Feature Integration Across Space, Time, and Orientation

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The perception of a visual target can be strongly influenced by flanking stimuli. In static displays, performance on the target improves when the distance to the flanking elements increases—presumably because feature pooling and integration vanishes with distance. Here, we studied feature integration with dynamic stimuli. We show that features of single elements presented within a continuous motion stream are integrated largely independent of spatial distance (and orientation). Hence, space-based models of feature integration cannot be extended to dynamic stimuli. We suggest that feature integration is guided by perceptual grouping operations that maintain the identity of perceptual objects over space and time.

Keywords: nonretinotopic processing, motion grouping, metacontrast masking, oblique effect, contrast polarity

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The processing and the perception of a visual target can be strongly influenced by stimuli presented at spatially adjacent locations (e.g., Badcock & Westheimer, 1985a, 1985b; Levi, Klein, & Aitsebaomo, 1985; Watt & Morgan, 1984; Westheimer & McKee, 1977). For example, Westheimer and Hauske (1975) showed that vernier offset discrimination deteriorates in the presence of adjacent flanking lines and that the strength of this interference decreases as the distance between the flankers and the target vernier increases. Typically, distance-dependent lateral inhibition has been assumed as a mechanism to explain this interaction (Figure 1a).

In feature pooling, for example, features of neighboring elements are combined according to a weighted average. Parkes, Lund, Angelucci, Solomon, and Morgan (2001) showed that observers cannot discriminate the orientation of a tilted Gabor patch surrounded by vertically oriented distractor Gabors. However, the whole group of Gabors appears to be slightly tilted in the direction of the central Gabor (see also, Baldassi & Burr, 2000). If the distractors are slightly tilted in the opposite direction as the central Gabor, the opposite tilt directions cancel out each other. This finding indicates that the orientation signals of the individual Gabors are pooled, an instance of feature integration. If the distance between the single Gabors is increased, no feature pooling occurs. This dependency on distance is typically modeled by a Gaussian weighting function (Figure 1b; e.g., Wilkinson, Wilson, & Ellemberg, 1997). Similar to the dependency on "spatial distance," feature pooling and lateral inhibition are also assumed to depend on the "distance" in the orientation domain.

While there has been extensive research documenting how these distance-dependent interactions influence the processing of *static* stimuli, only very little is known on how the features of *dynamic* stimuli are processed and integrated over space and time. Recently, we have introduced a paradigm, called sequential metacontrast, to study feature integration with dynamic stimuli (Otto, Ögmen, & Herzog, 2006; see also, Piéron, 1935). In sequential metacontrast, a central line is followed on either side by a sequence of flanking lines which are consecutively presented further away in space (Figure 2a). With this stimulation, observers perceive two diverging streams of flanking lines, one moving to the left and one moving to the right (Figure 2b; for an animation, see supplementary material). As expected from classical metacontrast masking (e.g., Bachman, 1994; Breitmeyer & Ögmen, 2006; Stigler, 1910), the visibility of the central line is strongly suppressed. Still, if the central line contains, as a feature, a small vernier offset, observers perceive a corresponding offset in the motion streams. For example, when we asked observers to report the offset of one *attended*[1] motion stream (e.g., the stream moving to the right; see Figure 2b),

[1] In our previous experiments as well as in the experiments reported in this article, observers attended to one pre-determined motion stream and reported the perceived vernier offset within this attended stream. Therefore, attention was always focused on the stream identified for the perceptual report. Because we did not manipulate independently the "attended stream" from the "stream for perceptual report," here we do not make any claims on the role of attention in dynamic feature integration.
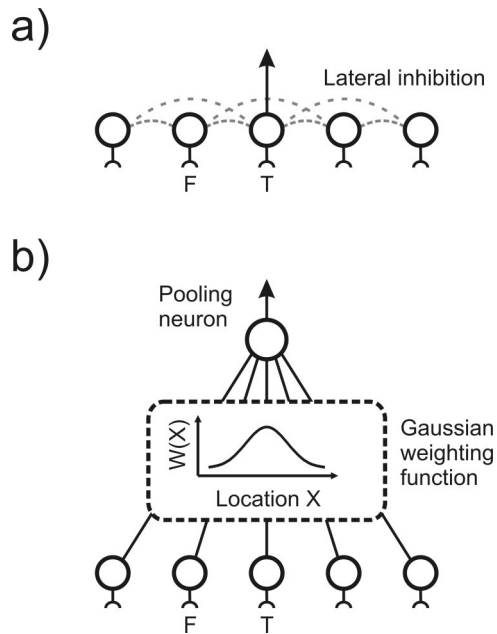
a)

b)

Figure 1. Mechanisms proposed to explain spatial interactions for static stimuli. Features are analyzed by a set of stimulus specific neurons. (a) Lateral inhibition. The central neuron is activated by the target stimulus (T). The neuron activated by a flanking stimulus (F) inhibits the neuron responding to T. The inhibitory interaction decreases as the distance between T and F is increased (as indicated by the dotted lines). (b) Pooling. Neurons are activated by T and F, respectively. A pooling neuron computes a weighted sum of the outputs of these sensory neurons. As with lateral inhibition, these excitatory interactions are distance dependent; that is, the magnitude of the weights decreases with distance, typically following a Gaussian function.

observers report an offset in the direction of the offset of the central line (Otto et al., 2006). If one of the flanking lines of the attended stream is offset in the opposite direction as the offset of the central line, the opposite offset directions cancel out each other. This finding indicates that the offsets of the individual lines within the motion stream are integrated. If one of the flanking lines of the unattended stream is offset, this flank offset does not affect performance. Hence, offsets of the single lines are only integrated if they are presented within the same motion stream (Otto et al., 2006).

Feature integration within a motion stream bears some similarity to feature pooling with static stimuli. In the latter case, feature pooling occurs when a set of single elements (as the Gabor patches in the experiments of Parkes et al., 2001) are grouped across space to a single Gestalt, like trees to a forest (c.f., Cavanagh, 2001). Analogously, in the former case, feature integration occurs when the single lines are grouped across space and time to one "moving" line. In both cases, observers seem to compute an accurate average of the features of the individual elements (see also, Ariely, 2001). This average is then attributed to the global percept. On the other hand, a solely space-based mechanism, as assumed for feature pooling with static stimuli, seems not applicable for feature integration with dynamic stimuli. When multiple objects are in motion, these objects can occupy the same space at different times. Consequently, if feature integration is extended in time, as required for the analysis of motion,

a solely space-based mechanism would incorrectly blend features of different objects. Hence, feature integration occurring with dynamic stimuli should be guided by the grouping of the single elements to one motion stream, which is defined by space and time, rather than by the pure spatial distance between elements. Because motion is ubiquitous in natural viewing conditions, from a theoretical standpoint, it is a fundamental necessity to understand feature integration, not just across space, but in space-time along the trajectories of moving objects.

In this contribution, we investigated spatiotemporal feature integration along motion trajectories by using the sequential metacontrast paradigm. We tested feature integration by presenting two offsets with opposite directions within the stimulus sequence and measured how the two offsets are integrated (see Figure 2). In Experiments 1–3, we varied the distance between the two offsets (1) by changing the position of the offsets in a fixed sequence, (2) by increasing the distance between consecutive lines, and (3) by increasing the length of the whole sequence. Moreover, in Experiment 4, we tested how offsets of different sizes yielding different performance levels are integrated. In Experiment 5, we presented lines of different contrast polarities (i.e., black or white lines on a grey background) to test whether the integration of offsets is limited to lines of the same contrast polarity. To test if the integration of offsets can also be extended to lines of different orientation, in Experiment 6, we presented lines along circular motion trajectories. Finally, in Experiment 7, we present sequences of only two lines but with the same spatiotemporal distances for which we found integration in Experiments 1 and 6. This manipulation allows us to test whether the smooth spatiotemporal continuity of lines is necessary for integration.

General Methods

Observers

Data were obtained from paid, naive observers and one of the authors (T.O.). After the general purpose of the experiments was explained, observers signed informed consent. Observers were told that they could quit the experiment at any time they wished. For each observer, we determined the visual acuity by means of the Freiburg visual acuity test (Bach, 1996). To participate in the experiments, observers had to reach a value of 1.0 at least for one eye (corresponding to a Snellen fraction of 20/20).

Apparatus

Stimuli appeared on an X-Y-display (HP-1332A, or Tektronix 608) controlled by a PC via fast 16-bit D/A converters. Stimuli were composed of dots drawn with a dot pitch of 250-350 μm at a dot rate of 1 MHz. The dot pitch was selected so that dots slightly overlapped; that is, the dot size (or line width) was of the same magnitude as the dot pitch. Refresh rate was 200 Hz. Stimulus luminance was 80 cd/m^2, as measured with a Minolta LS-100 luminance meter by means of a dot grid (same dot pitch and refresh rate as above). The room was dimly illuminated (approximately 0.5 lux) and background luminance on the screen was below 1 cd/m^2. Viewing distance was 2 m.

In Experiment 5, stimuli were presented on a Philips 201B4 CRT monitor driven by a standard accelerated graphics card. The
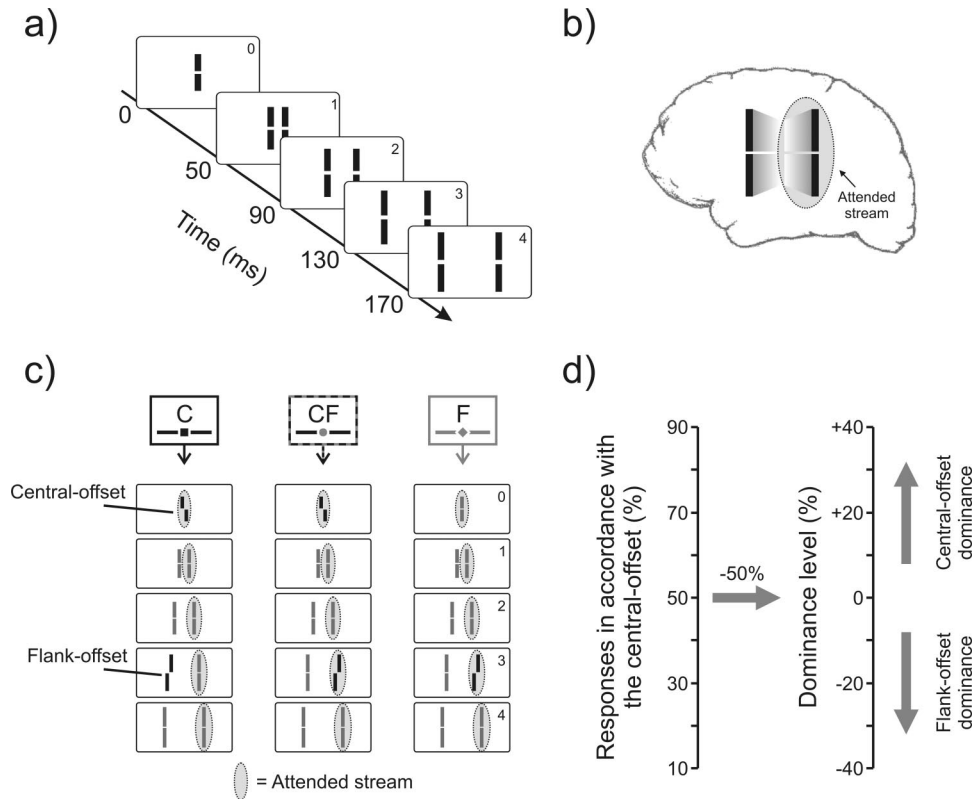
Figure 2. (a) Sequential metacontrast. In the standard sequence, a central line (frame 0) was followed by four successive pairs of flanking lines (frames 1–4; frame numbers were not displayed in the actual displays). Actual stimuli were bluish white on a dark background. (b) A motion percept of two streams of lines diverging from the center is elicited. The central line itself is largely invisible (Otto, Ogmen, & Herzog, 2006; for an animation, see supplementary material). In the experiments, we asked observers to attend only to one of the two streams (e.g., the right stream as highlighted by the grey ellipse). (c) We presented three basic offset conditions. In condition C, the central line contained a vernier-offset ("central-offset'), which was randomly offset either to the left or to the right in each trial. In addition, in the *unattended* stream, one of the flanking lines contained a vernier-offset ("flank-offset," here in frame 3). The direction of the flank-offset was always opposite to the direction of the central-offset (i.e., when the central-offset was to the right, the flank-offset was to the left, and vice versa). Condition CF is the same as condition C but the flank-offset was presented in the *attended* stream. In condition F, the flank-offset was presented in the attended stream while the central line was aligned. In all conditions, we asked observers to indicate the direction of the vernier-offset perceived in the attended motion stream (the ellipses are used for graphical purpose and were not presented in the actual displays). (d) We recorded the percentages of responses in accordance with the central-offset. Because the direction of the flank-offset was opposite to the central-offset, this percentage is expected to be below 50% when responses are determined by the flank-offset (e.g., when 30% of the responses are in accordance with the central-offset, actually 70% of the responses are in accordance with the flank-offset). To provide an intuitive performance measure, we converted these percentages into *dominance levels* by subtracting 50%. With dominance levels, the sign indicates whether the central- (+) or the flank-offset (–) dominates the responses. Moreover, the absolute value reflects the strength of the corresponding dominance. A dominance level of 0% indicates that the two offsets contributed equally to the responses.

screen size was adjusted to 360 by 288 mm with a screen resolution of 1280 by 1024 pixels. Refresh rate was 100 Hz. The white point of the monitor was adjusted to D65. The color space was computationally linearized by applying individual gamma corrections to each color channel (eight bits per channel). A Minolta CA-210 display color analyzer was used for calibration measurements. Stimulus luminance was adjusted individually as described below (see Contrast Polarity Calibration). The room was dimly illuminated (approximately 0.5 lux). Viewing distance was 5 m.

Stimuli and Procedures

Standard Sequence

We presented variations of the sequential metacontrast stimulus as introduced by Otto et al. (2006). The standard sequence started with a central line consisting of two vertical segments of 10.0′ (arcmin) length separated by a vertical gap of 1.0′ (Figure 2a). Four pairs of flanking lines followed one after the other. The segment length for the first pair of flanking lines was 11.7′ and

increased progressively by 1.7′ for the following lines. The centroid-to-centroid distance between the central line and the first flanking lines as well as between consecutive flanking lines was 3.3′.

Each line was presented for 20 ms. The stimulus onset asynchrony (SOA) between the central line and the first pair of flanking lines was 50 ms. The SOA between consecutive flanking lines was 40 ms. Hence, the SOA between the central line and the last pair of flanking lines was 170 ms. Consequently, the "speed" of the motion streams (see Figure 2b) was approximately 1.3 deg/s.

Task and Offset Conditions

Before the experiment proper, we asked observers to attend to one motion stream. Most observers attended to the stream moving to the right. In a binary task, we asked observers to indicate the perceived vernier-offset direction in this attended stream.

We employed a paradigm comprising three conditions (Figure 2c). In condition C, the central line was offset. The direction of this central line offset, hereafter the *central-offset*, was chosen randomly in each trial. In addition, one flanking line in the *unattended* stream also had a vernier offset (e.g., the flanking line in frame 3 as shown in Figure 2c). The direction of this *flank-offset* was chosen to be opposite to the central-offset. Hence, when the central-offset was to the left, the flank-offset was to the right, and vice versa. All other lines in the display were non-offset. Hence, in condition C, we presented only the central-offset in the attended stream.[2]

In condition CF, we presented the central- and the flank-offset as before. In contrast to condition C, the flank-offset was presented in the attended stream of lines (Figure 2c). Hence, in condition CF, we presented both the central- and the flank-offset in the attended stream.

In condition F, we presented only the flank-offset in the attended stream (Figure 2c). The central line was non-offset. For consistency, we labeled a response that was in accordance with the flank-offset to be *not* in accordance with the central-offset as in the previous conditions (see Data Analysis).

Offset Sizes

Before the experiment proper, we determined offset sizes individually to achieve comparable performance levels across observers. We determined offset discrimination thresholds for a single offset presented either at the central line (i.e., as in condition C but without the flank-offset in the unattended stream) or at the penultimate flanking line of the attended stream (i.e., as in condition F) using an adaptive staircase procedure (PEST; Taylor & Creelman, 1967). We estimated the threshold of the psychometric function (cumulative Gaussian) by means of a maximum likelihood analysis. In the actual experiments, we used constant offset sizes according to the individual threshold levels for the central- and the flank-offset, respectively.

Stimulus Presentation and Responses

Each trial was initiated with four markers at the corners of the screen together with a fixation dot in the center presented for 500 ms. A blank screen followed for 200 ms. Then, the actual stimulus

sequence was presented. After stimulus presentation, a blank screen appeared and observers responded by pressing one of two buttons. To indicate the offset direction of the attended stream, observers pressed the left/right button when they perceived the lower line segment offset to the left/right with respect to the upper segment. No feedback was given. A new trial was initiated 500 ms after the observer gave a response.

We presented stimuli in blocks of 80 trials. For each observer, we presented each condition in a total of 160 trials. While condition F was presented in two separate blocks, conditions C and CF were presented randomly interleaved within four blocks. Naive observers were neither told which condition was presented nor that only a subset of lines in the display was offset (even if observers are aware of the paradigm, they cannot indicate which line in the attended stream was offset; Otto et al., 2006). We randomized the order of blocks across observers to reduce the influence of hysteresis, learning, or fatigue effects in the averaged data.

Contrast Polarity Calibration

In Experiment 5, we presented lines with opposite contrast polarity on a uniform gray background. Luminance of black (negative contrast) and white (positive contrast) lines was 0.3 cd/m² and 115.0 cd/m², respectively, as measured with a GretagMacBeth EyeOne Display 2′ colorimeter. Before the experiment proper, the luminance of the gray background was adjusted individually for each observer to achieve comparable performance levels for both contrast polarities. We presented a sequence of three lines (i.e., each consisting of two line segments of 10.0′ length with a vertical gap of 1.0′) that were consecutively shifted by 3.3′ to the right. Each line was presented for 20 ms. The SOA between consecutive lines was 40 ms. The central line contained a probe-vernier. We presented a block of 100 trials with both contrast polarities randomly interleaved. We asked observers to indicate the offset of the line in apparent motion and determined offset discrimination thresholds for the probe vernier independently for either contrast polarity using an adaptive procedure (PEST; see Offset Sizes). If the thresholds for the two contrast polarities were not comparable, the background luminance was shifted in the direction of the contrast polarity yielding the lower threshold. We repeated this procedure until we found a background luminance yielding comparable thresholds for both contrast polarities. Individual values for the background luminance ranged from 48.5 to 56.3 cd/m² (mean: 53.5 cd/m²).

Data Analysis

For each trial, we analyzed if the observer's response was in accordance with the direction of the central-offset. For each condition and each observer, we recorded the percentage of responses in accordance with the direction of the central-offset. Note that the direction of the flank-offset was always opposite to the direction of the central-offset. Hence, when this percentage was below 50%, more responses were in accordance with the flank-offset. To provide an intuitive performance measure, we computed the *dom-*

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[2] The motion grouping between the central line and the first pair of flanking line is ambiguous. Hence, the central line can be grouped to the attended as well as to the unattended stream.

inance level by subtracting 50% from the percentage of responses in accordance with the central-offset (Figure 2d). With dominance levels, positive and negative signs indicated that more responses were in accordance with the central- or the flank-offset, respectively. Moreover, the absolute value indicated the strength of the corresponding dominance. A dominance level of 0% indicated that neither offset dominated performance. For each condition, we computed the mean dominance level and standard error of the mean (SEM) across observers.

Experiment 1: Flank-Offset Position

If feature integration within the attended motion stream is determined by the spatiotemporal distance between the elements, as assumed in retinotopic feature integration models (e.g., Wilkinson et al., 1997), offset integration should vary when the distance

between the two offsets in the sequence is varied. This hypothesis was tested in Experiments 1–3. First, we varied the distance between the central- and the flank-offset by presenting the flank-offset at different positions in a fixed stimulus sequence.

Methods

In the first part Experiment 1, we presented the standard sequential metacontrast sequence with four pairs of flanking lines. For the three basic offset conditions C, CF, and F, we presented the flank-offset block-by-block either in frame 1, 2, or 3 (Figure 3a). Hence, the centroid-to-centroid distances between the central- and the flank-offset were 3.3′, 6.7′, or 10.0′. Corresponding SOAs were 50, 90, and 130 ms, respectively. For six observers, individual offset sizes ranged from 0.8′ to 1.5′ (mean: 1.3′) for the central-offset and from 0.5′ to 1.0′ (mean: 0.8′) for the flank-
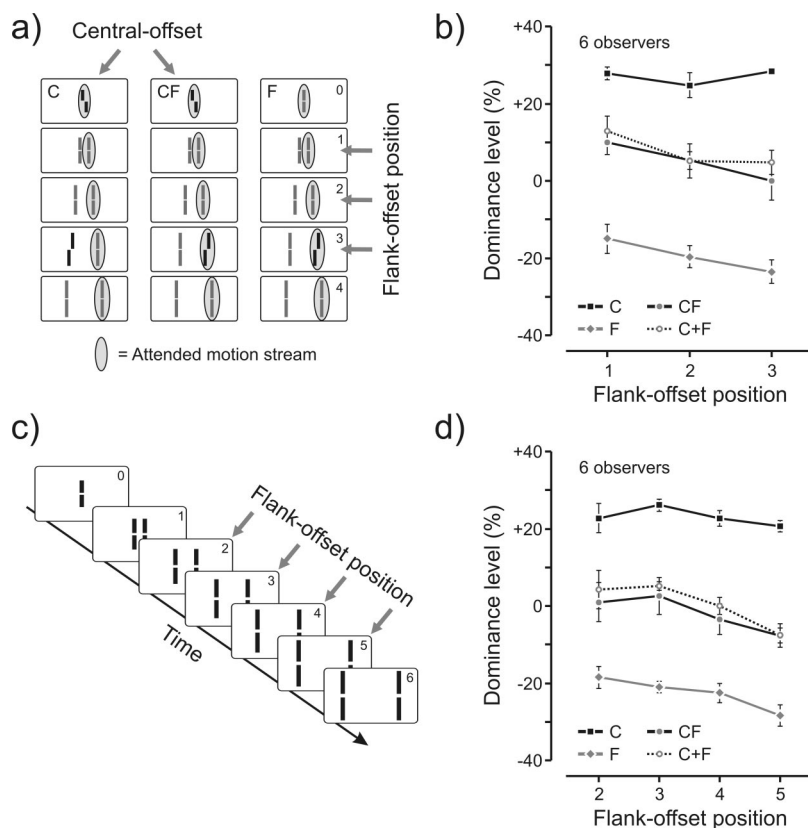

Figure 3. Flank-offset position. (a) We presented the standard sequence in the three basic offset conditions C, CF, and F (see also, Figure 2c). Block by block, we presented the flank-offset in frames 1, 2, or 3 (in this illustration, the flank-offset is shown in frame 3). (b) Dominance levels as a function of the flank-offset position. The sign of the dominance level indicates whether more responses were in accordance with the central- (+) or the flank-offset (−). The strength of the corresponding dominance is given by the absolute value (Figure 2d). In condition C, responses were dominated by the central-offset irrespective of the flank-offset position in the *unattended* stream. In condition F, responses were dominated by the flank-offset. This dominance was slightly stronger for flank-offsets presented later in the sequence. In condition CF, the dominance level was roughly between 0% and + 10% indicating an integration of the two offsets. The actual dominance level was well predicted by the sum (C + F) of the dominance levels achieved in the conditions C and F. Means and SEM of 6 observers. SEM can be smaller than symbol size. (c, d) We repeated the experiment with 6 pairs of flanking lines. We presented flank-offsets in frames 2, 3, 4, and 5, respectively (no offset is shown in this illustration). Results are similar to the conditions with 4 pairs of flanking lines. Means and SEM of six observers.

offset. The offset size for the flank-offsets was the same for the three flank-offset positions.

In the *second* part, in order to cover a larger spatiotemporal window, we repeated the experiment with a stimulus sequence comprising six pairs of flanking lines (Figure 3c). The duration of this sequence was 270 ms. Block by block, the flank-offset was presented in frame 2, 3, 4, or 5. Hence, the centroid-to-centroid distances between the central- and the flank-offset were 6.7′, 10.0′, 13.3′, or 16.7′. Corresponding SOAs were 90, 130, 170, and 210 ms, respectively. Six new observers participated. Individual offset sizes ranged from 1.0′ to 1.7′ (mean: 1.3′) for the central-offset and from 0.5′ to 1.2′ (mean: 0.8′) for the flank-offset. The size for the flank-offsets was the same for all flank-offset positions.

Results and Discussion

In condition C, the central-offset was presented in the attended motion stream and the flank-offset was presented at different positions in the unattended stream (Figure 3a). For the sequence with four pairs of flanking lines, dominance was roughly constant for the different flank-offset positions (Figure 3b, condition C). Similarly, for the sequence with 6 pairs of flanking lines, dominance levels seemed not to change with flank-offset positions (Figure 3d, condition C). Hence, with both sequences, dominance is rather not changed when we varied the position of the flank-offset within the *unattended* stream of lines.

In condition F, the flank-offset was presented in the *attended* stream and the central line was aligned (Figure 3a). In the sequence with four pairs of flanking lines, the flank-offset dominated responses (Figure 3b, condition F). When the flank-offset was presented in later frames, this dominance increased (linear regression analysis, slope: −4.3, SEM: 0.9, R^2 = 0.99). For the sequence with 6 pairs of flanking lines, we found a similar trend (Figure 3d, condition F; linear regression analysis, slope: −3.1, SEM: 1.0, R^2 = 0.92).

In condition CF, the central- and the flank-offset were both presented in the *attended* stream of lines (see Figure 2c). For the sequence with four pairs of flanking lines, the dominance level was roughly between 0% and + 10% (Figure 3b, CF). Hence, neither offset dominated too strongly. This finding indicates that the central- and the flank-offset were integrated (see also, Otto et al., 2006). For condition CF, we estimated the dominance level by the sum of the dominance levels achieved separately in conditions C and F. Interestingly, this estimated dominance level fitted the experimental data well for all flank-offset positions (Figure 3b, C + F). The same finding holds for the sequence with 6 flanking lines (Figure 3d, CF and C + F). Hence, when we presented the flank-offset in frame 5 (i.e., 16.7′ away from the central-offset and with a SOA of 210 ms), integration seemed not to differ, for example, from the condition with the flank-offset in frame 1 (i.e., 3.3′ away from the central-offset with a SOA of 50 ms only; see Figure 3b).

Experiment 2: Flank Distance

In Experiment 1, we investigated integration when the position of the flank-offset was varied within a fixed stimulus sequence. In Experiment 2, we varied the distance between the central- and the flank-offset by varying the distance between consecutive flanking lines.

Methods

We presented the standard sequence and used distances between consecutive flanking lines of 1.7′, 5.0′, and 8.3′, respectively. The distance between the central line and the first flanking lines was 3.3′ to ensure strong masking of the central line. Hence, the distance between the central line and the flanking lines presented last was 8.3′, 18.3′, or 28.3′, respectively. By increasing the distance between flanking lines while keeping the stimulus timing constant, we co-varied the speed of the motion streams from 0.8 deg/s (for a spacing of 1.7′) up to 2.8 deg/s (for a spacing of 8.3′). For 6 observers, individual offset sizes for the central- and the flank-offset ranged from 0.8′ to 1.9′ (mean: 1.3′) and from 0.5′ to 1.3′ (mean: 0.8′), respectively. The flank-offset was presented in frame 3. The procedure was the same as in Experiment 1 (see Figure 2c).

Results and Discussion

In condition C, responses were dominated by the central-offset and this dominance varied only slightly, if at all, when the flank distance increased (Figure 4, C). Similarly, in condition F, responses were dominated by the flank-offset (Figure 4, F). For larger flank distances, this dominance seemed slightly to decrease. These results are essentially similar to those of the Experiment 1 (Figure 3b).

In condition CF, the integration of two offsets changed depending on the flank distance. While dominance levels were roughly
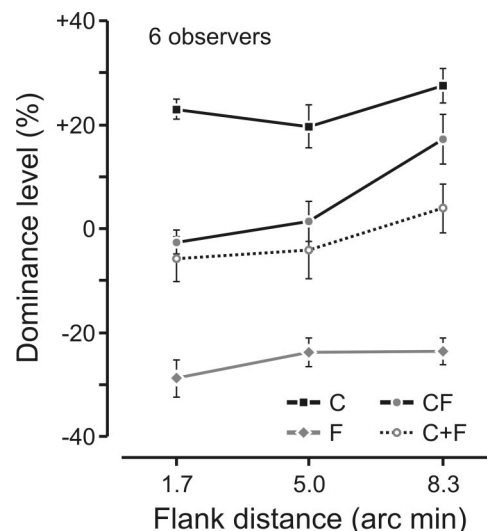

Figure 4. Flank distance. We presented the standard sequence with the flank-offset in frame 3 (see Figure 2). We varied the distance between consecutive flanking lines. For flank distances of 1.7′ and 5.0′, results are comparable to Experiment 1 with a flank distance of 3.3′ (Figure 3b). However, for the flank distance of 8.3′, the dominance level in the condition with both the central- and the flank-offset in the attended stream differed from the predicted dominance level (CF vs. C + F). Hence, offset integration is not linear for this distance. Means and SEM of 6 observers.

around 0% for flank distances of 1.7′ and 5.0′, more responses were in accordance with the central-offset for a distance of 500″ (Figure 4, CF). Moreover, for distances of 1.7′ and 5.0′, the dominance levels predicted by linear integration roughly fitted the experimental data (Figure 4, C + F). However, for the distance of 8.3′, the difference between the predicted and the experimental dominance levels was significant (mean difference: 13.3%; two-tailed, paired t-test; $p = .028$). Hence, for the flank distance of 8.3′, we did not observe linear integration as in Experiment 1.

Experiment 3: Sequence Length

To further investigate the spatiotemporal window over which integration operates, in Experiment 3, we varied the distance between the central- and the flank-offset by varying the length of the stimulus sequence.

Methods

We presented sequences with 4, 6, 8, or 10 pairs of flanking lines (Figure 5a). The SOA between successive flanking lines was 40 ms. The distance between successive flanking lines was 3.3′. Hence, for 10 pairs of flanking lines, the distance between the central line and the last flanking line was 33.3′ (i.e., more than 0.5 deg) with an SOA of 410 ms.

For five observers, individual offset sizes ranged from 0.8′ to 1.3′ (mean: 1.1′) for the central-offset and from 0.5′ to 1.0′ (mean: 0.7′) for the flank-offset (as determined with the standard sequence and the flank-offset in frame 3). Flank-offsets were presented in the penultimate frame; that is, by extending the sequence, we also increased the spatiotemporal distance between the central- and the flank-offset. The procedure was the same as in Experiments 1 and 2 (see Figure 2c). However, observers were explicitly asked to report the offset at the end of the motion sequence.

Results and Discussion

In condition C, using the same offset size, the dominance of the central-offset decreased when we increased the number of flanking lines (Figure 5, C; linear regression analysis, slope: −2.3, SEM: 0.9, $R^2 = 0.98$).

In the condition with 10 pairs of flanking lines, for one observer, the dominance level was even around 0%; that is, this observer did not perceive the central-offset at the end of the sequence anymore. In condition F, similarly, the dominance of the flank-offset decreased (Figure 5, F; linear regression analysis, slope: 1.2, SEM: 0.7, $R^2 = 0.99$). Hence, for both the central- and the flank-offset, the dominance level depended, at least partly, on the number of lines within the motion stream.

In condition CF, dominance levels were roughly around –5% to –10%; that is, responses were slightly dominated by the flank-offset (Figure 5, CF). As in Experiment 1, the actual dominance levels were well predicted by summing the dominance levels of conditions C and F (Figure 5, C + F). Notably, in the sequence with 10 pairs of flanking lines, the distance between the central- and the flank-offset (which was presented in frame 9) was 0.5 deg with an SOA of 370 ms. Hence, feature integration can extend over a substantial spatiotemporal window. Moreover, this finding indicates that the failure of the linear model to predict the dominance level in Experiment 2 (see Figure 4, CF and C + F) cannot be explained by the spatial distance between the central- and the flank-offset *per se*. We rather suggest that, in Experiment 2, the motion grouping of the single lines broke partially down (resulting also in a less vivid motion percept) because of the large distances between consecutive flanking lines. Hence, the smooth spatiotemporal continuity of single lines seems to be crucial for feature integration. This issue will be investigated further in Experiment 7.
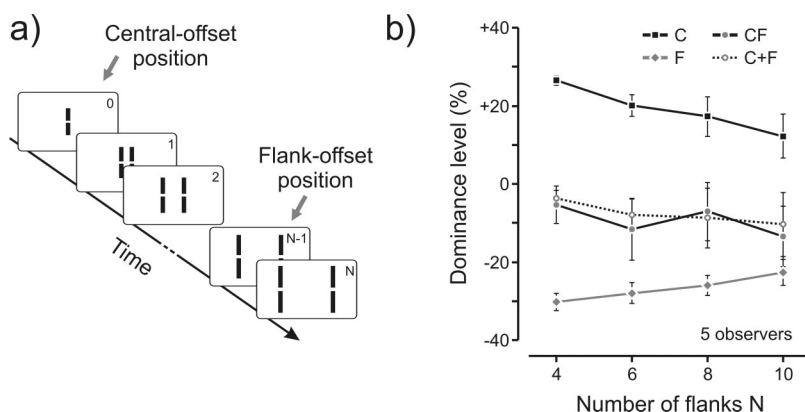

Figure 5. Sequence length. (a) We presented a sequence with 4, 6, 8, or 10 pairs of flanking lines. The flank-offset was always presented in the penultimate frame (no offset is shown in this illustration). (b) The dominance level as a function of the number of flanking lines. In condition C, the dominance of the central-offset decreased the more flanking lines were presented. Similarly, in condition F, slightly fewer responses were determined by the flank-offset. In condition CF, the dominance level was slightly negative. The actual dominance level was well predicted by the sum (C + F) of the dominance levels achieved in the conditions C and F. Hence, linear integration occurs within a substantial spatiotemporal window of up to 0.5 deg and almost 400 ms. Mean and SEM of five observers.

Experiment 4: Dominance Level

In Experiments 1–3, we kept the sizes for the central- and the flank-offset constant. Still, performance levels varied slightly depending on the manipulations of the stimulus sequence. In Experiment 4, we varied the offset sizes of the central- and the flank-offset to test feature integration at different performance levels explicitly.

Methods

We presented the standard sequence with four pairs of flanking lines (see Figure 2). The flank-offset was presented in frame 3. In order to achieve comparable dominance levels, we determined offset sizes according to the individual threshold level (ITL) as in Experiments 1–3. These offset sizes ranged from 0.5′ to 1.8 (mean: 1.1′) for the central-offset and from 0.3′ to 1.0′ (mean: 0.6′) for the flank-offset. In addition, we used offsets sizes of 50%, 75%, and 125% of the ITL. The procedure was the same as before. Five observers participated.

Results and Discussion

The dominance levels in conditions C and F were determined by the actual offset size; that is, the larger the offset size the more responses were in accordance with the central- and the flank-offset, respectively (Figure 6; conditions C and F). In condition CF, dominance levels for all offset sizes were well predicted by the sum of the dominance levels achieved in conditions C and F (Figure 6, CF and C + F). We tested only offset sizes yielding absolute values of the dominance levels in the range between 5% and 40%. For offset sizes yielding dominance levels beyond this
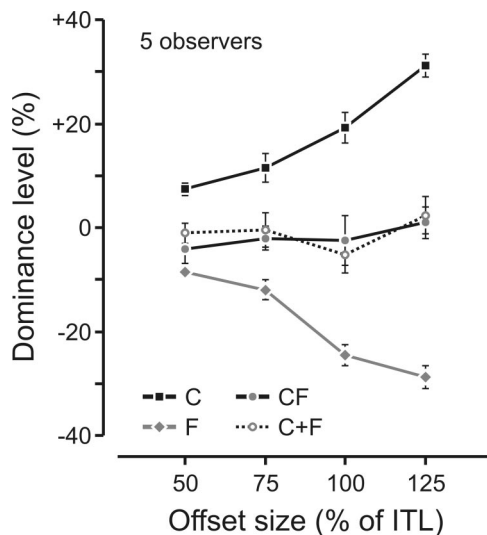

Figure 6. Dominance level as a function of offset sizes. In addition to the individual threshold level (ITL), we used offset sizes of 50%, 75%, and 125% of the ITL. In condition C, dominance of the central-offset increased for larger offset sizes. The same holds true for the dominance of the flank-offset in condition F. In condition CF, neither offset dominated. The dominance levels for condition CF are well predicted by the sum (C + F) of the dominance levels achieved in the conditions C and F. Means and SEM of five observers. SEM can be smaller than symbol size.

range, we expect integration to fail, for example, because of floor and ceiling effects.

Experiment 5: Contrast Polarity

Experiments 1–3 showed that integration occurs, within certain limits, independently of the spatio-temoral distance of the central- and the flank-offset. In Experiment 5, we presented the standard sequence with lines of either the same or opposite contrast polarity to test whether this manipulation changes feature integration.

Methods

We presented the standard sequential metacontrast sequence with four pairs of flanking lines (Figure 2a). Lines were either white (positive contrast polarity) or black (negative contrast polarity). The luminance of the grey background was individually adjusted to achieve comparable performance levels for both contrast polarities (see Contrast Polarity Calibration).

In the *first* part of Experiment 5, block-by-block, we presented the central line and the flanking lines in all four combinations of contrast polarity (i.e., a black/white central line was followed by black/white flanking lines; Figure 7a). For each combination of contrast polarity, we presented the three basic offset conditions as introduced in Figure 2c. For six observers, individual offset sizes ranged from 2.0′ to 2.7′ (mean: 2.4′) for the central-offset and from 0.8′ 1.3′ (mean: 1.1′) for the flank-offset.[3] We asked observers to report the offset perceived in the right motion stream irrespective of the contrast polarity.

In the *second* part, using the same combinations of contrast polarity (Figure 7a), we presented two sequential metacontrast sequences in two consecutive temporal intervals in each trial. The two intervals were separated by a blank screen presented for 500 ms. In random order, one sequence contained the standard sequence including the central line whereas the other sequence consisted only of the four pairs of flanking lines. All lines were non-offset. We asked observers to indicate which interval contained the central line by pressing one of two buttons (two interval forced-choice task). The same six observers of the first part participated.

In the *third* part, block-by-block, we presented only the sequences with opposite contrast polarities (see Figure 7a, bw and wb). We asked observers to attend to the central line, which had opposite contrast polarity compared to the other lines, and to report the offset of this line only. In half of the trials, only the central line was offset (condition C). In the other half, the central line was offset and we inserted a flank-offset to both lines in frame 3 (condition CF). For each combination of contrast polarity, conditions C and CF were randomly interleaved in 4 blocks of 80 trials. The same six observers of the first and second part participated and we used the same offset sizes as specified above.

Results and Discussion

In the *first* part of Experiment 5, we presented the standard sequence with different combinations of contrast polarity for the

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[3] These offset sizes were larger compared to Experiments 1–4. A likely explanation for this difference is the reduced contrast of lines compared to Experiments 1–4.
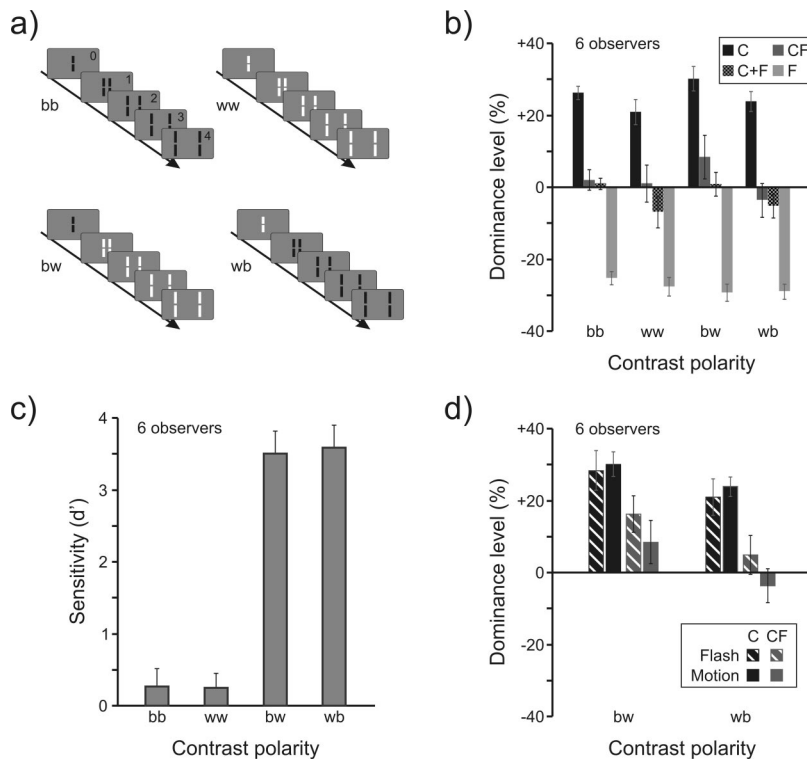
Figure 7. Contrast polarity. (a) We presented, block by block, central and flanking line with different combinations of contrast polarities. For example, both central and flanking lines could be black (bb) or a black central line could be followed by white flanking lines (bw). No offsets are shown in this illustration. (b) Dominance levels for the different combinations of contrast polarity in the conditions C, CF, and F (see Figure 2c). In condition C, responses were dominated by the central-offset and, in condition F, by the flank-offset. In condition CF, dominance was around 0% indicating an integration of the two offsets. The dominance level for condition CF was well predicted by the sum (C + F) of the dominance levels achieved in the conditions C and F. (c) Sensitivity of central line detection for the different combinations of contrast polarity. Sensitivity is almost at chance level ($d' = 0$) for sequences composed of lines with the same contrast polarity (bb and ww). Sensitivity is very high when the central and the flanking lines have opposite contrast polarities (bw and wb). (d) For the sequences with opposite contrast polarities, we asked observers to attend to the central line with opposite contrast polarity (Flash) and to indicate the offset of this line only. In condition C, only the central line was offset. In condition CF, in addition, both lines of frame 3 contained a flank-offset. Observers were not able to report the central-offset without taking the flanking lines into account as dominance level in conditions C and CF differed significantly. Moreover, dominance level seemed to be comparable to the analogous conditions when observers attended to one motion stream (Motion; data taken from b). Means and SEM of six observers.

central and the flanking lines (Figure 7a). In condition C, responses were primarily dominated by the central-offset. This indicates that the central offset is attributed to the motion stream irrespective of the contrast polarity of the lines. In condition F, the dominance of the flank-offset was comparable across all combinations of contrast polarity (Figure 7b, F). This result was expected because of the individual contrast calibration for positive and negative contrast polarities. In condition CF, the dominance level was roughly around 0% (Figure 7b, CF). Hence, neither offset dominated. For condition CF, we also estimated the dominance level by the sum of the dominance levels achieved in conditions C and F. These estimated dominance levels fitted the experimental data well (Figure 7b, C + F). Hence, these findings indicate that the central- and the flank-offset are integrated independently of the contrast polarity of the lines.

This is a surprising finding because, perceptually, the sequences of lines with opposite contrast polarities differed compared to sequences of lines with only one contrast polarity. For example, when a black central line was followed by white flanking lines, observers reported a black "flash" at the beginning of the motion stream. However, no such flash was perceived with only black lines. Hence, the visibility of the central line is increased in opposite contrast polarity sequences. To quantify this central line visibility, in the *second* part, we employed a two-interval forced-choice detection task. A one-way ANOVA with repeated measures showed a significant difference in detection sensitivity across the four combinations of contrast polarity ($F(3, 15) = 82.148$; $p < .001$; Figure 7c). Post hoc LSD comparisons revealed that sensitivity was lower in condition bb compared to bw (mean difference: -3.24; $p < .001$) and to wb (mean difference: -3.32; $p < .001$) as

well as in condition ww compared to bw (mean difference: –3.25; $p < .001$) and to wb (mean difference: –3.34; $p < .001$). Hence, observers can hardly, if at all, detect the interval containing the central line when all lines have the same contrast polarity (i.e., conditions bb and ww; see also, Otto et al., 2006). When the contrast polarity of the central line was opposite to the contrast polarity of the flanking lines (i.e., conditions bw and wb), observers' performance in detecting the central line was close to perfect.

With sequences of lines with opposite contrast polarity (i.e., conditions bw and wb in Figure 7a), observers reported a black or white "flash" in the center of the screen, which could be detected easily. Interestingly, when we asked observers to describe this flash, typical answers were "In the center, there is something black, maybe a line," "Sorry, but I cannot tell the form," or "I don't know, it's too fast." Hence, it is rather unclear whether the central line is detected because observers can detect a change in contrast polarity or because the central line is perceived as an individual line that is *not* grouped to the motion stream.

To test this further, in the *third* part, we changed the instruction and asked observers explicitly to attend to the black or white flash at the beginning of the sequence and to indicate the offset of this flash only. We presented the standard sequence with the central-offset. In half of the trials, both flanking lines in frame 3 contained a flank-offset (condition CF; we presented a flank-offset in either stream to control that observers attended only the central line and not one or the other motion stream), in the other half, they were not (condition C). Assuming that the central line is "ungrouped" from the following lines with opposite contrast polarity, observers should be able to report the central-offset independently of the presence of the flank-offsets. In this case, performance in conditions C and CF should be comparable. However, we found a significant difference in dominance levels between conditions C and CF for both contrast polarity conditions (Figure 7d; bw, mean difference: 12.1%, two-tailed, paired t-test: $p = .002$; wb, mean difference: 16.1%, two-tailed, paired t-test: $p = .001$). Hence, observers are not able to report the central-offset independently of the flanking lines. Performance for conditions C and CF of this part seems not to differ compared to the analogous conditions of the first part (Figure 7d). These findings indicate that offsets were integrated in the same way whether the single lines were presented with the same or with opposite contrast polarity.

Experiment 6: Orientation

In the Experiments 1–5, we presented sequences with vertical lines. Hence, the central- and the flank-offset activated possibly similar sets of orientation selective neurons. For static integration, it is assumed that features are not pooled when presented with large orientation differences (e.g., Parkes et al., 2001). To test if integration occurs with lines of different orientations, we presented sequences of lines that followed a circular motion trajectory. Hence, the central- and the flank-offset activated presumably different sets of orientation sensitive neurons.

Methods

In the *first* part of Experiment 6, we presented a stimulus sequence consisting of the central line followed by five pairs of flanking lines. Hence, the duration of the whole sequence was 230 ms. Lines were arranged with their center of gravity along a (virtual) circular motion trajectory (Figure 8a). The distance between consecutive flanking lines along this trajectory was about 3.3′. The central line was vertical. Flanking lines were perpendicular to the tangent of the trajectory. To manipulate the orientation difference between lines, we varied the radius of the trajectory using radii of 95.4′, 48.0′, 31.8′, and 24.0′, respectively. Hence, the orientation difference between the central line and the last flanking line was 10, 20, 30, or 40 deg. The orientation of the penultimate line with the flank-offset was 8, 16, 24, or 32 deg. Unlike Experiments 1–5, the length of the line segments was kept fixed at 11.7′ for all flanking lines. For five observers, individual offset sizes ranged from 1.2′ to 1.7′ (mean: 1.4′) for the central-offset and from 0.5′ to 1.2′ (mean: 0.8′) for the flank-offset presented in frame 4. All observers attended the right stream. The procedure was the same as introduced in Figure 2c.

In the *second* part, we used similar sequences but the central line was oblique and the last line of the attended stream was vertical (Figure 8c). This modification was achieved by rotating the stimulus sequence of the first part (Figure 8a) by the actual orientation difference counterclockwise. Hence, the orientation of the central line was 10, 20, 30, or 40 deg. The orientation of the penultimate line with the flank-offset was 2, 4, 6, or 8 deg. For another five observers, individual offset sizes ranged from 1.3′ to 1.7′ (mean: 1.5′) for the central-offset and from 0.6′ to 1.2′ (mean: 0.9′) for the flank-offset. All observers attended the right stream.

Results and Discussion

In the *first* part of Experiment 6, the central line was vertical and the last line of the attended stream was oblique (Figure 8a). In condition C, responses were dominated by the central-offset (Figure 8b, C). In condition F, responses were dominated by the flank-offset (Figure 8b, F). In condition CF, both the central- and the flank-offset were presented in the *attended* stream of lines (see Figure 2c). We found that the dominance level was roughly around 0% for all orientation differences (Figure 8b, CF). As in most experiments before, the dominance levels in condition CF were well predicted by the linear model (Figure 8b and d, C + F). Hence, the central- and the flank-offset seem to be integrated across large orientation differences as in Experiments 1–5 using vertical lines only. This finding indicates that feature integration in motion streams is not restricted to sets of neurons with the same orientation preference.

The dominance in conditions C and F seems slightly to decrease with increasing orientation differences (Figure 8b; C, linear regression analysis, slope: −0.43, SEM: 0.12, $R^2 = 0.94$; F, linear regression analysis, slope: 0.18, SEM: 0.06, $R^2 = 0.73$, note that the positive slope here indicates a decrease of flank-offset dominance). This decrease in dominance might have occurred because of the increasing orientation difference *per se* or because of an oblique effect (e.g., Appelle, 1972; Baud-Bovy & Gentaz, 2006; Westheimer, 2003) for the last line of the attended stream which was the more tilted the larger the orientation difference was. To investigate these possibilities, in the *second* part, we rotated the whole stimulus of the first part counterclockwise so that the last line of the attended stream was always vertical (Figure 8c). Compared to the first part, this manipulation did not change integration. The central- and the flank-offset were equally integrated indepen-
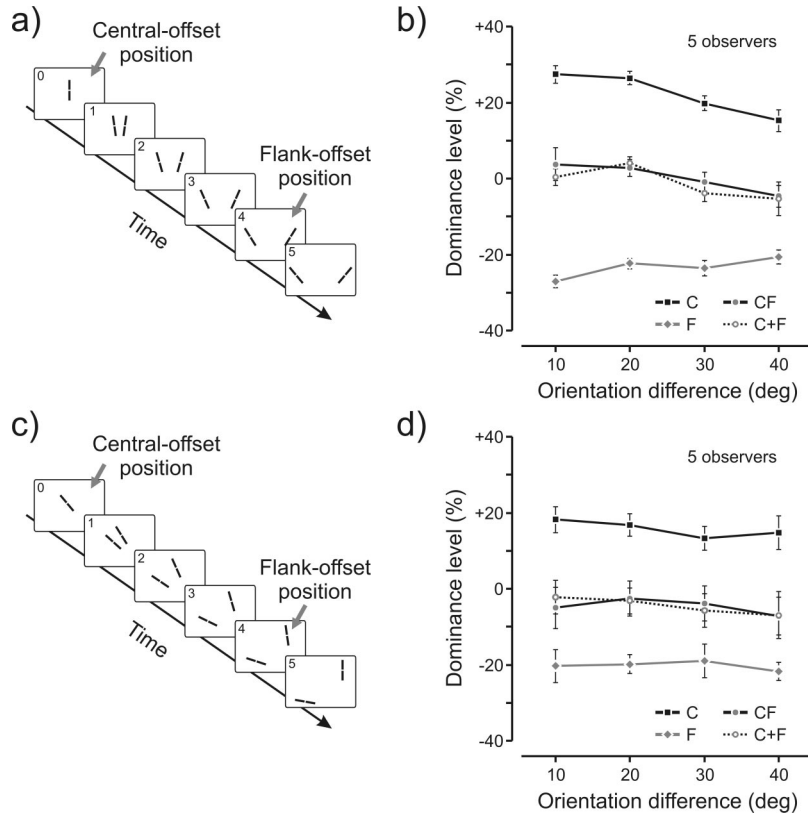
Figure 8. Circular motion. (a) We presented sequences with 5 pairs of flanking lines. Flanking lines were perpendicular to the tangent of a (virtual) circular motion trajectory. Depending on the radius of the trajectory, the orientation difference between the central line and the last flanking line was 10, 20, 30, or 40 degrees (deg). The flank-offset was presented in frame 4 (no offsets are shown in this illustration). (b) Dominance level as a function of the orientation difference between the central and the last line. In condition C, the dominance of the central-offset deteriorated slightly when the orientation difference was increased. Similarly, in condition F, the dominance of the flank-offset deteriorated slightly. The integration of the central- and the flank-offset was linear as in the previous experiments (CF and C + F). Means and SEM of five observers. (c) The same experiment as in (a) except for that the central line was oblique and the last line of the attended motion stream was vertical. (d) Results seem not to differ compared to (b). However, dominance levels in conditions C and F were largely unaffected by the orientation difference. Means and SEM of five observers.

dent of the orientation difference (Figure 8d; CF and C + F). However, regarding conditions C and F, the trend of decreasing dominance with increasing orientation difference seemed to be reduced (Figure 8d; C, linear regression analysis, slope: -0.14, SEM: 0.15, $R^2 = 0.67$; F, linear regression analysis, slope: 0.03; SEM: 0.06; $R^2 = 0.13$). The difference in slopes between the first and the second part was significant for condition F (mean difference: 0.21; two tailed, two sample t-test; $p = .045$) and revealed a trend for condition C (mean difference: -0.29). Hence, dominance seemed to depend not only on the orientation difference but also on the orientation of the whole stimulus sequence.

Experiment 7: Two Line Sequences

In Experiments 1–6, we investigated feature integration with stimuli that elicit a percept of continuous motion. One exception was Experiment 2 where we increased the distance between subsequent flanking lines to 8.3′. In Experiment 7, we investigated whether the close spatiotemporal continuity of lines is crucial for

feature integration. We presented stimulus sequences with the same spatiotemporal distances between the central- and the flank-offset for which we found integration in Experiments 1 and 6. However, we removed all flanking lines that were not offset. Hence, we presented sequences consisting of two lines only. With these stimuli, no continuous motion percept occurred. Observers were able to selectively attend either to the first or to the second line.

Methods

In the *first* part of Experiment 7 (see Figure 9a), the two lines corresponded to the central-line and the fourth attended flanking line of the sequence shown in Figure 8a (with an orientation difference of 40 deg). The first line (corresponding to frame 0) was oriented vertically and the second line (corresponding to frame 4) was tilted 32 deg clockwise. The distance between the lines along the (virtual) circular motion trajectory was 13.3′. The corresponding SOA was 170 ms.
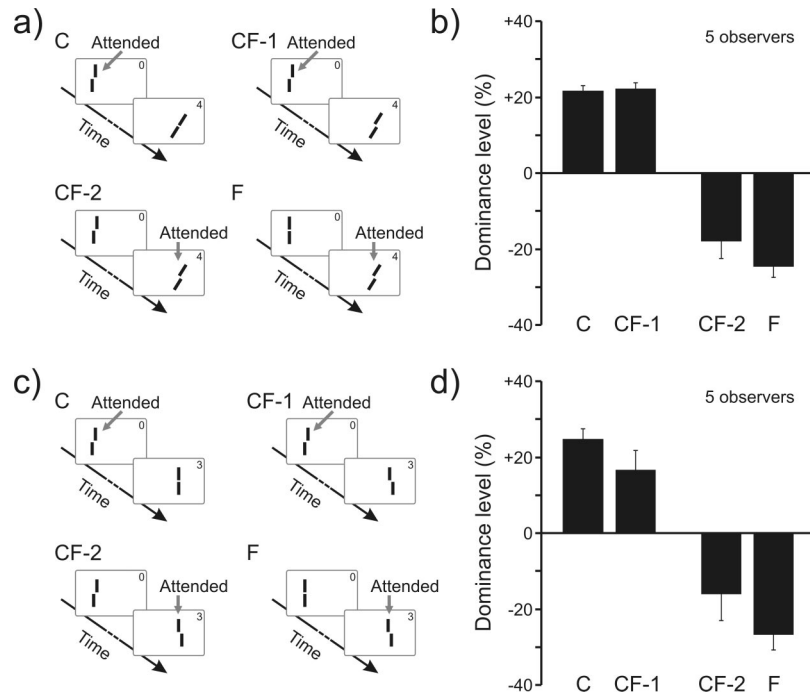
Figure 9. Two line sequences. (a) We presented consecutively two lines that corresponded to the central line and the fourth, attended line of the sequence shown in Figure 8a. In condition C, observers attended to the first line with the central-offset. In condition F, observers attended to the second line with the flank-offset. In both conditions, the unattended line was not offset. In conditions CF-1 and CF-2, we presented both the central- and the flank-offset. The two conditions were physically the same, only the focus of attention differed. Observers attended either the first or the second line. (b) When the first line with the central-offset was attended, responses were dominated by the central-offset whether (CF-1) or not (C) the flank-offset was presented. When the second line with the flank-offset was attended, responses were dominated by the flank-offset (F and CF-2). However, this dominance seemed to be slightly reduced in condition CF-2. (c) We repeated the experiment with two lines that corresponded to the central line and the third, attended flanking line of the standard sequence (see Figure 2). (d) Results were similar to (a). Dominance of the central- and the flank-offset was slightly reduced in conditions CF-1 and CF-2 compared to conditions C and F, respectively. Means and SEM of five observers.

We employed *four* offset conditions (see Figure 9a). In condition C, observers attended to the first line with the central-offset while the second line was not offset. In condition CF-1, observers attended to the first line with the central-offset while the second line contained a flank-offset. Condition CF-2 was the same as CF-1 but observers attended to the second line with the flank-offset. In condition F, observers attended to the second line with the flank-offset while the first line was not offset. Conditions C and CF-1 as well as F and CF-2 were presented randomly interleaved. Before the experiment proper, we determined individual offset sizes for the central- and the flank-offset. For five observers, individual offset sizes ranged from 0.3′ to 0.8′ (mean: 0.5′) for the central-offset and from 0.3′ to 0.8′ (mean: 0.5′) for the flank-offset. Please note that these offsets were smaller than in Experiments 1–6 to yield comparable dominance levels.

In the *second* part, we presented the two lines corresponding to the central line and the third flanking line of the standard sequence (Figure 9c). Hence, both lines were oriented vertically. The distance between the two lines was 10′. The corresponding SOA was 130 ms. The procedure was the same as in the first part. The same five observers as in the first part participated. Individual offset

sizes ranged from 0.3′ to 0.7 (mean: 0.4′) for the central-offset and from 0.2′ to 0.3′ (mean: 0.3′) for the flank-offset.

Results and Discussion

In the *first* part of Experiment 7, when the first line with the central-offset was attended, responses were dominated by the central-offset whether or not the flank-offset was presented at the second line (Figure 9b, C and CF-1). Similarly, when the second line with the flank-offset was attended, responses were dominated by the flank-offset (Figure 9b, F and CF-2). When we presented the central-offset at the first line (CF-2), this dominance seemed to be slightly reduced. The small difference in dominance levels in conditions F and CF-2 failed to be significant but revealed a trend (mean difference: 6.6%).

Interestingly, while conditions CF-1 and CF-2 were physically the same, the dominance level in these two conditions differed significantly (mean difference: 40.0%; two-tailed, paired t-test, $p = .002$). Hence, depending on attention, responses were dominated either by the central- or by the flank-offset. This finding

indicates that the two offsets were *not* integrated in this two line sequence.

In the *second* part, when the first line with the central-offset was attended, responses were dominated by the central-offset (Figure 9d, C). When we presented the flank-offset (CF-1), this dominance decreased (mean difference: 8.0%; two-tailed, paired t-test, *p* = .032). Similarly, when the second line with the flank-offset was attended, responses were dominated by the flank-offset (Figure 9d, F). With the central-offset (CF-2), it seemed that this dominance decreased. The difference in dominance levels between conditions F and CF-2 failed to be significant but revealed a trend (mean difference: 10.7%). In conditions CF-1 and CF-2, which were physically identical, the difference in dominance was significant (mean difference: 32.6%; two-tailed, paired t-test; *p* = .049). Hence, feature integration is strongly diminished.

To summarize, we presented the central- and the flank-offset with the spatiotemporal distances that yielded feature integration in Experiments 1 and 6. However, we removed the lines in-between and produced two-element sequences instead of multi-element motion streams. Our results indicate that no or, at least, less feature integration has occurred. Hence, Experiment 7 provides evidence that integration occurs only within a sequence of lines yielding a continuous motion percept.

General Discussion

Spatio-Temporal Feature Integration

In sequential metacontrast, a central line is followed by a sequence of flanking lines (Figure 2a). Observers do not perceive a sequence of single static lines but two streams in apparent motion (Figure 2b). The central line itself is completely masked but its offset is visible in the stream of lines (e.g., Figure 3, condition C; Otto et al., 2006). The central-offset can be integrated with offsets of the flanking lines. For example, when one line of the attended motion stream is offset in opposite direction to the central-offset, this offset cancels out the retinotopically mis-localized central-offset (e.g., Figure 3, condition CF; see also, Otto et al., 2006). Hence, feature integration across space and time has occurred.

At a first glance, this offset integration is similar to the spatial pooling of features as found in static displays. For example, when a set of Gabor patches is presented in the periphery, observers fail to report the orientation of a central tilted Gabor but perceive the entire group of Gabors to be tilted (Parkes et al., 2001). Analogously, in sequential metacontrast, observers perceive the attended stream of lines to be offset according to the average offset of the single lines. Hence, feature integration appears to be similar when single elements of a static stimulus are grouped across space and when single elements of dynamic stimuli are grouped across space and time. However, the weighting functions of features in the integration process are very different.

For static displays, spatial pooling depends on the distance between the single elements. This dependency is usually modeled by a Gaussian weighting function (Figure 1; e.g., Wilkinson et al., 1997). We found that offset integration in sequential metacontrast is rather independent of the distances between the central- and the flank-offset. For example, in Experiment 1, we varied the flank-offset position within the stream of lines. The central- and the flank-offset are integrated in the same way whether the flank-

offset is presented at the first flanking line with a distance of 3.3′ or at the fifth flanking line with a distance of 16.7 (Figure 3). In Experiment 3, the integration window extends even up to 0.5 deg (Figure 5). Moreover, this integration is largely linear because performance in condition CF is given roughly by the sum of performance in conditions C and F.

To yield comparable dominance level across observers, we determined offset sizes individually before the experiment proper. These calibrated offsets are integrated with equal weights (Figure 6; for performance levels below 5% or above 45%, we do not expect integration to be linear because of floor and ceiling effects). Remarkably, the size of the central-offset was usually larger than the size of the flank-offset. Hence, in terms of offset sizes, the magnitudes are not equal.

It may be possible that we compensated for differences of the different offset positions because of our calibration procedure. To tackle this issue, we presented sequences with either four or six pairs of flanking lines and determined offset discrimination thresholds systematically for offsets presented at the different positions (results not shown, methods as described in Offset calibration). We found that offset discrimination thresholds decreased slightly for offsets presented in later frames (correspondingly, the dominance for the flank-offset with a fixed offset size increased slightly when presented in later frames; see, Figure 3, conditions F). Still, these thresholds were rather comparable and by a factor of about five larger than thresholds achieved with a single, static line. One exception is the line presented last for which we found thresholds which were only slightly increased compared to thresholds achieved with a single, static line (see also, Fahle, 1995; Westheimer & McKee, 1975). Hence, assuming that the thresholds reflect the actual weighting of offsets, we find the highest weight (according to the lowest thresholds) for the lines presented last.

Offset integration in sequential metacontrast occurs in a temporal window of up to 400 ms (Figure 5). For luminance integration in apparent motion, Shimozaki, Eckstein, and Thomas (1999) proposed a weighting function with higher weights for features presented earlier in the sequence. In contrast, for offset integration, we found low but comparable weights for offsets presented within the sequence and the highest weight for the offset presented last (see above). This difference in results between the studies might be explained by the different feature domains.

Contrast Polarity

In Experiment 5, the central line could be presented with opposite contrast polarity compared to the flanking lines. Such opposite contrast polarities are assumed to break the grouping of lines in static displays. For example, in simultaneous masking, offset discrimination is strongly deteriorated when a target vernier is flanked by a grating of straight lines of the same contrast polarity[4] (Malania, Herzog, & Westheimer, 2007). This effect was attributed to the grouping of the vernier within a grating of similar lines. When the flanking lines are of different contrast polarity, this grouping breaks down and offset discrimination improves (Sayim, Westheimer, & Herzog, 2008). We found that integration is not

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[4] These stimuli are exactly a "static" copy of our present stimuli if all flanking lines are presented simultaneously with the central line.

changed when lines of opposite contrast polarity are presented compared to conditions with equal contrast polarity (Figure 7b). This finding might indicate that motion grouping does not depend on contrast polarity.

As shown in Figure 7c, detection of the central line is close to perfect when the flanking lines have opposite contrast polarity. Still, observers cannot discriminate the central-offset independently of the flanking lines (Figure 7d). These findings may be explained by separate grouping systems such as a brightness and a contour system (e.g., Gilchrist, Humphreys, Riddoch, & Neumann, 1997). Observers might detect the central line based on the brightness system, which is contrast polarity sensitive, whereas offset discrimination is based on the contour system, which is blind to it. Indeed, differences between detection and judging figural properties (Fehrer & Raab, 1962; Harrison & Fox, 1966; Ögmen, Breitmeyer, & Melvin, 2003; Schiller & Smith, 1966; Vorberg, Mattler, Heinecke, Schmidt, & Schwarzbach, 2003) as well as between brightness and contour properties (Breitmeyer et al., 2006; Petry, 1978; Stober, Brussel, & Komoda, 1978) of a target stimulus in metacontrast have been well documented and support the notion that observers can use different stimulus dimensions according to the task demands (see "criterion contents" in Breitmeyer & Ögmen, 2006). Finally, that *offset discrimination* is strongly affected by the flanking lines in the opposite contrast condition is in agreement with the findings that metacontrast occurs across contrast polarities (Breitmeyer, 1978; Breitmeyer, Tapia, Kafaligönül, & Ögmen, 2008; Sherrick, Keating, & Dember, 1974; cf., Becker & Anstis, 2004; Luiga & Bachmann, 2008).

Orientation

In static displays, feature integration is thought not only to be restricted to a narrow spatial range but also to a narrow range in the orientation domain. For example, the pooling model by Wilkinson et al. (1997) assumes that only the outputs of simple cells with similar orientations are pooled. Moreover, neurons in V1 make horizontal connections preferentially to neurons with the same orientation preference (e.g., Grinvald, Lieke, Frostig, & Hildesheim, 1994; Malach, Amir, Harel, & Grinvald, 1993; Singer, 1995). In this context, Parkes et al. (2001) predict not to observe orientation pooling when a single Gabor "pops out" because of orientation differences.

In Experiment 6, we tested orientation selectivity for offset integration in sequential metacontrast. Surprisingly, the central-offset is perceived in a stream moving along a circular trajectory. Although the two offsets were presented with orientation differences of more than 30 deg, integration occurred as in Experiments 1–5 with vertical lines only (Figure 8). Hence, within a motion stream, feature integration seems not to be limited to a narrow range in the orientation domain. Metaphorically speaking, features can go around the corner.

Experiment 5 with circular motion trajectories revealed another unexpected finding. We presented sequences either turning from vertical to oblique (Figure 8a) or vice versa (Figure 8c). Surprisingly, in conditions C and F, dominance levels seem to be more affected by the orientation difference when the last line of the sequence was oblique (Figure 8b) compared to vertical (Figure 8d). This finding may point to an oblique effect (i.e., performance is usually worse when an oblique stimulus is presented compared

to vertical or horizontal ones; e.g., Appelle, 1972; Baud-Bovy & Gentaz, 2006; Westheimer, 2003). Interestingly, in the first part of the experiment (Figure 8a, b), the orientation of the central line was always vertical and, hence, performance should *not* be affected by the oblique effect. Hence, our finding may point to an oblique effect that affects the readout of the integrated offset at the last line of the stream rather than the coding of the individual lines in the sequence.

Grouping and Attention

In Experiment 2, we did not observe integration when we increased the distance between consecutive flanking lines to 8.3′ (Figure 4). One explanation for this result may be that, because of the large spacing between consecutive lines, the motion grouping between consecutive flanking lines was weakened. Consequently, no integration occurred. In Experiment 7, to test this hypothesis, we presented the central- and the flank-offset with the same spatiotemporal distances for which we found integration in Experiments 1 and 6 and removed the other lines. With these two line displays, observers can attend to either line independently because the continuous motion percept is strongly reduced (c.f., Watson, Ahumada, & Farrell, 1986). As a consequence, we observed only little integration if at all (Figure 9). Hence, Experiment 7 provides evidence that feature integration in dynamic displays occurs only if the single lines are grouped into a continuous motion stream.

In a previous study, we have demonstrated that a flank-offset influences performance only if presented in the attended motion stream (Otto et al., 2006). In accordance with this finding, the dominance level does not change when the flank-offset is presented at different positions in the unattended stream (Figure 3, condition C). However, it remains an open question whether attention is the "glue" for feature integration (e.g., Treisman, 1998) or only a read-out mechanism of a pre-attentive grouping (see also, Hamker, 2007; Ma, Hamker, & Koch, 2006; Sharikadze, Fahle, & Herzog, 2005). Our data may also be explained by a model which combines attention and grouping (Roelfsema, 2006). This model is based on the idea that enhanced neuronal responses, caused by attention, propagate gradually along enabled connections, activated by pre-attentive grouping operations.

In contrast to static displays, we found that the integration of features within a motion stream is, within certain limits, independent of space, time, and orientation provided that the continuity of motion is preserved. This fundamental difference in feature integration strategies for static versus dynamic stimuli might reflect a qualitative difference in the underlying grouping processes. With static grouping, neighboring elements are combined to a whole whereby the single elements keep their identity. For example, a group of trees is combined into a forest, but each tree stays a tree. On the other hand, with motion grouping, consecutive elements are combined to a whole perceived as *one* element (e.g. one line), which is moving. Gestalt psychologists called this effect *"phenomenal identity"* (Ternus, 1926). In addition, when multiple moving elements are presented, they can also be spatially grouped, for example, when moving in parallel (e.g., Palmer, Brooks, & Nelson, 2003).

The different types of grouping are also very likely to be reflected in different neuronal correlates. Whereas static grouping probably involves early visual areas such as V2 (e.g, Qiu & von

der Heydt, 2005; Zhou, Friedman, & von der Heydt, 2000), motion grouping possibly involves motion areas as MT or MST (e.g., Duffy & Wurtz, 1991; Heeger, Huk, Geisler, & Albrecht, 2000; Perrone & Stone, 1998; Rees, Friston, & Koch, 2000; Tanaka et al., 1986).

The different feature integration strategies can be understood within the context of a computational framework. Because moving objects change their spatial position, distance-dependent operations are severely limited in their ability to compute the features of moving objects (Ögmen, 2007). This suggests that feature computation and integration for moving objects should extend over a relatively large spatial range. On the other hand, these computations cannot combine indiscriminately information from large spatial extents, because features of different objects occupying the same space would incorrectly blend into each other. In accordance with this proposition, our previous (Ögmen, Otto, & Herzog, 2006; Otto et al., 2006) and current findings indicate that feature integration for moving objects follows exactly the rules of motion grouping. However, this does not exclude that the grouping of multiple moving elements, at a later stage, can reveal similar characteristics as the grouping of multiple static elements (e.g., Verghese & Stone, 1996).

Related Work

In classical metacontrast, feature mis-localizations were already noted in previous research (e.g., Hogben & Di Lollo, 1984; Stewart & Purcell, 1970; Stoper & Banffy, 1977; Werner, 1935; Wilson & Johnson, 1985; for pattern masking, see also Herzog & Koch, 2001). Unfortunately, most cases were anecdotally described only (cf., Hofer, Walder, & Groner, 1989) and, usually, were treated as errors or limits of the visual system. On the contrary, we propose that non-retinotopic feature integration, as reported herein, follows rules of grouping precisely (Otto et al., 2006). Hence, our results with sequential metacontrast point to a fundamental computational strategy and not to errors of visual processing.

Our findings are strongly linked to other recent investigations showing that visual feature processing does not strictly depend on low-level *retinotopic* processing (e.g., Aydin, Herzog, & Ögmen, 2009; Cai & Schlag, 2001; Cavanagh, Holcombe, & Chou, 2008; Melcher, 2008; Moore & Enns, 2004; Moore, Mordkoff, & Enns, 2007; Muckli, Kohler, Kriegeskorte, & Singer, 2005; Nishida, Watanabe, Kuriki, & Tokimoto, 2007; Ögmen et al., 2006; Shimozaki et al., 1999; Watanabe & Nishida, 2007). Together with earlier findings showing that information is sampled along motion trajectories (e.g., Burr, 1979, 1981; Fahle & Poggio, 1981; Morgan, 1976), these and our results provide strong evidence that visual feature processing is guided by perceptual grouping operations that maintain the spatiotemporal continuity of objects (see also Kahneman, Treisman, & Gibbs, 1992).

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Call for Nominations:
Sport, Exercise, and Performance Psychology

The Publications and Communications (P&C) Board of the American Psychological Association and Division 47 (Exercise and Sport Psychology) of the APA have opened nominations for the editorship of *Sport, Exercise, and Performance Psychology* for the years 2011–2016. The editor search committee is co-chaired by Ed Acevedo, PhD, and Robert Frank, PhD.

Sport, Exercise, and Performance Psychology, to begin publishing in 2011, will publishes papers in all areas of sport, exercise, and performance psychology for applied scientists and practitioners. This journal is committed to publishing evidence that supports the application of psychological principals to facilitate peak sport performance, enhance physical activity participation, and achieve optimal human performance. Published papers include experimental studies, qualitative research, correlational studies, and evaluation studies. In addition, historical papers, critical reviews, case studies, brief reports, critical evaluations of policies and procedures, and position statements will be considered for publication.

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Candidates should be nominated by accessing APA's EditorQuest site on the Web. Using your Web browser, go to http://editorquest.apa.org. On the Home menu on the left, find "Guests." Next, click on the link "Submit a Nomination," enter your nominee's information, and click "Submit."

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