures, see Additional Data and Analyses in the Supplemental Material.

Discussion

This study was aimed at determining if the process of parsing cluttered visual information into discrete identifiable objects differs between visual perception and rapid visually guided movement planning. Specifically, we investigated how the planning of rapid reach movements is affected by perturbations of visual target information that are known to influence the segmentation of objects in perception.

We applied a pictorial illusion that involves connecting objects into pairs using single lines. To date, this illusion has been applied only to perceptual processes and has been found to result in underestimation of the total number of objects in a set (Franconeri et al., 2009; He et al., 2009). In the current study, we confirmed the effect on perception: Participants consistently and reliably underestimated the number of objects when they were connected into pairs. The primary aim of the study, however, was to determine how the visuomotor system segments scenes into separate objects; therefore, we had participants make speeded reaches toward target displays with connected pairs. The goal location of each reach was not made apparent until the onset of the movement, and therefore movement planning was based on the initial display. We found that there was no effect of the illusion on reach trajectories. Instead, the planning of the reaches was based on the true number of potential targets. For example, when there were no connected pairs, reach trajectories were biased toward the averaged lateral spatial location of the potential targets across the display. Remarkably, participants behaved exactly the same way when potential targets were connected. In other words,

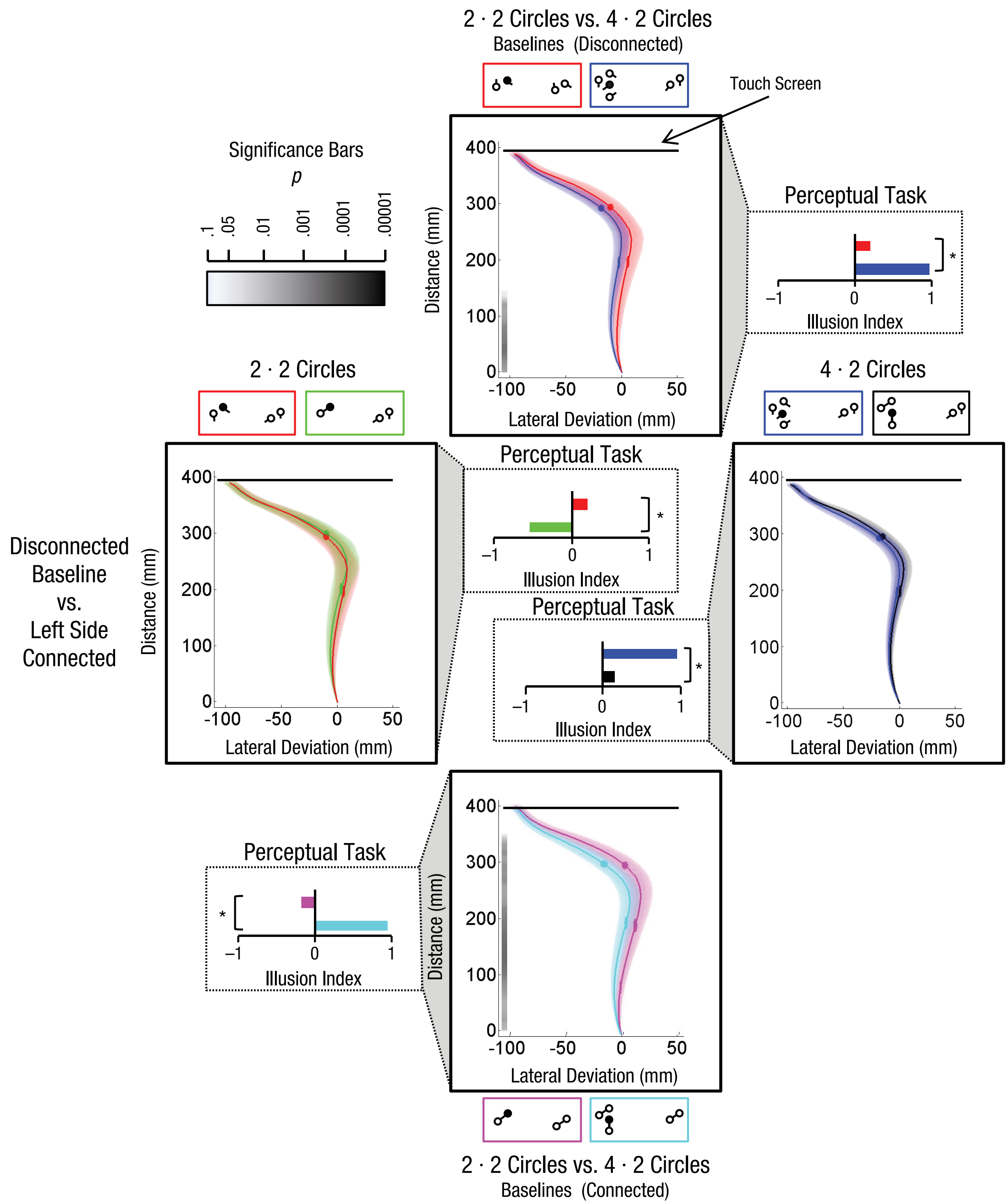

Fig. 2. Results from the rapid-reaching and perceptual tasks for trials on which the goal target appeared on the left: Part I. The graphs in this figure show results for trials on which there were either two or four circles on the left side of the display and two circles on the right side of the display. Averaged reach trajectories as viewed from above are presented for baseline trials (i.e., trials on which the circles were disconnected on both sides of the display or connected on both sides of the display) and for trials on which circles on the left side of the display only were connected. Example displays (not drawn to scale) are shown for each plot. In each example, a goal target is filled in for purposes of illustration, but the results shown are collapsed across all possible endpoints on the left side of the display. The solid black horizontal line in each plot indicates the location of the touch screen. Shading around each trajectory represents the average standard error across subjects. The colored ovals along each trajectory indicate two temporal properties of the reach: First, they are placed at 25%, 50%, and 75% of the reach distance to show how the reach evolved in time; second, the dimensions of each oval are proportional to the velocity in the x and y dimensions at that point in the trajectory. For points at which the compared trajectories differed significantly, the degree of significance is indicated by the gray-scale bar to the left of the plot. The bar graphs show corresponding performance on the perceptual task, averaged across all participants. Performance was assessed with the illusion index, calculated as follows: (number of "more" responses − number of "less" responses)/(number of "more" responses + number of "less" responses). Thus, a value of −1 indicates that all responses were "less" responses, a value of 1 indicates that all responses were "more" responses, and a value of 0 indicates equal proportions of "more" and "less" responses. A value of 0, then, does not necessarily indicate the absence of the illusion; rather, it indicates that participants believed, overall, that there were equal numbers of targets on the two sides. Asterisks indicate a significant difference between conditions ($p \leq .01$, based on post hoc analyses). See Figure S1 in the Supplemental Material for results when the goal target appeared on the right side of the display.

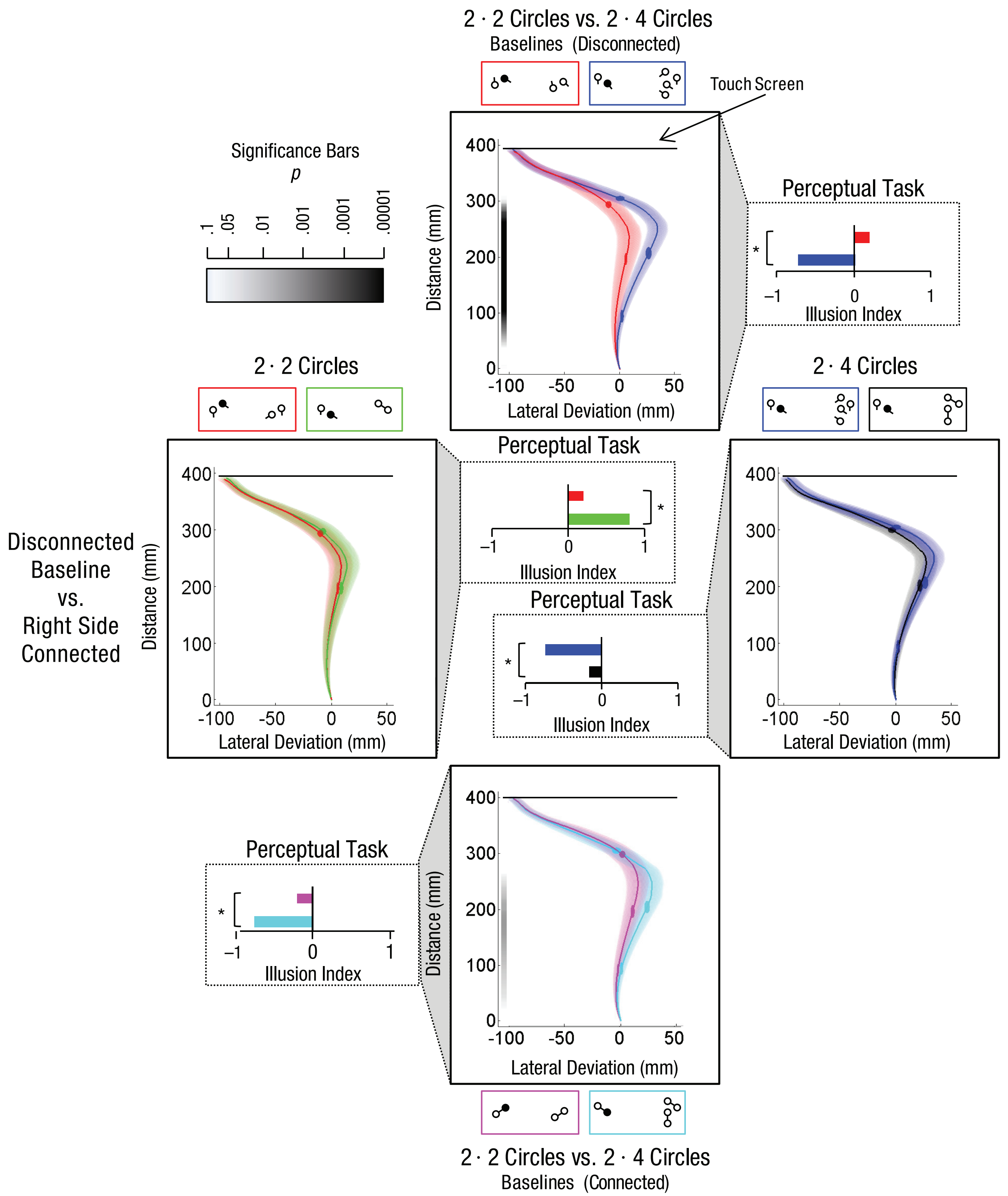

Fig. 3. Results from the rapid-reaching and perceptual tasks for trials on which the goal target appeared on the left: Part II. The graphs in this figure show results for trials on which there were two circles on the left side of the display and either two or four circles on the right side of the display. Averaged reach trajectories as viewed from above are presented for baseline trials (i.e., trials on which the circles were disconnected on both sides of the display or connected on both sides of the display) and for trials on which circles on the right side of the display only were connected. The bar graphs show corresponding performance on the perceptual task, averaged across all participants. See Figure 2 for details. See also Figure S2 in the Supplemental Material for results when the goal target appeared on the right side of the display.

the visuomotor system was able to effectively parse the individual objects, and then plan and execute the reaches accordingly. This means that the visuomotor system must either have access to alternate sources of visual information or deal with the information in a way that is quite different from the perceptual processing that creates the illusion and influences how the objects are parsed perceptually.

In fact, the idea of separate segmentation mechanisms for perception and action is consistent with the basic tenets of the two-visual-streams theory (Goodale & Milner, 1992). This theory proposes that visual input to the brain is processed along two separate but interacting cortical streams: The ventral stream is responsible for vision-for-perception, and the dorsal stream is responsible for vision-for-action. By definition, the ventral stream is responsible for extracting lasting and detailed information about objects; it often employs top-down processes to make sense of the environment. The dorsal stream, in contrast, must make real-time computations and have access to accurate object information in order for the observer to interact appropriately with the environment at any given moment.

Two-visual-streams theory, however, is still incomplete when it comes to understanding object segmentation for purposes of movement planning. Although the two streams certainly interact to some extent (especially considering the role of the ventral stream in goal identification), using functional analyses allowed us to show that the perceptual bias in scene segmentation induced by object connectedness did not influence visuomotor processes at any stage of movement, from planning to execution to on-line control—a finding that contradicts previous work (e.g., Crajé, van der Kamp, & Steenbergen, 2008; Franz, 2003; Franz, Gegenfurtner, Bülthoff, & Fahle, 2000; Glover, 2002; Glover, Rosenbaum, Graham, & Dixon, 2004; Mendoza, Hansen, Glazebrook, Keetch, & Elliot, 2005). Instead, our results indicate (at least as far as segmentation of the scene into separate objects is concerned) that the visuomotor system plans movements accurately very early on, despite the fact that goal selection may be based on a biased perceptual representation. The fact that the visuomotor system could effectively parse the objects suggests that the movement to each of the potential targets was somehow computed independently from perceptual selection. This strongly supports the idea that each potential target was being prepared for action (Cisek & Kalaska, 2002, 2005; Pastor-Bernier & Cisek, 2011) and that the planning of the movement did not simply rely on information based on a perceptual representation of the goal, even though these processes must operate in parallel.

According to the two-visual-streams literature, the dorsal stream is engaged only when one is actively attending to and acting on a goal object. One could argue, then, that the processes underlying the strategic reaching behavior in the current study must not have relied on dorsal-stream mechanisms because no single target for action was identified when the movement was initiated. It is possible, however, that the dorsal premotor neurons that have been shown to encode the spatial locations of multiple potential targets (Cisek & Kalaska, 2002, 2005; Pastor-Bernier & Cisek, 2011) communicate with the dorsal stream when an action toward those targets is initiated. That said, it is true that almost all imaging and patient studies of the dorsal stream's role in the control of action have used paradigms in which only a single goal object is presented. Future research needs to address how the dorsal stream handles situations in which there are multiple potential targets for action.

The segmentation of a scene into separate objects—especially for determining numerosity—has been thoroughly studied in perception (for examples of different theories of counting and estimation, see Allik & Tuulmets, 1991; Burr & Ross, 2008; Dehaene & Cohen, 1994; Durgin, 2008; Trick & Pylyshyn, 1993), but has been studied to a much lesser extent in action. A particularly relevant process in perceptual numerosity judgments is subitization, the rapid and accurate enumeration of small set sizes (the exact boundary of this range is debated but thought to be around 3 or 4; Kaufman, Lord, Reese, & Volkmann, 1949). We recently showed that this same capacity limit may apply to the enumeration of targets in rapid motor planning (Gallivan et al., 2011). One concern we had when planning the current experiment, then, was whether or not the pictorial illusion would influence performance within the subitizing range. Because subitizing is thought to be controlled by preattentive processes, researchers have assumed that it cannot be easily compromised or disrupted (Trick & Pylyshyn, 1994). More recent research, however, has suggested that subitizing is not preattentive and can indeed be disrupted by attentional demands (Burr, Turi, & Anobile, 2010; Vetter, Butterworth, & Bahrami, 2008). In other words, attentionally demanding tasks disrupt subitizing, and participants revert to other ways of estimating number, such as counting (Burr et al, 2010). Given these findings, it is entirely possible that the same variables that affect counting can still operate in the subitizing range, but perhaps with less force and precision, and only in attention-demanding tasks.

The fact that we found a robust effect of connectedness on perception in the subitizing range suggests that perhaps our experiment was so attentionally demanding that the illusion could be effective even with small set sizes. Nevertheless, the fact that the attentional demands of the perceptual and reaching tasks were quite similar suggests that the absence of an effect of the illusion on rapid reaching movements was due to differences in the way the objects in the scene were segmented.

In addition to testing whether differential segmentation mechanisms underlie visual perception and rapid movement planning, the current experiment allowed us to address criticisms of the use of pictorial illusions to compare processes underlying perception and action in general. One particular criticism is that task demands are not equated. For example, it has been suggested that actions are immune to the effects of illusions simply because the motor response does not require processing anything other than the target, whereas perception involves processing the entire display (Franz et al., 2000). Our paradigm, however, directly addressed this criticism because participants were required to view and process the entire display in both tasks; the final target remained ambiguous until the initiation of a response. In the perceptual task, all potential targets had to be enumerated in order for participants to compare magnitude. Similarly, in the reaching task, all potential targets had to be represented for action because each location had an equal likelihood of becoming the goal target. Therefore, not only were our tasks matched on general demands (e.g., timing constraints, button release, target-cue onset), but the response demands for both tasks required the processing of the entire display.

In summary, our results provide support for differential mechanisms underlying scene segmentation in perception and action. Whereas perceptual comparisons of magnitude were dramatically influenced by manipulations of object grouping, the visuomotor system was able to effectively parse the individual objects and accurately plan, execute, and control rapid reaching movements to multiple potential targets. These results are especially compelling considering that initial movement planning may be based on a perceptual representation of the goal. The segmentation of a scene into separate objects must be a process of particular importance to movement planning if the motor system is able to effectively bypass the biases of perception in situations in which rapid planning and execution is paramount.

Author Contributions

J. L. Milne, C. S. Chapman, J. P. Gallivan, and D. K. Wood designed the experiment. J. L. Milne collected and analyzed the data with the use of code written by C. S. Chapman. J. L. Milne prepared the manuscript. J. C. Culham and M. A. Goodale supervised the project and edited the manuscript. All authors approved the final version of the manuscript for submission.

Declaration of Conflicting Interests

The authors declared that they had no conflicts of interest with respect to their authorship or the publication of this article.

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Supplemental Material

Additional supporting information may be found at http://pss.sagepub.com/content/by/supplemental-data

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