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Attentional Signatures of Perception: Multiple Object Tracking Reveals the Automaticity of Contour Interpolation

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Multiple object tracking (MOT) is an attentional task wherein observers attempt to track multiple targets among moving distractors. Contour interpolation is a perceptual process that fills-in nonvisible edges on the basis of how surrounding edges (inducers) are spatiotemporally related. In five experiments, we explored the automaticity of interpolation through its influences on tracking. We found that (1) when the edges of targets and distractors jointly formed dynamic illusory or occluded contours, tracking accuracy worsened; (2) when interpolation bound all four targets together, performance improved; (3) when interpolation strength was weakened (by altering the size or relative orientation of inducing edges), tracking effects disappeared; and (4) real and interpolated contours influenced tracking comparably, except that real contours could more effectively shift attention toward distractors. These results suggest that interpolation's characteristics—and, in particular, its automaticity—can be revealed through its attentional influences or "signatures" within tracking. Our results also imply that relatively detailed object representations are formed in parallel, and that such representations can affect tracking when they become relevant to scene segmentation.

Keywords: contour interpolation, illusory contours, occluded contours, multiple object tracking, attention

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A glance up from this paper will reveal that most objects in the field of view are only partly visible. The visual system is thus faced with the daunting task of having to determine which visible fragments belong to the same object. Central to this reconstruction is contour interpolation, which connects fragments on the basis of how their edges are spatiotemporally related (Kellman, Garrigan, & Shipley, 2005; Kellman & Shipley, 1991; Palmer, Kellman, & Shipley, 2006). Although there are other means for creating order in the visual array, interpolation stands out as one of the most important. It extracts properties like object shape and cardinality, as when a canonical Kanizsa square is viewed as one square on top of four circles, rather than four disconnected wedged-circles (Kanizsa, 1979). It also determines whether objects persist, as when an object moving behind foliage is observed as a single enduring thing rather than a series of small objects that go in and out of existence (Grossberg, 1998; Keane, Lu, & Kellman, 2007; Palmer et al., 2006).

Given the role of interpolation in recovering fundamental scene characteristics, it is not surprising that the process is early in every sense of the term. It is ontogenetically early in that human infants in the first weeks of life can interpolate (Johnson & Aslin, 1995; Kellman & Spelke, 1983; Valenza, Leo, Gava, & Simion, 2006). It is phylogenetically primitive in that creatures such as owls, bees, mice, and fish engage in perceptual completion (Kanizsa, Renzi, Conti, Compostela, & Guerani, 1993; Nieder, 2002; Sovrano & Bisazza, 2007). Finally, the earliest visual processing centers (V2 and V1) are involved in interpolation (e.g., Peterhans, von Der Heydt, & Baumgartner, 1984; Sugita, 1999; for a review of fMRI findings, see Seghier & Vuilleumeir, 2006), although later areas (e.g., LOC) are also incorporated (Kellman et al., 2005; Murray, Foxe, Javitt, & Foxe, 2004).

Interpolation as an Attention-Driving Process? Or Vice Versa?

Because interpolation is an early process that is crucial for ordinary scene perception, one would think that it should strongly guide attention. Evidence from a visual search paradigm supports this view. He and Nakayama (1992) had observers search for an L target among a set of reversed L distractors, where both kinds of tokens bordered the sides of adjacent squares. When the squares were stereoscopically positioned in front of the L's, the targets and distractors themselves appeared as amodally completed squares, and search slopes became steep (suggesting a serial search process). When the target and distractor L's were placed stereoscopically in front of their adjacent squares, targets and distrac-

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tors no longer were equated through completion, and search slopes became shallow (suggesting a greater involvement of parallel processing). Even though interpolation was always objectively irrelevant to the search, interpolation automatically created shapes, which in turn made it more difficult to rapidly focus on the target. Similar outcomes were obtained in pictorial displays (Rensink & Enns, 1998), in displays with illusory contours (Davis & Driver, 1998; though, see Li, Cave, & Wolfe, 2008), and in electrophysiological studies (Senkowski, Röttger, Grimm, Foxe, & Herrmann, 2005; for a review, see Davis & Driver, 2003).

Object priming studies corroborate the foregoing. When observers were shown a bar, the middle portion of which was modally or amodally completed, and when one side of that bar was momentarily brightened, items appearing on the other end of the bar were given attentional priority relative to equidistant locations not on the bar (Moore, Yantis, & Vaughn, 1998; for physiological evidence, see Martinez, Ramanathan, Foxe, Javitt, & Hillyard, 2007; Martinez, Teder-Salejarvi, & Hillyard, 2007).

Whereas the locus of attention depends on interpolation, there are mixed reports as to whether the converse is true. Some studies suggest little, if any, dependency. Patients who were unable to attend to items within their left hemifield were nevertheless able to utilize inducers within the neglected field for the purposes of interpolation (Vuilleumier, Valenza, & Landis, 2001; see also, Mattingley, Davis, & Driver, 1997; Vuillemier & Landis, 1998). In a neurophysiological study, neurons in areas V1 and V2 exhibited enhanced firing when presented with interpolated figures, and this response occurred even when those figures were not attended (Marcus & van Essen, 2002). Computational models, based on bottom-up, local-grouping mechanisms, can accurately predict human performance on certain interpolation tasks (Geisler, Perry, Super, & Gallogy, 2001; Kalar, Garrigan, Wickens, Hilger, & Kellman, 2010).

Other studies indicate that attention can at least modulate interpolation strength. Montaser-Kouhsari and Rajimehr (2006) showed that the degree to which observers became adapted to illusory lines depended on whether the lines were attended. In the aforementioned single unit study, V2 neurons exhibited weak facilitation when interpolated figures were attended (Marcus & van Essen, 2002). Finally, and perhaps most strikingly, when two Gabor patches collinearly flanked a central, low-contrast Gabor target, detection thresholds for the target decreased, but only if the patches were attended (Freeman, Sagi, & Driver, 2001). These findings are all consistent with others that highlight the importance of attention on early visual processing (e.g., Ito & Gilbert, 1999; Motter, 1993; Papathomas, Gorea, Feher, & Conway, 1999; Roelfsema, Lamme, & Spekriejse, 1998).

Method and Motivations

In the current study, we investigated whether interpolation characteristics—and in particular, its automaticity—could be revealed via multiple object tracking (MOT).[1] Originally introduced by Pylyshyn and Storm (1988), MOT involves attending to a subset of initially stationary visual objects, following the members of that (target) subset for some duration as all objects on the screen independently move, and then reidentifying the targets with a mouse pointer at the end of a trial. The paradigm has yielded over a hundred papers to date and has been invoked to explore a range of issues on object perception, including how we attribute properties to objects (Bullot & Droulez, 2008), group objects (Yantis, 1992), and recover objects that momentarily disappear (e.g., Keane & Pylyshyn, 2006). The paradigm's popularity owes to the robust effects that it produces, its relevance to normal seeing, and the capacity being interesting in its own right (Scholl, 2009).

The specific variation of MOT that we developed to explore interpolation is multiple vertex tracking (MVT). MVT resembles ordinary MOT in that eight moving disks are tracked, but differs in that, first, one target and one distractor continuously orbit a central point (barycenter) in each quadrant, and, second, disks appear as sectored circles for most of the movement phase (see Figure 1). These sectors are positioned and oriented so that targets can occasionally interpolate with one another or with distractors, potentially improving or degrading tracking performance, respectively.

There are a number of reasons to use MVT. One is that it is methodologically novel. Tracking is typically employed as a means for studying high-level vision, but here we show that interpolation can be revealed through its attentional influences, which can be considered as *signatures* or correlates of the underlying perceptual process. Studying interpolation via its effects on tracking also helps to place the large literature on interpolation in a functional/ecological context: The stimuli are presented over the course of seconds rather than fractions of a second; participants act on (rather than merely judge) the stimuli; and the interpolating figures are continuously in flux, which may be more reflective of how they are actually witnessed in ordinary contexts.

MVT can also potentially show interpolation effects that cannot be revealed in other ways. It can show, for example, that interpolation occurs with items that participants know beforehand that they must ignore (Flombaum, Scholl, & Pylyshyn, 2008; Pylyshyn, 2006). This stands in contrast to visual search, where participants do not know in advance what regions to ignore, and to object priming, where participants attend to all inducers before target onset.

Finally, although our main goal was to investigate interpolation's automaticity, MVT can serve to adjudicate between inconsistent claims in the interpolation and attention literatures. On the one hand, interpolation is thought to automatically guide attention, as discussed. On the other hand, scene representation, and object tracking, in particular, are thought to *not* depend on the featural properties of tracked objects (e.g., shape or orientation; Pylyshyn, 2003; Rensink, 2000; Scholl, 2007). For example, one study has shown that features of about 2 objects (Horowitz, Klieger, Fencsik, Yang, Alvarez, & Wolfe, 2007) can be utilized when the task requires tracking on the basis of appearance. No study (that we know of) has shown similar

[1] In this paper, we operate on the premise that if attentional allocation depends on interpolation, and if this dependence obtains regardless of the wishes of the observer, then attention reveals the automaticity of interpolation. We acknowledge, however, that a process can be both automatic and irrelevant to attention.

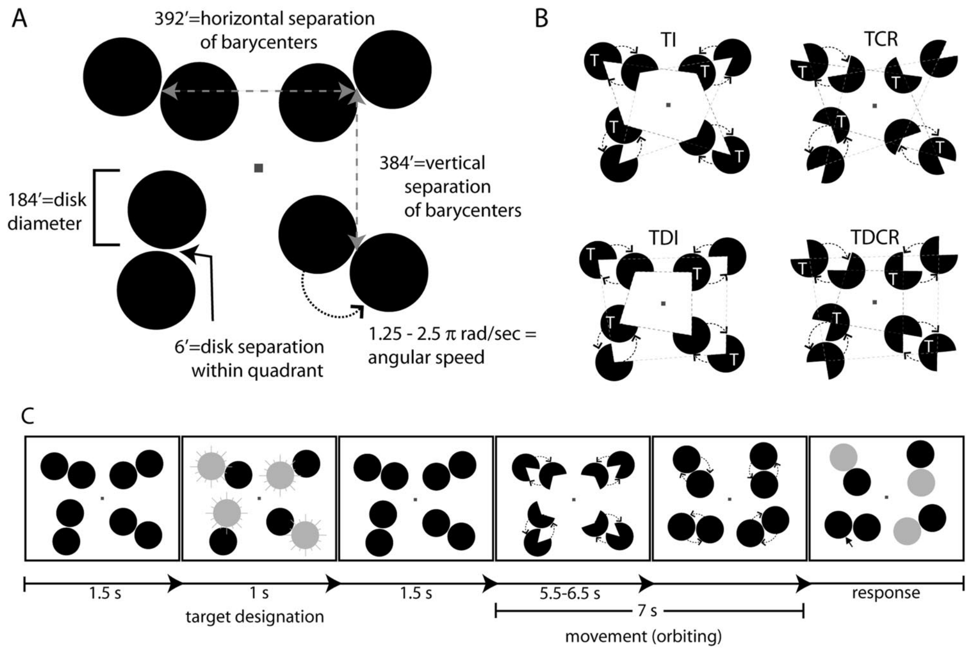

Figure 1. Stimuli and trial sequence in Experiment 1. (A) In all trials, a pair of black disks appeared within each quadrant of a white screen. Disks within a quadrant orbited about a central point (barycenter) at a random speed and direction (clockwise or not). Speed varied between, not within, quadrants. (B) During a portion of the trial, white notches (sectors) appeared on all disks. The orientation and angle of sectors defined the four conditions. All conditions involved collinear edge relations between objects in adjacent quadrants (depicted by dotted lines). These edges could interpolate (TI and TDI) or not (TCR and TDCR). Targets ("T"s) could be grouped together (TI and TCR) or with distractors (TCI and TDCR). (C) In each trial, one disk in each quadrant blinked, denoting it as a target. When movement began, white sectors appeared over all disks (here, the TI condition is shown). Disks orbited for 5.5 s. At a random point within the following second, sectors disappeared. After a total of 7 s of orbiting, all objects stopped, and participants attempted to identify the targets with a mouse. Stimuli and trial sequences in the remaining experiments were variations of those depicted here.

effects when appearance is irrelevant to the task instructions. Because interpolation strongly depends on features like orientation, alignment, and junction structure (e.g., Kellman et al., 2005; Kellman & Shipley, 1991; Rubin, 2000), either parallel tracking is indifferent to object appearance and hence interpolation; or it is automatically sensitive to interpolation by being sensitive to features. The experiments in the current study will decide which is correct.

Experiments and Predictions

Automatic effects of interpolation on tracking were explored in five experiments. All experiments were a variation of Experiment 1, which itself had four conditions. In the target interpolate (TI) condition, all targets transformed into sectored disks that were oriented into a single illusory quadrilateral, and the four distractors did the same. Each quadrilateral continuously morphed in shape, as a result of the different speeds assigned to each quadrant pair. The target distractor interpolate condition (TDI) was just like the TI condition, except that two opposite corners of each quadrilateral were targets. The target contour relation (TCR) and target distractor contour relation (TDCR) served as controls; they were just like the TI and TDI, respectively, except that the sectored disks were reflected outward so that angular relations of contours were preserved, but the elements prohibited boundary completion. Whereas objects in adjacent quadrants could group through a collinear edge relation in all four conditions, only in the TI and TDI conditions could those edges form illusory contours.[2]

There were three predictions for Experiment 1. First, when all targets shared a collinear contour relation, tracking would be better when those contours induced interpolation. The rationale was that relatable edges (edges that support interpolation), but not other sorts of edges, promote automatic grouping (Kellman & Shipley, 1991). This grouping can effectively reduce the number of objects to track, which, in turn, would improve performance (Allen, McGeorge, Pearson, & Milne, 2004; Yantis, 1992). The second prediction was that when the edge relations of targets and distractors failed to induce interpolation (as in the TCR and TDCR), such edges would be irrelevant to tracking. The appearance of objects generally plays little or no

[2] The demo movies (in supplementary materials) clearly reveal the effects described and are thus highly recommended. See also www.briankeane.org

role in tracking (Horowitz et al., 2007; Scholl, 2007), and so the same was expected in the control conditions. The third prediction was that when targets and distractors formed illusory contours with one another, tracking performance would deteriorate relative to the TDCR condition. The rationale here was that when targets and distractors automatically group, they would become more confusable and harder to track (Scholl, Pylyshyn, & Feldman 2001; Yantis, 1992), but only edge relations that induce interpolation would cause such grouping. Since contour integration can be attentionally abolished in at least some cases (Freeman et al., 2001) and because there is no evidence (that we know of) that indicates that features of distractors can be utilized in tracking (as would be required for them to interpolate), this last prediction was the most speculative of the three.

Experiment 2 was just like Experiment 1, except that it considered to what extent *occluded* (or amodal) contours automatically drive attention. An amodal appearance was approximated by adding thin (1 arcmin) rings around all disks in all conditions. Although this was not an ideal amodal display in that it contained potential cue conflicts relating to the depth assignment of surfaces (as discussed below), previous studies successfully employed it (Gold, Murray, Bennett, & Sekuler, 2000; Lee & Nguyen, 2001; Murray et al., 2004; Ringach & Shapley, 1996), and so was expected to reveal amodal effects. We predicted qualitatively the same results as Experiment 1. Predictions were motivated partly because modal and amodal completion generate similar (if not identical): object-based priming (Moore, Yantis, & Vaughn, 1998), shape discrimination precision (Kellman et al., 2005; Ringach & Shapley, 1996; though see, Zhou, Tjan, Zhou, & Liu, 2008), alignment detection precision (Palmer, Kellman, & Shipley, 2006), and filling-in (Gold et al., 2000; though see Davis & Driver, 2003). The processes also invoke similar responses in ERP and single unit recording studies (Lee & Nguyen, 2001; Murray, Foxe, Javitt, & Foxe, 2004). Conceptual considerations further suggest that—at least in some cases—modal and amodal completion are produced by a single mechanism (Kellman, Garrigan, Shipley, & Keane, 2007; Kellman, Yin, & Shipley, 1998).

The primary goal of Experiment 3 and Experiment 4 was to show that interpolation effects on tracking could be modulated in a bottom-up, stimulus-driven fashion. In Experiment 3, the modulation was in the form of support ratio (Petry & Meyer, 1987; Shipley & Kellman, 1992). In Experiment 4, inducer rotation angle altered tracking effects. In both experiments, only versions of the TI and TDI conditions were examined, and the prediction was that as interpolation strength decreased, differences between TI and TDI would decrease as well. These two experiments were also set up to distinguish more decisively whether results depended on interpolation or generic grouping strategies.

Experiment 5 aimed to provide upper and lower limits on the extent to which contours can affect behavior in our kind of task. This last experiment involved the TI and TDI conditions, as before, and two otherwise identical conditions that incorporated luminance-defined (real) contours. Here, we had no specific predictions other than that the two kinds of contours would exercise similar effects on tracking (e.g., Ringach & Shapley, 1996). This last experiment was also expected to elucidate why only modest benefits were achieved in the TI conditions of the prior experiments.

Experiment 1: Automatic Effects of Illusory (Modal) Contours on Tracking

The purpose of Experiment 1 was to reveal the automaticity of illusory contour formation via tracking. The predictions were that: (1) when targets maintained a collinear edge relation, such a relation would help most when those edges induced interpolation; (2) when contour relations did not support interpolation, they would be irrelevant to tracking; and, more speculatively, (3) when targets and distractors maintained collinear edge relations with one another, interpolation would lower performance.

Method

Participants. Sixteen undergraduate students of University of California, Los Angeles participated in a ~45 minute session for class credit. All participants had normal or corrected-to-normal vision. One additional participant, whose overall tracking performance fell at 3 *SD*s below the mean, was excluded from the analysis.

Apparatus. The displays were presented on one of three 16 × 12" ViewSonic Graphic Series G225f computer monitors, each with a resolution of 1,024 × 768 pixels and a refresh rate of 75 Hz. Participants viewed the displays at 54 in from the monitor, so that each pixel subtended a viewing angle of 1 arcmin. Black, gray, and white roughly corresponded to luminance values of <1, 50, and 100 cd/m^2, respectively.

Stimuli. Throughout each trial, there was a red fixation square (side = 20 arcmin) in the middle of a white screen. At the beginning of a trial, exactly two black disks (radius = 92 arcmin) appeared quasi-randomly within each quadrant of the screen. The centers of disks within a quadrant were separated by 190 arcmin (3.2 deg) (see Figure 1A). Barycenters of the four quadrants formed a fixed rectangle that spanned 392 arcmin (6.5 deg) along the horizontal dimension, and 384 arcmin (6.4 deg) along the vertical dimension. Exactly one disk in a quadrant was designated a target.

During the motion phase, objects within a quadrant circularly orbited with equal speed and in the same direction about their barycenter. Each quadrant pair was randomly assigned a clockwise or counterclockwise direction and a random speed ranging between 1.25 and 2.5[1] πrad/s (or between 3 and 6 deg of angular rotation per frame). As objects began to move, a sector of each disk became the same color as the background (white). The angular size and orientation of a disk's sector continuously changed depending on the condition and the relative locations of the other disks in the display.

The four conditions were differentiated in terms of how target and distractor sectors were angled and oriented (see Figure 1B). In the target interpolate (TI) condition, the sectors of the targets could form illusory edges of one quadrilateral, and the sectors of the four distractors could form edges of a second illusory quadrilateral. In other words, for each disk set (the target set, and distractor set) the angles of the sectors were drawn as if the vertices of a white quadrilateral were centered in each disk. The TDI condition was the same as the TI condition, except that two targets always appeared in opposite corners of each quadrilateral, so that each target interpolated with two distractors and each distractor, with two targets. Because the TI and TDI conditions could contain two morphing illusory quadrilaterals during the motion phase of a trial, the conditions were indistinguishable after target designation.

The target contour relation (TCR) and target distractor contour relation (TDCR) conditions served as controls, and were the same as the TI and TDI condition, respectively, except that the sectors were positioned opposite to the interior angles (see Figure 1B). This set-up at once prohibited interpolation and ensured that the angular relations of sectors were the same between the TI and TCR, and also between the TDI and TDCR conditions.

Procedure and design. Participants were seated with a chinrest in a darkened room. Instructions appeared on the introductory screen and participants were informed that they would need to track four initially blinked moving disks among four moving distractors. It was emphasized that they should try their best to keep fixated on the red fixation square throughout each trial. There was no mention of illusory figures, quadrilaterals, or contour interpolation in the instructions or in the recruitment phase of the experiment. After reading the instructions, participants pressed the space bar to begin.

On each trial, objects appeared as stationary disks for 1.5 s (see Figure 1C). Then, one randomly chosen object from each quadrant turned gray for 200 ms, and turned black for 200 ms. This blinking sequence, which designated an object as a target, repeated a total of five times. Exactly 1.5 s after the blinking ended, white sectors appeared on all disks, and the display remained static for another 80 ms thereafter. This brief pause was necessary to avoid a "flash-jump" effect, where objects appear to jump ahead when they abruptly move and change form at the same time (Eagleman & Sejnowski, 2007). Objects then orbited within each quadrant for 5.5 s. At a random point within the following second, all objects simultaneously transformed back into undifferentiated disks. After 7 s of motion, all objects stopped and participants attempted to identify the targets with a mouse. Upon entering their four responses, participants were told how many they got right on that trial, and the cumulative percent correct for their current block. A space-bar button-press began the subsequent trial.

Each experiment consisted of one target grouping block, which contained the TI and TCR conditions, and one target-distractor grouping block, which contained the TDI and TDCR conditions.[3] Each condition consisted of 40 trials. Trial types appeared randomly and with equal frequency within the two blocks, and blocks were counterbalanced across participants. When the experiment ended, participants completed a short questionnaire about what they saw in the experiment (besides sectored disks) and what strategies they used.

Results

Data for Experiment 1 were submitted to a 4 (quadrant) × 2 (grouping) × 2 (interpolation) within-subjects analysis of variance (ANOVA). Results are shown in Figure 2. There was a main effect of quadrant, $F(1, 15) = 3.08$, $p < .04$, $\eta_p^2 = 0.171$, in that performance overall was better in the upper left quadrant and worst

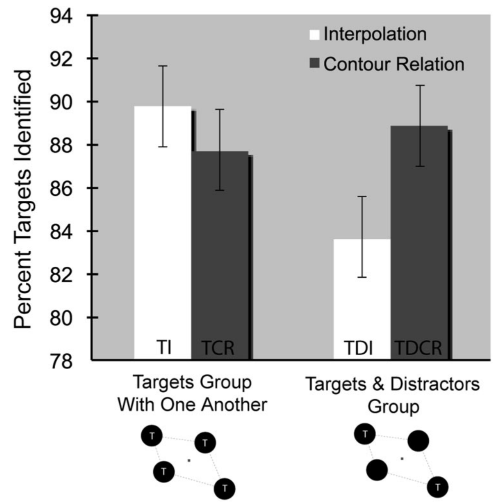

Figure 2. Mean accuracy and error bars (95% confidence intervals) for each condition in Experiment 1. Error bars for this graph and all other graphs do not include between-subject variance (Loftus & Masson, 1994).

in the lower right quadrant. A similar sort of preference has been shown before, and could indicate a general attentional advantage for the upper left quadrant (Gold et al., 2000; though see Carlson, Alvarez, & Cavanagh, 2007). Because the quadrant variable did not interact with any other, data for this and all other experiments were collapsed across quadrant.

There was also a main effect of grouping in that targets that grouped together were tracked better than targets that grouped with distractors, $F(1, 15) = 6.32$, $p = .02$, $\eta_p^2 = 0.296$. Most importantly, there was an interaction: when targets maintained an edge relation, interpolation boosted performance; otherwise, interpolation lowered performance, $F(1, 15) = 19.21$, $p = .001$, $\eta_p^2 = 0.562$.

A main effect of interpolation was lacking ($F(1, 15) = 2.82$, $p = .11$, $\eta_p^2 = 0.158$), but planned comparisons suggested that interpolation hurt performance, more than it helped. That is, while the TI condition was *not* reliably better than its control, $t(15) = 1.42$, $p = .18$, $d = 0.29$ (all t tests two-tailed, unless noted), the TDI condition *was* reliably worse than its TDCR control, $t(15) = 5.01$, $p < .001$, $d = 0.74$. Finally, the TCR accuracy ($M = 87.6$, $SEM = 2.1$) was slightly *lower* than the TDCR ($M = 88.8$, $SEM = 1.7$), indicating that—when targets shared only a collinear contour relation—there was no benefit relative to when targets and distractors maintained the same relation.

Discussion. Grouping effects strongly depended on the presence of illusory contours. This suggests that edges that produce interpolated contours, but perhaps not other sorts of edge relations,

[3] Strictly speaking, all targets (and distractors) shared a constant contour relation in all four conditions. For two subsequent frames of motion, once the condition was specified and once the edges and target status of one sectored circle were given, the edges and target status of all objects could be logically deduced. Nevertheless, for the purposes of the first two experiments, we assumed that a set of objects could be grouped if and only if every adjacent pair of objects within that set consistently shared a collinear edge relation.

spontaneously bind objects together. Most surprisingly, the majority of the interaction owed to the tendency of interpolation to interfere with tracking. Scholl, Pylyshyn, and Feldman (2001) documented a related "target-merging" effect, in which luminance-defined connections between targets and distractors reduce tracking performance. Our results go beyond target-merging, and reveal that there need not be any intervening information for the interference to obtain. The properties of the objects themselves can cause automatic grouping. This suggests that feature relations of targets and distractors automatically affect tracking, but only if those relations are relevant to interpolation. Implications for theories of object tracking and scene representation will be considered in the General Discussion.

We were surprised to find that performance in the TI condition failed to differ significantly from its partner control. As noted in the Introduction, interpolation was expected to periodically bind targets together and thereby reduce the number of objects to track (Allen et al., 2004; Yantis, 1992). The null result could owe to a reduction in interpolation strength when inducers are continually attended (perhaps as a result of adaptation); or it could simply mean that, in this kind of task, contours are generally are not very helpful in maintaining attention. These possibilities will be further considered in Experiment 5.

Experiment 2: Automatic Effects of Occluded (Amodal) Contours on Tracking

The purpose of Experiment 2 was to reveal whether occluded contours form automatically during tracking. The stimuli in Experiment 2 were just like those of the first experiment, except that thin black rings were placed around all objects, so that the illusory phenomenology disappeared. Behavioral similarities between modal and amodal completion as well as certain conceptual considerations (Kellman et al., 2007) motivated us to make the same predictions as before: superior performance in the TI condition relative to its TCR control, inferior performance in the TDI relative to its TDCR control, and little, if any, difference between the controls.

As noted in the Introduction, these predictions may be qualified by the fact that ringed amodal stimuli, while appealing in that they differ minimally from their modal counterparts, contain cue conflicts that may weaken interpolation strength. First, the amodal organization of the display requires segmenting the ring around each inducer from the identically colored (black) area within the ring (which must be part of a depth layer behind the interpolated figure). Homogeneous areas typically would be assigned as being connected and at a common depth, especially in 2D cases such as this, in which other depth information is absent. Second, the match of the surface color of the interpolated figure and the surround (both white) allows a competing surface interpolation process (Yin, Kellman, & Shipley, 1997), which could produce a different organization of the surfaces than completion of an amodal figure behind the white surround. Nevertheless, displays of this type have been successfully used in a number of other studies of interpolation (Gold et al., 2000; Lee & Nguyen, 2001; Murray, Foxe, Javitt, & Foxe, 2004; Ringach & Shapley, 1996), and are expected to reveal whether amodal contours exercise an effect on tracking.

Method

Subjects. Thirty-two undergraduate students at University of California, Los Angeles each participated in a 1-hr session for class credit. All participants had normal or corrected-to-normal vision.

Apparatus. The displays were the same as Experiment 1.

Stimuli. The stimuli were the same as Experiment 1, except that black annuli with a width of 1 arcmin were drawn around each disk in all conditions (see Figure 3).

Procedure and design. The procedure and design were the same as Experiment 1.

Results

The results of Experiment 2 are shown in Figure 4. The data were submitted to a 2 (grouping) $\times$ 2 (interpolation) ANOVA. The only significant effect of this analysis was the predicted interaction, $F(1, 31) = 5.01$, $p = .03$, $\eta_p^2 = 0.139$. That is, when targets maintained an edge relation with one another, interpolation appeared to improve performance; otherwise, interpolation reduced tracking accuracy. Planned comparisons once again showed that whereas the TI condition was not significantly better than its control ($t(31) = 1.21$, $p > .23$, $d = 0.07$), the TDI condition was reliably worse than its control, $t(31) = 2.15$, $p < .02$, one-tailed, $d = 0.13$.[4] As found in Experiment 1, there was no benefit of all targets forming a noninterpolated quadrilateral: participants performed slightly worse in the TCR ($M = 81.2$, $SEM = 2.4$) than in the TDCR condition ($M = 82.5$, $SEM = 2.3$).

To gain power and to compare the attentional effects of the stimuli in the two experiments, we performed a 2 (experiment) $\times$ 2 (grouping) $\times$ 2 (interpolation) mixed-model ANOVA. Performance was overall lower in the presence of interpolation, $F(1, 46) = 4.17$, $p < .05$, $\eta_p^2 = 0.083$, which suggests that contours affected performance more when they linked targets and distractors rather than targets and targets. The direction of interpolation's effect once again depended on how targets grouped: in the presence of target grouping, interpolation raised performance; otherwise, it lowered performance, $F(1, 46) = 24.41$, $p < .001$, $\eta_p^2 = 0.347$. This interaction itself was stronger when the contours were illusory rather than occluded, $F(1, 46) = 5.70$, $p < .03$, $\eta_p^2 = .110$. The rings did not reliably affect overall accuracy, $F(1, 46) = 3.01$, $p = .09$, $\eta_p^2 = .06$. (When only the control conditions of the two experiments were compared, there was also no main effect of experiment.)

To determine whether the three-way interaction owed to reduced distraction in the amodal TDI condition or reduced improvement in the amodal TI condition, a two-way ANOVA was performed for each level of the grouping variable. As expected, the added rings did not alter the relation between the TI and TCR conditions, $F(1, 46) = 0.64$, $p > .42$, $\eta_p^2 = 0.014$; however, the rings reduced the difference between the TDI and TDCR conditions, $F(1, 46) = 7.48$, $p < .01$, $\eta_p^2 = 0.14$. These follow-up tests also revealed a result that we previously predicted: An advantage of the TI relative to the TCR (null-interpolation) control, $F(1, 46) = 4.10$, $p < .05$, $\eta_p^2 = 0.08$.

[4] A one-tailed test was used here since the same comparison yielded an extremely significant effect in Experiment 1 ($p < .001$) and since the testing conditions between the two experiments were nearly identical.

Discussion

The most important result of Experiment 2 was that occluded contours affected tracking in qualitatively the same way as illusory contours. When targets maintained collinear edge relations, performance was slightly (but not significantly) better in the presence of interpolation; when targets and distractors maintained such edge relations, performance was significantly worse in the presence of interpolation. Thus, whether contours are occluded or illusory, interpolation automatically directs attention during parallel tracking.

Another finding was that the amodal stimuli were slightly less effective at directing attention than the modal. As noted above, this weakening may owe to cue-conflicts that make a consistent scene interpretation more difficult (c.f., Kellman, Guttman, & Wickens, 2001). For example, ringed amodal Kanizsa figures do not pop-out in visual search (Davis & Driver, 1994), whereas other kinds of 2D and 3D occluded figures do (He & Nakayama, 1992; Rensink & Enns, 1998). Other amodal variants (e.g., those involving 3D) will need to be considered before conclusions can be drawn about differential effects of modal and amodal completion on tracking.

Cue conflicts aside, combining and comparing the modal and amodal data was informative in three ways. First, and most relevantly, it provided the power to detect the (modest) tracking advantage offered by target-linking contours. The TCR (control) and TI conditions were randomly interleaved, so the benefit plausibly cannot be attributed to strategy differences. The reason for the small magnitude of the improvement will be considered further in Experiment 5.

Comparing the experiments was useful also in that it furnished information about the relation between phenomenology and objective performance. In the postexperiment questionnaires, the percentage of participants seeing quadrilaterals of some sort (box, square, etc.) was 62% (8 of 13 participants) and 25% (7 of 28) in the modal and amodal experiment, respectively.[5] Tracking accuracy differences therefore predict how well the contours are noticed. Being that illusory contours were both more noticed and more distracting than occluded contours, recognizing interpolation does not appear to abate its negative influence. The simplest explanation is that interpolation effects are automatic and operate despite the intentions of the observer.

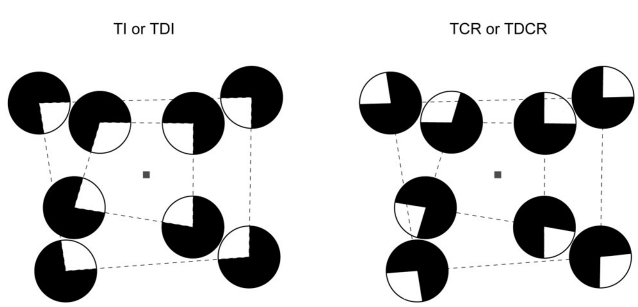

Figure 3. Stimuli in Experiment 2. Stimuli were the same as those in Experiment 1, except that each disk in all conditions was accompanied by a 1 arcmin ring around its circumference. To the left is a possible snapshot of either the TI or TDI condition; to the right, a possible snapshot of either the TCR or TDCR condition. Dotted lines reveal how the sectors of adjacent disks were related, and are for illustration only. The small central square was the fixation point.

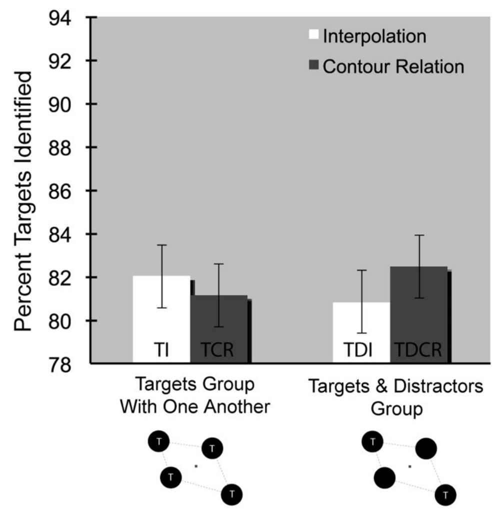

Figure 4. Mean accuracy and 95% confidence intervals for each condition of Experiment 2.

Identification of reduced interpolation effects in Experiment 2 also renders unlikely a possible objection, viz., that blurring in low spatial frequency channels, rather than interpolation, created the effects observed thus far (Ginsburg, 1975). Just as blurring failed to explain pop-out of Kanizsa figures in visual search (Davis & Driver, 1994), it also fails to explain our results. A 1 arcmin annulus produced phenomenological and behavioral differences in our experiments, implying that the visual system does not simply blur object boundaries without regard to what appears in between.

Experiment 3: Automatic Effects of Support Ratio on Tracking

In the next experiment, we aimed to confirm and extend the previous findings by showing that interpolation effects depend on support ratio (physically specified edge length divided by total edge length), a major determinant of interpolation strength (Banton & Levi, 1992; Shipley & Kellman, 1992). In Experiment 3, interpolation strength was measured as the accuracy difference between the TI and TDI conditions. We predicted that if disks were reduced in size and all other factors remained the same (to reduce the support ratio; see Figure 5), then the difference between these two conditions would lessen as well.

A secondary purpose of Experiment 3 was to address a possible objection to the first two experiments, namely, that collinear contours, rather than interpolation, produced the pattern of results uncovered thus far. On this view, the control conditions failed to affect performance only because sector edges in the TCR and TDCR had a greater eccentricity than the edges in the TI and TDI condition. When sectors are oriented toward the fixation point, collinear edge groupings may affect performance regardless of support ratio.

[5] Some participants had to leave the experiment early and could not complete the questionnaires.

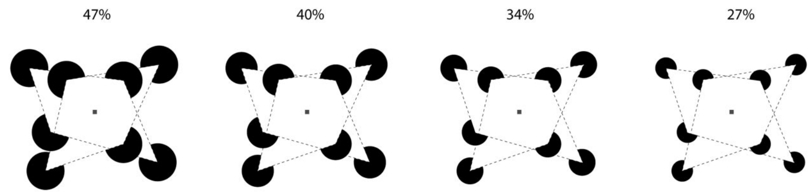

Figure 5. Stimuli in Experiment 3. Versions of the TI and TDI conditions were each examined at four different average support ratios. Since the average distance between disks was always the same as Experiment 1, average support ratio values completely depended on disk size. The prediction was that as disks became smaller, interpolation strength would decrease, and so too would the accuracy difference between the TI and TDI conditions.

Method

Participants. Eighteen undergraduate students of University of California, Los Angeles participated in 1-hr sessions for class credit. All had normal or corrected-to-normal vision.

Apparatus. The apparatus was the same as Experiment 1.

Stimuli. Stimuli in this experiment were the same as in the first experiment, except that the contour relation conditions (TCR and TDCR) were removed, and disks had one of four radii: 92, 78, 65, and 52 arcmin. Because objects were on average located at their respective barycenters, there were four average support ratios, 47, 40, 34, and 27%. Informal observations guided the selection of these values: the smallest support ratio was the largest value that produced a negligible phenomenal trace of illusory contours; the largest support ratio was the same as Experiment 1; and, the two intermediate support ratios were middle points between the large and small extremes.

In contrast to the previous experiments, one of four speeds was assigned without replacement to each quadrant: 1.25, 1.67, 2.08, or 2.5[1] πrad/s (or alternatively, 3, 4, 5, or 6 deg of rotation per movement frame). In addition, exactly two quadrants were randomly assigned a counterclockwise rotation. The foregoing changes prevented the targets from grouping by a common angular speed or direction (Yantis, 1992, especially pp. 319–322), which participants claimed in the postexperiment questionnaires to have used to their advantage. Analyses on Experiment 1 data further confirmed that common motion reduced differential effects in the interpolation conditions.

Procedure and design. The procedure was the same as in the previous experiments, with the following differences. Each session consisted of an 80 trial TI block and an 80 trial TDI block, and block orderings were counterbalanced across observers. The four support ratios were presented with equal frequency and randomly within each block.

Results

As shown in Figure 6, results of Experiment 3 strongly depended on interpolation and, in particular, support ratio. A 2 (grouping) $\times$ 4 (support ratio) ANOVA confirmed the trends depicted in the graph. There was a main effect of grouping, in that performance was overall better when targets interpolated with one another rather than with distractors $F(1, 17) = 4.61$, $p < .05$, $\eta_p^2 = 0.213$. This shows that even when support ratio, and thus contour salience, is on average quite modest, interpolation can still automatically guide the flow of attention. More importantly, the benefit of all targets interpolating one quadrilateral, rather than two, increased as support ratio increased, $F(3, 51) = 3.95$, $p < .02$, $\eta_p^2 = 0.188$. To examine whether the interaction owed more to changes in the TI or TDI conditions, two follow-up ANOVAs were performed. Among the TI trials, performance decreased slightly with decreasing support ratio, but the trend was not reliable $F(3, 51) = 0.64$, $p > .59$, $\eta_p^2 = 0.036$. Among the TDI conditions, accuracy significantly improved as support ratio was reduced, $F(3, 51) = 3.16$, $p = .03$, $\eta_p^2 = 0.157$.

Discussion

Results from Experiment 3 extend and confirm the findings of the first two experiments in four ways. First, and most importantly, they show that the tendency of interpolation to automatically direct attention depends on support ratio, a well-known determinant of interpolation strength. Second, the bulk of this effect owed to the ability of interpolation to distract, rather than enhance, attention. Third, the effect of contour interpolation on tracking is robust; it does not simply disappear when disk sizes are reduced. Finally, because the differences between TI and TDI strongly depended on support ratio, eccentricity of group-able contours, by itself, is not a likely explanation for why the control conditions failed to affect performance in the first two experiments.

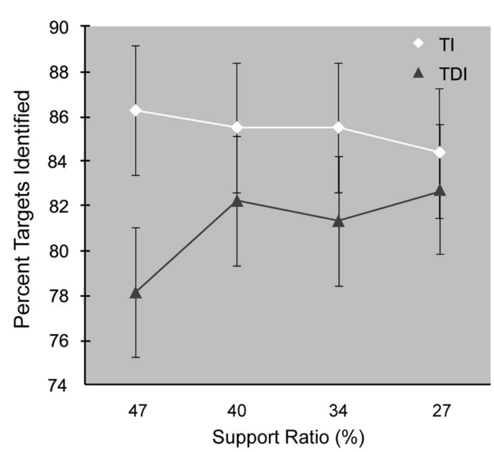

Figure 6. Mean accuracy and 95% confidence intervals for each support ratio for both the TI and TDI conditions in Experiment 3. Support ratio is plotted from highest (stronger predicted interpolation effect) to lowest.

Experiment 4: Automatic Effects of Inducer Rotation Angle on Tracking

In Experiment 4, we again tested whether tracking effects depend on interpolation strength, but this time, instead of modulating support ratio, we modulated inducer rotation (see Figure 7). The sharper that an interpolated contour must bend to connect two inducers, the lower the objective probability that those edges form a common contour (Geisler et al., 2001), and the less strongly they interpolate (Fulvio, Singh, & Maloney, 2006; Grossberg & Mingolla, 1985; Kellman & Shipley, 1991, p. 179; Rock & Anson, 1979). Some evidence suggests that interpolation effects go to zero when the relative angle between inducers is acute (<90 deg; Field, Hayes & Hess, 1993; Kellman & Shipley, 1991). We therefore predicted greatest interpolation effects when inducers were unrotated, no effects when inducers created a turning angle exceeding 90 deg, and intermediate effects, otherwise. As before, interpolation strength was gauged by TI/TDI differences.

Experiment 4 also addressed a potential objection. In Experiment 3, the correlation between grouping effects and object size could be attributed not to interpolation per se, but to the fact that smaller inducers provided less information with which to group. If object size is held constant, and eccentricity is always inward (so that information for grouping is always comparably accessible), then tracking should proceed regardless of inducer rotation or interpolation strength.

Method

Participants. Eighteen undergraduate students of University of California, Los Angeles participated in 1-hr sessions for class credit. One additional participant was excluded from the analysis for not following directions. All had normal or corrected-to-normal vision.

Apparatus. The apparatus was the same as Experiment 1.

Stimuli. Conditions were the same as the TI and TDI conditions of Experiment 1, except that sectored disks were individually rotated. In all cases, rotations for the upper right and lower left inducers were clockwise, and the remaining inducers rotated counter-clockwise. Thus, when two edges formed an illusory contour in one rotation condition, the average orientation of those edges would be the same in any of the other rotation conditions. There were three rotation angles. The 48 deg rotation was chosen since previous work suggests that interpolation cannot overcome such a sharp turning angle (Kellman & Shipley, 1991). The 12 deg rotation magnitude was selected on the basis of pilot studies, which revealed an intermediate effect of interpolation. The 0 deg rotation angle was expected to yield the strongest interpolation effects. To avoid ceiling effects, the duration of the movement phase was extended to a total of 9 s (Oksama & Hyönä, 2004). Velocity assignment to the different quadrants was the same as Experiment 3.

Procedure and design. One TI block (consisting only of TI trials) and one TDI block (consisting of only TDI trials) occurred in each half of a session, creating a four block experiment. The block order in the first half of the experiment was repeated for the second half. Every other observer began a session with a TI block. Within each 36-trial block, the three rotation angles occurred randomly and with equal frequency.

Results and Discussion

Visual inspection of Figure 8 reveals that interpolation and rotation angle were relevant to tracking performance. A 2 (grouping) × 3 (rotation angle) ANOVA confirmed this observation. There was a main effect of the grouping variable, in that performance was overall better when targets interpolated with one another rather than with distractors $F(1, 17) = 5.55$, $p = .03$, $\eta_p^2 = 0.246$. This shows once again that the interpolation effect is robust, and cannot easily be eliminated. More importantly, the benefit of all targets forming one quadrilateral, rather than two, decreased with rotation angle, $F(2, 34) = 3.56$, $p = .04$, $\eta_p^2 = 0.173$. This result supports those of the previous experiment and indicates that when interpolation strength is weakened, so too are the effects of interpolation on attention. Inducer information was comparably accessible in all conditions, but only when the inducers were oriented to interpolate did grouping become relevant. To verify whether the interaction owed more to changes in the TDI condition, two follow-up ANOVAs were performed. When all targets interpolated, performance decreased slightly as inducer rotation increased, but the trend was not significant, $F(2, 34) = 0.41$, $p > .66$, $\eta_p^2 = 0.023$. When targets and distractors interpolated, effects on tracking were greatest for smaller values and decreased to nearly zero for turn angles just exceeding 90 deg, $F(2, 34) = 3.60$, $p < .04$, $\eta_p^2 = 0.175$. Because the versions of the TDI condition were randomized within the same block, the specific interaction further underscores the stimulus-driven character of contour interpolation.

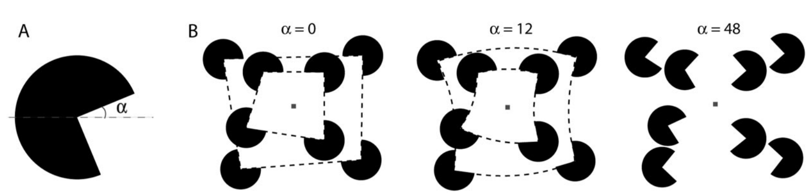

Figure 7. Stimuli in Experiment 4. (A) Inducers were individually rotated with an angle α from where they would have been in the TI or TDI condition. The upper right and lower left quadrant inducers could only rotate clockwise; the other inducers could only rotate counter-clockwise. (B) Possible snapshots of either the TI or TDI condition are shown for each of the three rotation angles: 0, 12, and 48 deg. Dotted lines indicate how the edges of adjacent inducers were related, and are for illustration only.

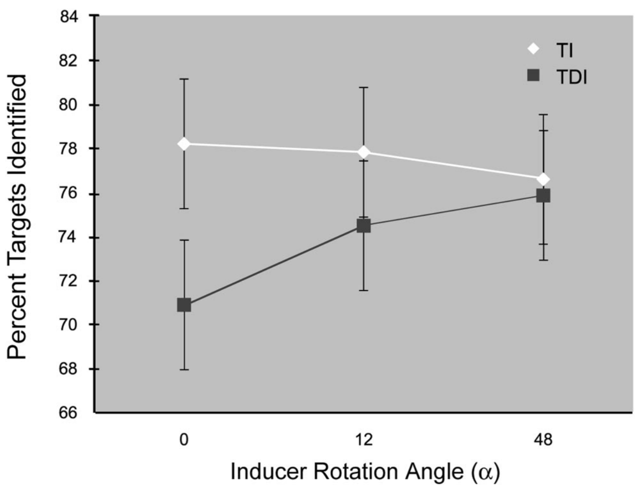

Figure 8. Results in Experiment 4. Accuracy and 95% confidence intervals are plotted for the TI and TDI conditions for each of the three inducer rotation angles. Doubling the inducer rotation angle gives the turn angle required for an interpolated contour to connect a pair of inducers.

Experiment 5: Comparing Automatic Effects of Real and Illusory Contours on Tracking

The fifth and final experiment had two purposes. First, we aimed to determine why interpolation improved tracking only slightly in the TI conditions. One possibility is that illusory contours are not as effective as ordinary contours at maintaining attention towards linked items. For example, interpolation strength may spike within the first few hundred milliseconds of attending inducers (Lee & Nguyen, 2001), and weaken quickly thereafter, perhaps as a result of adaptation (Ramachandran, Ruskin, Cobb, Rogers-Ramachandran, & Tyler, 1994). Another possibility is that *any* kind of contour will be of limited use when binding targets with one another, at least in a display where there is frequent overlap between the objects and connecting contours.

A second more exploratory question was how illusory and real contours compare in their ability to direct attention. Illusory contours affect performance slightly less than real contours in a number of other tasks (Keane et al., 2007; Ringach & Shapley, 1996), and so a similar outcome can be expected for tracking.

To address these questions, the TI and TDI were compared with a target real (TR) and target distractor real (TDR) condition. These new conditions were just like the TI and TDI, respectively, except that a black line connected pairs of notched circles exactly when the sectors were present (see Figure 9). If illusory contours are unique in affording only a slight advantage when connecting targets, then performance in the TR condition should exceed that of the TI. Furthermore, if real contours exert a similar but more intensified effect on tracking, then there should be a main effect of grouping and an interaction.

Method

Participants. Sixteen undergraduate students of University of California, Los Angeles participated in ~45 minute sessions for class credit or for monetary compensation. All had normal or corrected-to-normal vision.

Apparatus. The apparatus was the same as Experiment 1.

Stimuli. The stimuli were similar to Experiment 1, except that the TCR and TDCR conditions were replaced by the TR and TDR conditions. The TR and TDR were just like the TI and TDI, respectively, except that black lines (width = 1 arcmin) connected the centers of the disks exactly when the sectors were present. To increase contour effects, movement duration and quadrant velocity assignment were the same as in Experiment 4.

Procedure and design. The procedure and design were the same as Experiment 1, except there were only 32 trials per condition (to reduce fatigue effects that subjects reported in the previous experiments). In addition, in the instructions, participants were told that black lines would occasionally connect the pac-men, and that regardless of these lines, they should try their best to track the targets.

Results

Results are shown in Figure 10. A 2 (grouping) × 2 (contour type) ANOVA and follow-up *t* tests revealed that both illusory and real contours were highly influential. More precisely, while performance was overall better when targets formed contours with one another ($F(1, 15) = 71.3$, $p < .001$, $\eta_p^2 = 0.826$), this effect was more pronounced for real contours, $F(1, 15) = 8.34$, $p = 0.01$, $\eta_p^2 = 0.357$. This interaction did not owe to a difference between the TI and TR conditions ($t(15) = 0.33$, $p = .75$, $d = 0.05$); instead, it owed to lower performance in the TDR than in the TDI condition, $t(15) = 4.11$, $p = .001$, $d = 1.15$. The high difficulty of the TDR condition was enough to produce a main effect of contour type, $F(1, 15) = 13.3$, $p = .002$, $\eta_p^2 = 0.470$.

Discussion

Added difficulty of the TDR condition relative to the TDI condition was expected on the basis of strong "target-merging" effects found in previous tracking studies (Scholl et al., 2001), and also heightened real contour effects with other tasks (Keane et al.,

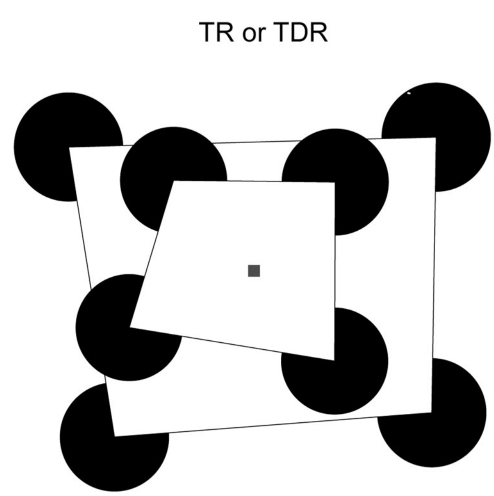

Figure 9. Possible snapshots of either the TR or TDR conditions in Experiment 5. The TR and TDR were just like the TI and TDI, respectively, except that thin black lines were drawn between the centers of the disks exactly when the disk sectors were present.

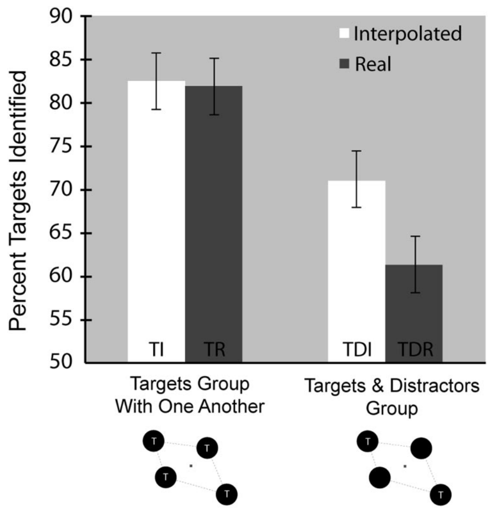

Figure 10. Results in Experiment 5. Mean accuracy and 95% confidence intervals are plotted for when the grouping contours were interpolated or real, and for when targets grouped with one another or with distractors.

2007; Ringach & Shapley, 1996). An unexpected finding, however, was that real and illusory contours afforded about the same improvement when linking targets. The absence of a TR advantage probably cannot be blamed on inadequate power since (1) the difference in means was in the wrong direction and favored the TI condition (82.5 vs. 81.9%), (2) only 6 of the 16 subjects performed better in the TR condition, and (3) TI/TDI differences were almost twice as large as Experiment 1 (12 vs. 6%), implying that differential effects of contours on behavior should have been easier to detect than before. Real contours may better direct attention in other circumstances, but here our results suggest that when inducers are attended (perhaps to boost interpolation strength; Grossberg, 2001) contours formed in the mind can act just like those that are luminance-defined.

An important implication of the near equivalence between the TI and TR conditions is that reduced interpolation benefits in the previous experiments cannot be attributed to weak interpolation. Any kind of contour will provide lessened advantages, at least in our set-up. The exact reason will need to be explored in future studies, but one possibility is that inter-target contours are less helpful when they periodically intersect with contours formed between distractors.

General Discussion

In the course of five experiments, the automaticity of interpolation was revealed via multiple object tracking. We showed that illusory and occluded contours impaired tracking performance when connecting targets and distractors, and improved performance when connecting targets with one another. Such effects depended on factors that alter interpolation strength (support ratio and inducer rotation angle), and rivaled those found with real contours, although real contours were more effective at shifting attention toward distractors. These outcomes, as a whole, could not be explained by blurring at low spatial frequencies or generic grouping strategies.

The foregoing support five new (or at least controversial) claims regarding contour interpolation and object-based attention: (1) Contour interpolation automatically directs attention during tracking, and occurs even when certain elements that engender interpolation are ignored; (2) illusory contours facilitate attention towards targets no less than real contours, at least in some cases; (3) relations between features of neighboring objects can affect tracking; (4) features of distractors matter for tracking; and (5) so-called "attentional" paradigms, such as MOT, can be modified to reveal the relatively subtle properties that guide lower-level perceptual processes, such as interpolation.

In the following, we discuss in more detail the ability of interpolation to automatically affect tracking. We then consider implications for theories of object tracking. The paper concludes with suggestions on how attentional paradigms can be modified to further uncover interpolation characteristics.

Automatic Effects of Interpolation on Attention

Overall, interpolation effects in our study were robust. When interpolation strength was consistently at its peak (Experiments 1 and 5), 94% (30/32) of subjects performed better in the TI than in the TDI condition. The difference could reach magnitudes as high as 12% (Experiment 5) and was reliable enough to withstand support ratios that were on average quite modest (Experiment 3).

The most obvious interpolation effect was the shifting of attention from targets to distractors. Participant L.K. unwittingly describes the difficulty of the TDI condition in her postexperiment questionnaire:

> What mostly confused me was the one target that would pair up with another circle and they would start moving together at a fast pace. In that case I had to dedicate most of attention to that one target in which case I would lose track of the other ones and not get a perfect score.

The ability of distractors to interpolate is striking given the instructional irrelevance of interpolation, and given also that distractor information is plausibly inhibited (rendered less accessible) during MOT (Flombaum, Scholl, & Pylyshyn, 2008; Pylyshyn, 2006). To our knowledge, ours is the first behavioral study to show that ignored items engage in modal and amodal completion.

Interpolation also aided observers when it linked targets. This was predicted on the ground that interpolation would tie targets together, and effectively reduce the number of objects to track (Allen et al., 2004; Yantis, 1992). The improvement was no less than when real contours connected targets. Future studies will need to consider whether the benefit arises more through preventing the loss of targets or through boosting the recovery of targets momentarily lost.

The relative advantage of targets participating in one rather than two quadrilaterals is broadly consistent with the single object advantage, according to which attending to the world is essentially easier with only one referent. For example, Duncan (1984) showed that simultaneous visual judgments were more accurate when they concerned one thing rather than two. Baylis and Driver (1993) similarly showed that judging the relative location of two contours was easier if they belonged to one rather than two things (see also, Egly, Driver, & Rafal, 1994). Our results extend this literature and indicate that interpolation can build the objects that guide attention during tracking; that this guidance can be used to index interpolation characteristics (especially its automaticity); and that such guidance can reveal the manner in which objects are represented, a point which to which we now turn.

Implications for Theories of How We Track and Represent Objects

According to Pylyshyn's FINST model (Pylyshyn, 2003), the visual system comes equipped with a series of pointers that preattentively indicate the whereabouts of objects without encoding featural properties. On Pylyshyn's view, while general features that determine an object's identity (such as boundedness and cohesion) are important for tracking, featural properties that simply modify an objects appearance (e.g., size, shape, orientation) are not. Scholl (2007) has since put forth a related view, according to which featural properties play only a very minor role in tracking (see also, Rensink, 2000). As evidence, when participants attempt to utilize object appearance to identify the locations of featurally rich, momentarily occluded objects during MOT, they can do so only for about 2 targets (Horowitz et al., 2007). When single objects move stroboscopically (Burt & Sperling, 1981; Dawson, 1991; Kolers, 1972; Ullman, 1985) or behind occluders, feature changes exert only a small effect on the perception of continuity (Jusczyk, Johnson, Spelke, & Kennedy, 1999; Michotte, Thinès, & Crabbé, 1964/1991; see also, Mitroff & Alvarez, 2007). Change blindness studies (where observers are not able to identify large changes to successively presented scenes) further suggest impoverished visual object representation (Simons & Levin, 1997).

The experiments in our paper imply that features of a scene are represented more than previously suspected, and affect tracking to a greater degree than previously thought. Tracking performance varied systematically with junction structure (Experiments 1 and 2), disk size (Experiment 3), and disk orientation (Experiment 4). This information derived not only from targets, but also from distractors, indicating that content-specific representations are plausibly formed for many objects at a time. In our paradigm, the system did not merely detect features or feature summaries (Parkes, Lund, Angelucci, Solomon, & Morgan, 2001); it precisely encoded what feature appeared on what object (or fragment), and assessed (at least implicitly) whether the geometric conditions of interpolation obtained (e.g., Kellman & Shipley, 1991). These sophisticated[6] operations were performed automatically, and (often) against the will of the observer.

The causal link between interpolation features and tracking need not contradict the view that tracking mechanisms by-and-large ignore object appearance. If tracking mechanisms (e.g., FINSTs) are prompted by visual objects, and if contour interpolation determines *what counts* as a visual object, then the features that determine interpolation should also determine how we track. In our experiments, featural properties clearly affected tracking only when they induced or altered interpolation. Therefore, we propose a *segmentation-relevance principle*, according to which features that spontaneously affect tracking are precisely those that help define what a visual object is. On this view, features like orientation and size are continually encoded, but become efficacious primarily when they force scene segmentation.[7] Future studies will need to consider the extent to which this principle holds true, for example, by investigating whether properties irrelevant to objecthood (e.g., common color) can produce automatic grouping during tracking.

Attentional "Signatures" of Perception: MVT and Beyond

MOT is considered by many to be a paradigm for studying attention, but here we have shown that one variant—what we call multiple vertex tracking (MVT)—can also reveal contour interpolation characteristics. *Any* property that at least moderately affects interpolation strength can most likely be revealed via tracking. Such properties include, but are not limited to: tangent discontinuities (e.g., the "sharpness" of L-junctions; Shipley & Kellman, 1990), misalignment in 2D (Kellman & Shipley, 1991), misalignment and torsion in 3D (Kellman et al., 2005), contrast polarity (Davis & Driver, 2003; Grossberg & Yazdanbakhsh, 2005), and the spatial distribution of inducing edge information (Maertens & Shapley, 2008), to name a few.

MVT advantages notwithstanding, nontracking paradigms can also reveal the attentional signatures of interpolation. For example, in visual search, the degree to which Kanizsa triangles pop-out (RT slopes) or the speed of pop-out (RT intercepts) may vary directly with other properties that modulate interpolation strength, such as support ratio, inducer rotation angle, etc. Illusory line bisection among patients with hemispatial neglect, and object-specific priming among healthy adults may also depend on properties relevant to completion. By extending attentional paradigms in this way, we can better understand how attention and perception relate and, more generally, how the fundamental referents of perception (objects) are represented and acted upon in ordinary experience.

[6] Interpolation is considered "sophisticated" because it depends upon a host of subtle stimulus properties including junction structure (Rubin, 2000), contrast polarity relations (Grossberg & Yadanbakhsh, 2005), spatiotemporal relations (Palmer et al., 2006) and alignment in 3-dimensional depth (Kellman et al., 2005), among others. The relevance of these properties does not obviously follow from (for example) the Gestalt rule of good continuation. Others have also described interpolation as "sophisticated" (Driver, Davis, Russell, Turatto, & Freeman, 2001, p. 89; Sugita, 1999, p. 71).

[7] There are also conceptual arguments for why earlier visual representations contain abundant information about the distal world (Keane, 2008).

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