Japanese Psychological Research THE JAPANESE PSYCHOLOGICAL ASSOCIATION

Japanese Psychological Research
2010, Volume 52, No. 4, 268–280

doi: 10.1111/j.1468-5884.2010.00442.x

Spatiotemporal integration and contour interpolation revealed by a dot localization task with serial presentation paradigm[1]

HIDEYUKI UNUMA[2]* *Kawamura Gakuen Woman's University*

HISA HASEGAWA *Aoyama Gakuin University*

PHILIP J. KELLMAN *University of California, Los Angeles*

Abstract: The visual system seems to integrate information that is presented over time in a spatially fragmented fashion, with the result that observers are able to report the whole shape of objects. This research considers relations in space and time that allow the integrated percepts of complete objects. Specifically, temporal characteristics for spatiotemporal integration of illusory contour and spatial characteristics of interpolated contour are examined. A serial presentation paradigm and a dot localization task were used in two experiments; observers localized a probe dot relative to a perceived contour of an illusory object. Each of four inducing figures was briefly presented in a serial order to observers and the total time of the series was manipulated. In Experiment 1 short time ranges varied up to 180 ms, whereas longer times were examined in Experiment 2. Overall, the results demonstrate that a short time allows spatiotemporal integration, and that the perceived location of contour consistently shifts with time range. These experiments suggest that the mechanism of spatiotemporal integration operates on spatial integration as a limiting case.

Key words: illusory contours, spatiotemporal integration, interpolation, localization, object perception.

Visual interpolation is an everyday phenomenon. Because objects in our daily environment are commonly occluded by other objects, we typically perceive them based on incomplete information. Visual edges and parts of the object's contour are missing, yet the visual system allows a percept of the shape of these objects. Some have argued that a visual interpolation process plays an important role in supplying the missing edges (Kellman, Guttman, & Wickens, 2001; Nakayama, Shimojo, & Silverman, 1989; Neumann & Mingolla, 2001). Considerable research has improved our understanding of the processes that underlie the visual interpolation of contour in two-dimensional or stationary scenes (Fantoni & Gerbino, 2003; Geisler, Perry, Super, & Gallogly, 2001; Kellman & Shipley, 1991).

*Correspondence concerning this article should be sent to: Hideyuki Unuma, Department of Psychology, Kawamura Gakuen Woman's University, Sageto, Abiko 270-1138, Japan. (E-mail: hide.unuma@kgwu.ac.jp)

[1]This research was supported by Kawamura Gakuen Woman's University Grant-in-Aid for Scientific Research and Education 2007, 2008, and 2009 to Hideyuki Unuma.

[2]We thank Dr Mari Jones for helpful suggestions and comments on earlier versions of this article.

Furthermore, other research has begun to consider interpolation in three-dimensional space (Kellman, Garrigan, & Shipley, 2005) and in the spatiotemporal domain (Keane, Lu, & Kellman, 2007; Palmer, Kellman, & Shipley, 2006).

With respect to contour perception, a useful way to understand the processes that enable connections among visible parts of a whole shape entails investigating the emergence of a shape representation over time in particular spatiotemporal conditions (Palmer et al., 2006; Unuma & Tozawa, 1994). For example, Palmer et al. (2006) observed that moving parts or edges enabled viewers to perceive shapes under an occluding surface. The authors proposed a geometric account of spatial and temporal relations between visual edges which predicts contour interpolations. The resulting model, termed the dynamic visual icon (DVI), assumes that the process involves object representations that are based on the spatiotemporal integration of fragmented edges. According to DVI, spatiotemporal integration is accomplished by a combination of visual persistence and position updating of sequentially viewed edges (Palmer et al., 2006, pp. 516–519). This model offers a unified account of the interpolation process for static, dynamic, occluded, as well as illusory objects. Two aspects of a dynamic representation, however, remain to be explored. One involves the persistence of a dynamic visual icon, in particular its temporal characteristics. The other involves the fidelity of a contour interpolation that depends on a spatiotemporal integration process (Palmer et al., 2006, p. 538).

Considerable research suggests that the temporal characteristics of stimulus presentations constrain the viewers' tendency to integrate visible edges (Guttman & Kellman, 2004; Reynolds, 1981; Ringach & Shapley, 1996; Takahashi, 1994). Although the time-course of temporal integration of visible edges and the emerging, or microgenetic, process (Sekuler & Palmer, 1992) of perceptual representation of shapes has received significant study, this research has relied largely on temporal manipulations that involve exposure times of static stimuli, that is, stimuli in which edge fragments are simultaneously visible. While the time required to generate an illusory contour in static displays has been estimated to range from 120 ms to 160 ms (Guttman & Kellman, 2004; Reynolds, 1981; Ringach & Shapley, 1996), the temporal characteristics that may apply to the process of connecting fragmented edges, both spatially and temporally, remain poorly understood.

Accordingly, in this research, we address the temporal characteristics of integration using visual edges that are fragmented in both space and time. It is this postulated connection process that we call spatiotemporal integration. There is evidence that spatiotemporal integration is temporally limited to relatively brief time intervals (Shipley & Kellman, 1994; Takemoto & Ejima, 1997; Unuma & Tozawa, 1994). For instance, Shipley and Kellman (1994) examined boundary formation and shape identification using spatiotemporal transformations of spatially separated elements, and found that spatiotemporal integration appears to be less efficient when temporal ranges exceed 165 ms. Unuma and Tozawa (1994) used a serial presentation paradigm in which each inducing part of an illusory contour figure was presented individually in a particular serial order, and analyzed causal relations between perceived brightness-change, contour-clarity, and depth-change. They found that an illusory contour figure could be perceived from fragmented edges within a total temporal range that was greater than 260 ms, as given by the stimulus-onset asynchrony (SOA) between two successive inducing elements. In light of this, Unuma and Tozawa (1994) suggested that illusory contours can be perceived from fragmented elements over relatively long temporal ranges, and that the perception of brightness change appears to be independent of the perception of illusory contour. The fact that estimates of temporal limits appear to vary across experimental reports suggests that the time required for spatiotemporal integration may be influenced by several factors, such as task demands, stimulus attributes, observers' knowledge, and the particular behavioral measures employed.

Takemoto and Ejima (1997) examined temporal limits for additive contrast effects using illusory contour figures as stimuli. They measured the perceived contrast of illusory contour figures as a function of SOA between inducing elements, and found that the perceived contrast decreased gradually with increasing SOA and leveled off at an SOA of 372 ms. This estimate of temporal limits in Takemoto and Ejima (1997) provides evidence for the persistence of local information and temporal integration in illusory contour perception. At the same time, the estimate itself appears to depend on the perceptual attributes of the task.

Although previous estimates of temporal limits in spatial and temporal integration were obtained using different methods and from different perceptual attributes, these estimates, including those involved in both static illusory contour figures and occluded figures, seem to suggest a coherent explanation for the time course of contour and surface processes (Grossberg & Mingolla, 1985) in visual interpolation. Assuming that the temporal characteristics of spatiotemporal integration of visible edges, fragmented both in space and time, are closely related to the microgenetic process (Sekuler & Palmer, 1992) of spatial interpolation with static displays, contour interpolation seems to develop within 200 ms (Keane et al., 2007; Ringach & Shapley, 1996; Shipley & Kellman, 1994). In contrast, surface processes have been proposed to require further processing time (Ringach & Shapley, 1996; Sekuler & Palmer, 1992; Takemoto & Ejima, 1997; Unuma & Tozawa, 1994). Therefore, the present research aims to clarify the fidelity of interpolated contours with spatiotemporal integration that entails two different temporal phases. Here we refer to an initial phase that takes less than 200 ms as the short range, and a second phase that takes more than 200 ms is referred to as the long range.

In the present study, using an illusory contour figure (Figure 1) and a dot localization task (Guttman & Kellman, 2004; Guttman, Sekuler, & Kellman, 2003), we explore the differences in contour interpolation for the short- and long-range process using the serial presentation paradigm (Figure 2). Perception of an illusory figure is considered to yield an index of spatiotemporal integration of fragmented edges in the serial presentation paradigm; this is because illusory figures have functional and phenomenological equivalences to figures with physical boundaries and they appear to share common interpolation mechanisms with amodal completion (Kellman & Shipley, 1991; Kellman, Yin, & Shipley, 1998). In short, if a perceptual representation is formed from fragmented edges, an illusory figure should be observed in the serial presentation paradigm.

Instead of the subjective report method used by Unuma and Tozawa (1994), here we employ three objective measures of performance: location, error in location, and imprecision. These measures are used to assess the location of a perceived contour as well as the precision of a given interpolated contour. We used a dot localization task in the current experiments, in which a small dot is presented near the illusory contour. Observers then judge whether the dot appears on the inside or the outside of the illusory figure's perceived boundary (Figures 1, 2). Two interleaved staircase procedures are used to estimate the location and precision of contour perception. The location measure is defined as the midpoint of the inside thresholds and the outside thresholds. The error in the location measure, calculated from the absolute values of location, indicates performance accuracy as assessed relative to a contour outline that is physically consistent with the visible edges. Finally, the imprecision measure is

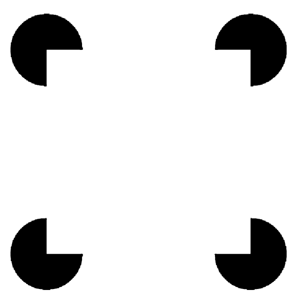

Figure 1 An illusory contour stimulus used in Experiments 1 and 2.

defined as the difference between the inside and outside thresholds. The greater this difference, the less precisely the contour is located.

We assume that the strength of the perceived contour is indexed by an observer's precision in identifying interpolated line locations, as measured using dot localizations in the serial presentation paradigm. This is because the imprecision measure has been shown to correlate highly with other measures of contour strength, such as reaction times (Guttman et al., 2003) and perceptual classification performance (Guttman & Kellman, 2004). Moreover, the imprecision measure represents an objective and intuitive metric for contour strength in static displays (Guttman & Kellman, 2004). Consequently, first we seek evidence that interpolated contours are strongly represented in a serial presentation paradigm, as measured by high precision. We refer to this hypothesis as the "precision hypothesis". Related to this hypothesis, we also assess whether the strength of an interpolated contour decreases as the time intervals between presentations of successive edges increase (i.e. beyond 200-ms limits). In the spatial domain, the precision of dot localization has been shown to decrease systematically with increasing amounts of spatial occlusion (Guttman et al., 2003). Analogously, if contour interpolation is time-limited, given temporal limits suggested by the dynamic visual icon model, then in the current paradigm the precision of contour representations should decrease with longer time intervals between successive visible edges beyond the 200-ms limits.

Secondly, we ask whether the putatively interpolated contour is an accurate reflection of the theoretical location. By "theoretical location" (Guttman et al., 2003), we mean an outlined contour physically consistent with the visible edges. Guttman et al. (2003) found that the judged location of a contour profile systematically changed from outside to inside the theoretical location as the amount of spatial occlusion increased. The reason for these shifts is not clear. However, Guttman et al. (2003) suggested that the contour interpolation

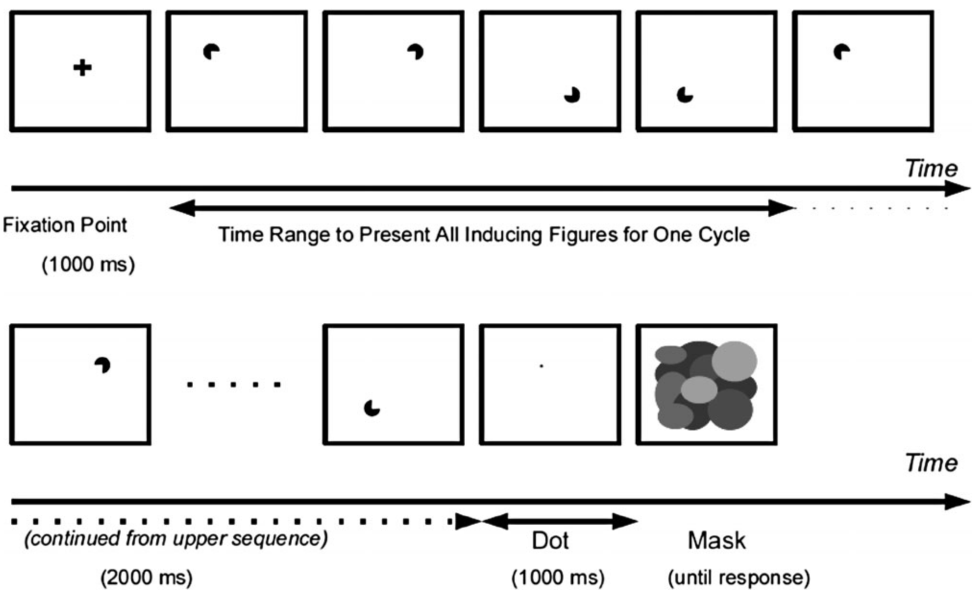

Figure 2 Trial structure for Experiment 1 and 2: Following a fixation point, each inducing element was presented one by one. After presentation of the inducing elements for 2 s, the probe dot appeared for 1 s, and then the mask was presented until the observer responded. The dot in the experiment was significantly smaller than the dot in Figure 2 relative to the stimulus.

process might take into account the broader stimulus context. For example, localization of a dot may be drawn toward the center of the entire stimulus. Further, they proposed an identity hypothesis, which posits that the operation of common boundary interpolation mechanisms is involved both in occluded contour completion and illusory contour formation (Guttman & Kellman, 2004).

In line with the identity hypothesis of occluded and illusory contours, we hypothesize that interpolated contours are less likely to accurately reflect the theoretical contour location within the temporal limits of the dynamic visual icon than in the simultaneous, that is, static, display. More specifically, we hypothesize that interpolated contour location should appear to be located more inside the theoretical location in dynamic displays than a comparable interpolated contour in static displays (Guttman et al., 2003). This is because a dynamic visual icon involves a joint interpolation over both a temporal and a spatial gap. Further, global processing of visual edges (Guttman et al., 2003), which results in localizing a dot towards the center of the entire figure, should also operate in spatiotemporal integration within the temporal limits. We refer to this second hypothesis as the "inaccuracy hypothesis". Although precision and inaccuracy of contour interpolation are distinct hypotheses, it should be noted that they seem to work in a coordinated fashion in static displays (Guttman et al., 2003). Accordingly, we hypothesize a unified representation of interpolated contour that incorporates both precision and inaccuracy in spatiotemporal integration.

In the present experiments, we manipulated the total time involved in presenting a series of inducing corner edges (of an illusory square) for which individual SOAs between successive edge presentations were constant within each of four temporal conditions. In two experiments, the different sets of time ranges were involved. In Experiment 1, following previous work, the total time to present a stimulus series varied from 0 to 180 ms (Ringach & Shapley, 1996; Shipley & Kellman, 1994). This is the short-range condition. The total time in Experiment 2 ranged from 240 to 1920 ms (Takemoto & Ejima, 1997; Unuma & Tozawa, 1994); this is referred to as the long-range condition.

According to the precision hypothesis, a dynamic visual icon should readily integrate visual edges in the short-range condition; moreover, an interpolation mechanism should form a precise representation of an interpolated contour, which is reflected in relatively precise dot-localization performance (Guttman et al., 2003). In Experiment 1, it is possible that short time-spans will keep high precision and, for similar reasons, this hypothesis also predicts lower precision for all the long-range conditions in Experiment 2.

The inaccuracy hypothesis leads to an expectation that viewers are more likely to erroneously report the location of illusory interpolated edges as being inside of the illusory occluding figure in Experiment 1. This is because observers are expected to locate a dot based on a precise but inaccurate contour representation, and because global processing is expected to lead to locating a contour shifted toward the inside of a figure rather than its theoretical location. In addition, the levels of inward shift of contour location may be higher in short-range (Experiment 1) than in long-range conditions (Experiment 2), because more inaccurate illusory contour representation can be used to locate a dot in short-range conditions.

Experiment 1

Method

Observers. Six university undergraduate students (six women), ranging in age from 18 to 23 years (mean age = 20.4 years) and naive to the hypotheses, participated in the experiment. The observers had normal or corrected-to-normal vision.

Apparatus. The experimental trials were generated using a program written in MacProbe 1.702 (Hunt, 1994) on a Macintosh Performa 5320 with a 100-MHz processor. Observers viewed stimuli on a 15-in. color monitor (67 Hz; 640 × 480 pixels) and responded by pressing one of two keys on the keyboard. Observers sat 57.3 cm from the screen with their heads stabilized in a chin and forehead rest.

Stimuli. Figure 1 depicts the stimuli used in the present experiment. The illusory contour stimuli consisted of four black sectors, that is, inducing elements, of 15.2 cd/m^2, each 2.0 deg in diameter, and missing a 90-deg notch measuring 1.0 deg along each edge, on a white background of 92.9 cd/m^2. The center-to-center distance between the inducing elements measured 5.7 deg, which yielded a support ratio of 0.35 (Shipley & Kellman, 1992).

Design. The experimental design was a 4×2 factorial design with two repeated-measures variables. Four levels of total time (0, 60, 120, 180 ms) were crossed with two levels of staircase direction (inside or outside). The 0 time-range condition implies that all inducing elements were presented simultaneously. The time range was determined by presenting equal SOAs between four inducing elements in four levels (0, 15, 30, 45 ms). Thus, each observer completed eight interleaved staircases, with trials from each staircase presented in random order.

Procedure. A schematic illustration of the trial structure appears in Figure 2. Each trial began with the presentation of a 1-s fixation point. Next, four inducing elements (corner edges) appeared successively with identical SOAs (determined for each time condition). The successive presentation of inducing elements continued for 2 s; the exposure duration of each inducing stimulus was held constant (15 ms), except for the exposure duration in the simultaneous condition, in which all inducing corner edges were presented for 2 s. Each inducing stimulus was presented along the profile line of the illusory square, and there were two kinds of serial orders, clockwise and counter-clockwise, which were randomly presented. Each trial began with a presentation of one of the four corner-edge stimuli (randomly determined). After the inducing element sequence, a small red dot (5.4 min of arc $\times$ 5.4 min of arc; 25.3 cd/m^2) was presented for 1 s near the contour of the illusory shape. The small dot was located near the center of an illusory contour line; the line was randomly chosen from among four profile lines of the illusory square. Finally, a mask that covered the whole stimulus area appeared following presentation of the final item and lasted until a response occurred.

The observers reported whether the red dot appeared on the inside or the outside of an imagined or perceived profile line of the illusory shape by pressing one of two keys; no feedback was given. For each stimulus, the position of the probe dot varied based on two interleaved staircases around each of the four profile lines of the illusory square. An inside (2-up/1-down) staircase converged on the point of the underlying psychometric function at which the observer was 0.707 likely (Falmagne, 1985) to respond that the dot appeared “inside” the shape’s boundary; an outside (2-down/1-up) staircase converged on the point of the psychometric functions at which the observer was 0.707 likely to respond that the dot appeared “outside” the shape’s boundary.

The probe dot always appeared along one of the imaginary vertical or horizontal lines, halfway between the two adjoined inducing elements. Completion of the staircase required 10 reversals, with the dot shifting position. The experiment continued until all staircases converged. Most observers required approximately 60 min to complete the task. Observers received a short break every 100 trials.

Analysis. For each staircase, the dot locations giving rise to the final 10 reversals were averaged; these points represent the inside threshold and the outside threshold. We derived three measures for each temporal condition. First, the location measure was designed to estimate the imagined location of a boundary line of the illusory object; this measure was based on the average of the inside and the outside thresholds. A zero location value indicates that an observer imagined the profile line at its exact theoretical location (i.e. the extension of the physical edges). Second, the error in location measure was calculated as the absolute value of location; it indicated the overall accuracy of the performance. Means of the error in location measure across observers were not necessarily identical to the absolute values of the mean of location measure; this is because the means of error in location were calculated from the absolute values of location measure for each observer. Finally, the imprecision measure was defined as the absolute distance between the inside and the outside thresholds. Consistent localization of the dot would produce small values of imprecision; conversely, large imprecision values would reflect lower precision in dot localization.

The data from two observers were discarded from the following analysis. The data from one observer were discarded because of high levels of imprecision in each condition, including simultaneous display, which suggested misunderstanding of or inability in the task. The data from a second observer were discarded because two staircases failed to converge within a 1.5-h session. The location, error in location, and imprecision data from four remaining observers were used to calculate ANOVAs, with the time factor as the within-subject variable.

Results

The imprecision measure indicated that dot localization in the serial presentation condition was as precise as localization in the simultaneous condition (Figure 3a). That is, imprecision of dot localization in the serial presentation conditions did not significantly differ from imprecision in the simultaneous condition, $F(3,9) < 1, p > .50, \eta^2_p = .11$. The estimate of imprecision averaged across observers in Experiment 1 was 16.7 min of arc.

Figure 3b depicts the judged location of contour, averaged across observers, as a function of the time range. Negative values indicate that the estimated location of contours was inside of their theoretical positions (based on actual physical edges). The reported contour location in the serial presentation condition significantly shifted inward compared with location measures in the simultaneous presentation condition, $F(3,9) = 49.43$, $p < .001$, $\eta^2_p = .94$. Planned comparisons supported this trend (P-values < .05 for all t-tests between the serial versus the simultaneous conditions). No significant differences were observed between the different serial presentation conditions ($p > .10$). However, in the serial presentations, the estimates for the locations of profile lines, averaged across observers, shifted 27.5 min of arc inward the illusory square, with a 95% confidence interval of $-31.1 < \mu < -24.0$. This estimate was

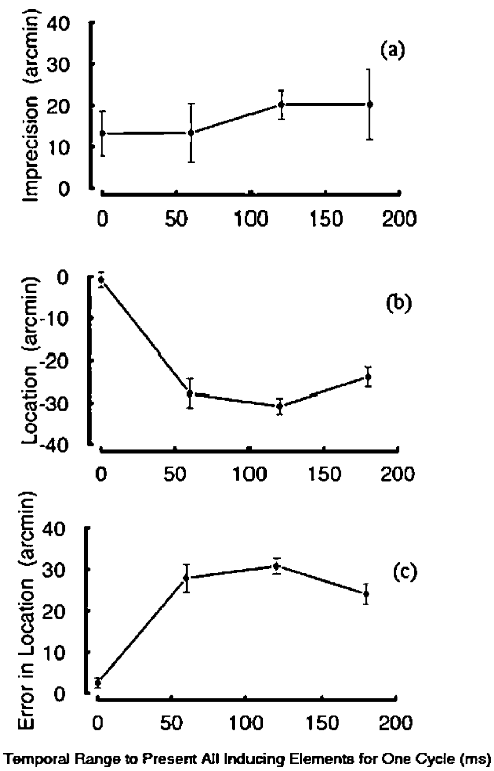

Figure 3 Results of Experiment 1: (a) imprecision as a function of the time range to present all the inducing elements for one cycle; (b) location as a function of the time range to present all inducing elements for one cycle, where the positive values indicate perception of the contour as outside of its theoretical position and the negative values indicate perception of the contour as inside of its theoretical position; and (c) the error in location as a function of the time range to present all the inducing elements for one cycle. Error bars represent plus or minus one standard error of the mean across all observers.

significantly different from the theoretical position (i.e. 0), $t(11) = 17.04$, $p < .05$, $d = 4.92$, whereas the estimate for contour location in the simultaneous condition was 0.81 min of arc, with a 95% confidence interval of $-6.56 < \mu < 4.94$, which includes 0, the theoretical position.

The error in location measure (Figure 3c) also reflected elevated inaccuracy in the serial presentation conditions. Serial presentation of inducing figures produced significantly less accurate dot localization than simultaneous presentation, $F(3,9) = 42.65$, $p < .001$, $\eta^2_p = .93$. Planned comparison (*t*-tests conducted with $\alpha = .05$) indicated that serial presentation led to less accurate dot localization than simultaneous presentation (all *P*-values < .05), but the three serial presentation conditions did not significantly differ from each other (all *P*-values > .05).

Discussion

The results of Experiment 1 support the precision hypothesis that a spatiotemporal integration process generates a precise representation of contours. This is demonstrated by the imprecision measure, which showed that serial presentation of edge fragments produced dot localizations that were comparable in precision to those observed in the simultaneous presentation. These results are consistent with the notion that observers judge the location of the dot based on a contour representation formed in the spatiotemporal integration process. However, the imprecision measure in Experiment 1 suggests that the level of imprecision in the current experiment, 16.7 min of arc on average, is higher than the levels reported in previous studies using a static illusory contour (Guttman & Kellman, 2004). However, there are several reasons for higher imprecision in the present experiment. First, the probe dot appeared near one of four sides of an illusory square that was determined randomly in Experiment 1, while in Guttman and Kellman (2004), the dot always appeared near the same side. Randomly located presentation of the probe dot may produce a higher level of imprecision than presentation in a restricted area. Second, the ratio of size of the inducing elements to the distance between inducers, 0.35, which is referred to as the support ratio (Shipley & Kellman, 1992), is lower than the ratio in Guttman and Kellman (2004), which was 0.50. The lower support ratio should yield weaker or more imprecise interpolation (Shipley & Kellman, 1992).

The location measure addresses the perceived location of the illusory contour. The results of contour location in Experiment 1 support the inaccuracy hypothesis, which holds that inaccurate judgments of perceived shape boundaries should be manifested by dot locations with an inward shift, given a spatiotemporal interpolation process. Here, we propose two alternative hypotheses to explain the process of localizing the dot inaccurately. First, it is possible that observers localize the dot based on a perceptually interpolated contour representation; we refer to this hypothesis as the perceptual representation hypothesis. The results of the imprecision measure also suggest a process in which observers use a precise figural representation to localize the dot. The global process of spatiotemporal integration, which can result in a shift of contour location toward the center of the whole figure, may be affected by the way viewers process static displays (Guttman et al., 2003).

An alternative hypothesis about the location data in Experiment 1 holds that observers tend to respond "outside" rather than inside in a serial presentation paradigm; this is the response bias hypothesis. If observers tend to respond outside in a dot localization task, the location measure should result in the inward location of the contour. The reason why observers do not respond inside but outside remains to be explained, but it is possible to hypothesize that observers have difficulty in judging the location of a dot in a descending series, that is, outside the illusory square. This is because in such cases the visual edges of the inducing figures, four 90-deg notches turned inward to create an illusory figure, and the circular or outer areas of the inducing figures provide more ambiguous cues than the inner notches of the inducing elements for locating a dot. When observers have difficulty in judging the location of a dot, they tend to repeat the same "outside" response; in turn, the location measure will register this response tendency as reflecting inward shifts.

Experiment 2

In Experiment 2, we examined whether the precision or strength of a contour representation, as gauged by a precision measure, decreases with increasing the temporal range. If spatiotemporal interpolation processes cease to operate beyond a postulated temporal limit, then the imprecision measure in this task should increase, because observers may have difficulty locating the dot based on the precise contour representation.

Method

Ten university undergraduate students (10 women), none of whom participated in Experiment 1, observed the stimuli in this experiment. Observers ranged in age from 18 to 22 years (mean age = 20.1 years), and they had normal or corrected-to-normal vision. As in Experiment 1, observers were unaware of the experimental hypotheses.

The experimental stimuli and procedure were identical to those of Experiment 1, except that four time ranges to present all four inducing elements for one cycle (240, 480, 960, 1920 ms) were used. The total amount of time for presenting the inducing stimuli in each trial was held constant (2 s), as in Experiment 1. The data of three measures, location, error in location, and imprecision, from ten observers were examined using a repeated-measures ANOVA with time range as the independent variable.

Results

Figure 4a plots imprecision as a function of the time range in which all four inducing figures are presented for one cycle. The imprecision of dot localization depended on the time range to present all the inducing figures, $F(3,27) = 3.28$, $p < .05$, $\eta^2_p = .27$. Planned comparison (*t*-tests conducted with $\alpha = .05$) indicated no significant differences between the conditions. However, with increments in time range, the imprecision measure tended to increase from 15.8 to 25.9 min of arc. The level of imprecision at the shortest end of the time range (240 ms) in Experiment 2 was close to the average level of imprecision in Experiment 1 (16.7 min of arc), while imprecision at the longest time range (1920 ms) was more than 1.6-fold the level of imprecision at the shortest time range.

In contrast, the location measure data did not depend on the time range (Figure 4b), $F(3,27) = 1.56$, $p > .05$, $\eta^2_p = .15$. The estimate of dot location averaged across time ranges was 11.1 min of arc, which was closer to the theoretical position than the estimate in the serial presentation conditions in Experiment 1

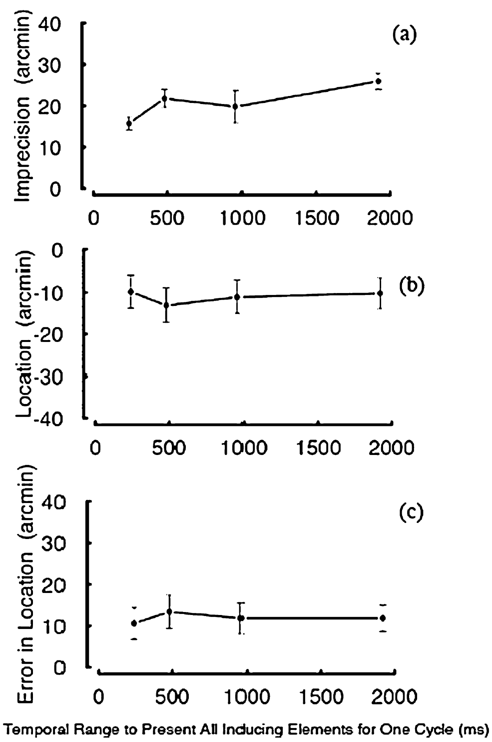

Figure 4 Results of Experiment 2: (a) imprecision; (b) location; and (c) the error in location. Each measure is plotted as a function of the time range to present all the inducing elements for one cycle in the same way as in Figure 3. Error bars represent plus or minus one standard error of the mean across observers.

(27.5 min of arc). The 95% confidence interval of the location measure calculated from the pooled data in Experiment 2 was $-15.0 < \mu < -7.2$, which does not overlap with the confidence interval for the location measure in the three serial presentation conditions from Experiment 1, which was $-31.1 < \mu < -24.0$. The error in the location measure did not depend on the time range (Figure 4c) as well as the location measure, $F(3,27) = 1.12$, $p > .05$, $\eta^2_p = .11$. The estimate for the error of location averaged across the time ranges was 11.9 min of arc, which was significantly different from zero, $t(39) = 6.57$, $p < .05$, $d = 1.04$.

Discussion

The results of the imprecision measure in Experiment 2 support and extend the precision hypothesis. The levels of imprecision in Experiment 2 were equal to or greater than the imprecision measures found in Experiment 1. These findings are consistent with the notion that precise contour representations can be formed within a limited time range; therefore, the precision (strength) of a contour representation should be reduced when a 200-ms temporal limit is exceeded. However, the fact that the level of imprecision in the 240-ms condition was equal to the level in the serial presentation condition in Experiment 1 needs to be considered together with the results of the contour location, as discussed below.

Compared with the results for Experiment 1, the location and the error in location measures in Experiment 2 showed that observers locate the dot closer to the theoretical position. These findings are consistent with the notion that observers in short time ranges locate the dot based on a precise perceptual representation of illusory shape, whereas in longer time ranges they may rely on a strategy such as locating the dot on the extension of the visual edge. The lower values for the shifts in dot localization in the long-range condition also suggest that imprecision in this condition may not be affected by a perceptual representation of the illusory square. It remains possible that the response-bias hypothesis, which assumes a tendency toward repetition of "outside" responses in a descending series, may provide an explanation for slight inside shifts of dot localization. For example, if observers locate a dot using locations of inducing elements that blink separately with long intervals, dot localization appears to be difficult in the long temporal range.

The level of location error in the 240-ms condition is consistent with neither the location errors in the simultaneous condition nor these errors in the serial presentation conditions in Experiment 1. The levels of location errors and imprecision measures in the 240-ms condition are contradictory and insufficient for the evidence of contour interpolation. Although the results for the imprecision measures may suggest some kind of representation of perceived shape, this interpretation requires careful consideration because the observers in the current experiment were different from those in Experiment 1. We suggest that dot localization in 240 ms is not affected by precise representation of the illusory figure that can be formed in the short time-range in Experiment 1.

General discussion

In the present study, our goal is to understand the spatiotemporal integration and contour interpolation process in the general framework of object perception. Following Palmer et al. (2006), we hypothesize that a DVI model explains spatiotemporal integration of visible edges and the resulting formation of an illusory contour representation. According to this view, this is accomplished by a combination of visual persistence and position updating of sequentially viewed edges. In this research, persistence in the DVI is crucial for preserving contour and location information during the temporal gaps between successive inducing elements. (Positional updating is not required in the present displays because the illusory object is formed in a constant observer-relative position.) Our specific aim was to further clarify the temporal and spatial characteristics of the dynamic visual icon. The precision hypothesis proposes that, for a limited range of time intervals, a dynamic visual icon forms a precise contour representation. In turn, this implies that the precision of a contour representation should decrease with increasing temporal range beyond some limit. Assuming that observers can form a precise contour representation (with shorter time intervals), the inaccuracy hypothesis nonetheless predicts, based on earlier findings, that the specific loci of the perceived contour lines will reflect an overall shrinkage of the illusory object within a limited temporal range. To test predictions from these hypotheses, two experiments were conducted using a dot localization task in conjunction with serial presentation of inducing edges of an illusory contour figure.

In both experiments, the imprecision measure suggested that observers located probe dots with precision for short temporal ranges. To give an intuitive understanding of precision, the smallest imprecision values observed (approximately 13.3 min of visual angle) correspond to localizing the contour within approximately a 2.2-mm range at a viewing distance of 57.3 cm. The location and the error in location measures showed that the reported location of contour shifted toward the inside boundaries of the illusory shape in conditions with a short temporal range, suggesting that within temporal limits, viewers perceived the object to shrink. Dot localizations in the conditions with longer temporal ranges showed smaller inward shifts of the contour than dot localizations in shorter temporal conditions; this suggests a more accurate, yet imprecise, representation of contour in longer temporal ranges. These results, taken together, support the precision hypothesis and the inaccuracy hypothesis about spatiotemporal integration and formation of contour representation in a limited, 180-ms, temporal range. The 180-ms temporal range, the longest condition in Experiment 1, allows precise contour representation that is consistent with the estimates reported in previous research with dynamic displays, such as an 175-ms estimate from Keane et al. (2007) and an 165-ms estimate from Shipley and Kellman (1994).

It should be noted that the relative roles of contour or boundary formation and surface-spreading processes have been modeled (Grossberg & Mingolla, 1985), and that a fast contour-formation system (15 Hz) and a slower surface-discrimination system (<7 Hz) have been reported (Rogers-Ramachandran & Ramachandran, 1998). While illusory contours (Guttman & Kellman, 2004) and occluded contours (Sekuler & Palmer, 1992) take a longer time to develop than real contours, empirical results suggest that illusory and occluded contours depend on a common contour/boundary interpolation process (Kellman et al., 2001; Kellman & Shipley, 1991). Complete interpolation of occluded contours develops over time and seems to require at least 200 ms (Sekuler & Palmer, 1992). Ringach and Shapley (1996), using illusory figures, estimated that local contour processing requires approximately 120 ms, whereas global processing, including surface-spreading processes, requires an extra 140–200 ms.

In the current research, we observed an inconsistency between imprecision and the location and the error in location measures in the 240-ms condition in Experiment 2. The reason for this is not clear. Although different observers from those in Experiment 1 participated in Experiment 2, the level of imprecision measured in the 240 ms condition in Experiment 2 suggests that the precision or strength of a representation was comparable with that observed in the short-range conditions. But the levels of the location and the error in location measures show a higher accuracy, which indicates a different characteristic of representation. Taking into consideration the difference in the temporal characteristics of the contour system and the surface-spreading system (Ringach & Shapley, 1996), the surface-spreading system might operate in the 240-ms condition. The notion of the difference of the temporal characteristics of the contour system and the surface-spreading system is consistent with the estimates of spatiotemporal integration, approximately 300 ms, using brightness change as a measure (Takemoto & Ejima, 1997; Unuma & Tozawa, 1994). The unit representation of objects (Kellman et al., 1998, 2001) might be related to such a surface representation. In the 240-ms condition, the surface-spreading system seems to allow surface representation, which leads to low imprecision and accurate performance in the dot-localization task.

The temporal characteristics of spatiotemporal integration within short time ranges (i.e. less than 180 ms) appear to be analogous to numerous findings with static displays in which all inducing elements appear simultaneously (Guttman & Kellman, 2004; Ringach & Shapley, 1996; Sekuler & Palmer, 1992; Shipley & Kellman, 1994). Hereon, we consider relations between spatiotemporal integration and spatial integration that have been examined in research with static displays. According to neural network models that hypothesize an interactive network of orientation-sensitive units (Field, Hayes, & Hess, 1993; Pillow & Rubin, 2002), spatial integration and interpolation revealed by dot-localization performance may be explained as follows (Guttman et al., 2003). Spatial integration depends on the successive activation of neural units; however, the final activation levels of units corresponding to dot or interpolated-contour location are assumed to decrease with increasing spatial distance from visible edges. Building on this rationale, it is possible that if the activation of units corresponding either to the dot or to the contour location decreases with increments in the temporal range of the inducing figures, dot localization in serial presentation situations will become correspondingly less precise as temporal range increases beyond a particular temporal limit. In this way, spatial integration can be understood as a limiting case of spatiotemporal integration (Keane et al., 2007; Palmer et al., 2006), where temporal gap or persistence has zero value.

The inaccuracy hypothesis, which posits that illusory shapes are perceived to shrink, requires a more developed rationale. Inaccurate contour location in spatiotemporal integration is analogous to the inaccuracy of the occluded contour in static displays (Guttman et al., 2003). In both spatiotemporal and spatial integration of visible edges, global as well as local processes may be involved (Sekuler, Palmer, & Flynn, 1994). For example, evidence for global processing is found in the apparent shrinkage of a global contour; this is consistent with the idea that fragmented edges are integrated toward the center of an illusory square. In sum, the current results support the idea that the same contour interpolation mechanism that operates in spatiotemporal integration also operates in the static or spatial integration.

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(Received May 5, 2009; accepted January 30, 2010)