**Fine temporal properties of center-surround interactions in motion revealed by reverse correlation**

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<th>Journal of Neuroscience</th>
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<td>Manuscript ID:</td>
<td>JN-RM-4253-05</td>
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<tr>
<td>Manuscript Type:</td>
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<tr>
<td>Manuscript Section:</td>
<td>Behavioral/Systems/Cognitive - John Maunsell</td>
</tr>
<tr>
<td>Date Submitted by the Author:</td>
<td>05-Oct-2005</td>
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<td>Complete List of Authors:</td>
<td>Tadin, Duje; Vanderbilt University, Department of Psychology; Vanderbilt University, Vanderbilt Vision Research Center Lappin, Joseph S.; Vanderbilt University, Department of Psychology; Vanderbilt University, Vanderbilt Vision Research Center Blake, Randolph; Vanderbilt University, Department of Psychology; Vanderbilt University, Vanderbilt Vision Research Center</td>
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<tr>
<td>Keywords:</td>
<td>Vision, Contrast, visual motion, Inhibition, center-surround, reverse correlation</td>
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<td>Themes &amp; Topics:</td>
<td>Processing of visual motion &lt; Vision &lt; Theme C: Sensory and Motor Systems</td>
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Fine temporal properties of center-surround interactions in motion revealed by reverse correlation

(Abbreviated title: Center-surround interactions in motion perception)

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Manuscript contains: 5 figures, 1 table and 25 pages

Keywords: Vision; visual motion; center-surround; contrast; reverse correlation; inhibition

Acknowledgments: Supported by NIH EY07760
Abstract

Center-surround interactions are a key property of neural motion mechanisms. Using a temporal reverse correlation method, we investigated perceptual interactions between a brief center motion (~20 ms) and a surround that moved up/down with a new direction chosen randomly every 5 ms. The aim was to reveal interactions between center and surround motions and their dependency on relative direction, contrast and timing. Hypothesizing that surround computation involves different neural circuitry than the center response, we manipulated surround contrast to affect the relative timing of center and surround signals. The reverse correlation analysis yielded temporal profiles of surround influence indicating, in 5 ms steps, the time course of the surround’s effect on the discriminability of center motion. The resulting temporal profiles varied systematically with contrast: as surround contrast decreased, both the latency and duration of its influence increased. This finding, consistent with longer and more variable neural response latencies at low contrast, psychophysically reveals fine-scale temporal interactions between center and surround signals. Additionally, the strength of surround influence was correlated with psychophysical thresholds for discriminating center motion. The directionality of this relationship, however, depended only on center contrast. When the center motion was high contrast, poor direction discrimination was associated with increased probability of same-direction surround motions. Low-contrast center motion, however, was more discriminable when surrounded by motion in the same direction, regardless of surround contrast. This suggests that the previously reported adaptive nature of center-surround interactions in motion is driven largely by the visibility of the center motion signals.
A significant portion of the neural analysis of visual input transpires within 150 ms after the stimulus onset (Thorpe, Fize & Marlot, 1996). Within that time, different visual properties, such as color and motion, may be processed and perceived at different times (Moutoussis & Zeki, 1997; Nishida & Johnston, 2002; Bedell et al, 2003). Delayed signals arrive via feedforward, feedback, and lateral connections, and together those signals play a fundamental role in neural processing of visual input (Lamme, Super & Spekreijse, 1998). Furthermore, stimulus properties such as contrast and velocity affect neuronal latencies (Nowak & Bullier, 1997), introducing stimulus-dependent delays. This hodgepodge of delays and asynchronies, though often obvious at the single cell level, typically is hidden from phenomenal experience and is only revealed psychophysically by carefully designed experiments.

Similarly intricate temporal interactions exist at the level of neural circuits. A textbook example is the so-called Reichardt detector: a model of motion perception where delayed signals from one retinal location are necessary for the computation of motion (Reichardt, 1961). In the present study, we are interested in fine temporal properties of another ubiquitous neural circuit: the interactions between the center and surround regions of the receptive field. Center-surround processing is inaugurated in the retina and it recurs at subsequent stages of visual processing (Allman et al., 1985a). In motion perception, center-surround interactions are found at all major stages of motion processing (Tadin & Lappin, 2005a) and are particularly prominent in MT (Allman et al., 1985b, Born & Tootell, 1992; Raiguel et al., 1995; Born, 2000) — a cortical area vitally involved in motion perception (Born & Bradley, 2005). A typical center-surround neuron responds strongly when its receptive field center is stimulated with the appropriate motion stimulus. But, if the spatial extent of this stimulation is enlarged to include the neuron’s surround, neural response attenuates — the neuron exhibits surround
suppression. Such surround suppression, however, is typically restricted to high contrast stimuli (Pack et al., 2005). At low contrast, surround’s suppressive influences weakens and spatial summation increases — a potentially adaptive mechanism that employs suppressive interactions only when the signal is sufficiently strong (Marr, 1982). These center-surround interactions enable neurons to perform complex operations, but also likely require additional synaptic processing to incorporate surround signals (Raiguel et al., 1999). Indeed, the inhibitory component of the surround response in MT lags about 10 ms after the excitatory center response (Borghuis et al., 2003).

Importantly, center-surround interactions seem to have measurable perceptual correlates (Tadin et al., 2003; Betts et al., 2005; Paffen et al., 2005), thus enabling us to study them psychophysically. Revealing temporal properties of surround suppression using psychophysical methodology, however, is likely to be difficult. One potentially profitable strategy is to employ stimulus manipulations that will differentially affect processing speed of center and surround signals. Such manipulations may affect the interaction between the center and surround, especially if the signals themselves are very brief. To implement this strategy, we designed a reverse correlation study where the stimulus consisted of a brief (~20 ms) center motion and a surround whose motion direction was randomly chosen every 5 ms (Fig. 1A,B). We then investigated whether the discriminability of center motion is influenced by surround motions occurring at different times relative to the center stimulus. Of particular interest was whether the timing of the surround’s influence changes with changes in surround and center contrast. This experimental question was motivated by observations that neuronal latencies and their variability depends on contrast (Lennie, 1981; Maunsell & Gibson, 1992; Maunsell et al., 1999; Reich, Mechler & Victor, 2001).
METHODS

Stimuli

Stimulus patterns were created in MATLAB with the Psychophysics Toolbox (Brainard, 1997) and Video Toolbox (Pelli, 1997) and shown on a linearized monitor (800 x 600 resolution, 200 Hz). To obtain 200 Hz refresh rate, which was important for the present experiment, we used a high-speed PROCALIX monitor (Totoku, Irving, TX) driven by a MP 960 graphics card (VillageTronic, Berlin, Germany). Viewing was binocular at 83 cm (yielding 2 x 2 arcmin per pixel). Ambient illumination was 3.4 cd/m². Background luminance was 42.3 cd/m². Stimuli were moving random-dot textures. The size of each dot was 6 x 6 arcmin; a given dot could be dark or light, with equal probability. Three observers participated in the experiment (first author and two naïve individuals). All procedures complied with institutionally reviewed guidelines for human subjects.

A moving random-dot surround (Fig. 1B) was presented in a spatial envelope consisting of a uniform disk surrounded by a blurred border (the spatial gradient of the border was a half cycle of the raised cosine function). The diameter of the uniform disk section was 8.2° and the width of the blurred border was 2.05°, resulting in the 12.3° stimulus diameter. In the center of the moving random-dot texture was a small hole (diameter = 1.3°) where the center random-dot pattern was briefly presented on each trial. The small size of this center region ensured that the center stimulus on its own evokes little or no surround suppression (Tadin & Lappin, 2005b). The center contrast was ramped on and off with a temporal Gaussian envelope whose peak contrast was 92%. In four different conditions, the surround contrasts were 92%, 27%, 6.5%, and 1.7%.

The temporal sequence of events is illustrated in Figure 1A. The surround pattern was presented for 500 ms, during which the dots in the surround texture moved
uniformly upward or downward at 20°/s (i.e., randomly jittered up-down). A new direction (up or down) was randomly selected every 5 ms (every frame on a 200 Hz monitor). At a randomly chosen time during the central 150 ms, the center stimulus was briefly presented and moved either up or down at 20°/s. The observers’ task was to identify the direction of motion of the center pattern. Performance was maintained near 70% correct by two interleaved adaptive staircases adjusting the center pattern duration (duration is defined as one standard deviation (σ) of the temporal Gaussian envelope controlling center contrast). The temporal Gaussian envelope offers a temporal equivalent of subpixel sampling, permitting motion durations (1σ) below 5 ms. Duration thresholds in this experiment were very low (as low as 3 ms) largely because of the fast center speed. For example, a 3.91 ms threshold would be shown in 5 video frames with contrasts that are 3.8%, 44.1%, 100%, 44.1%, and 3.8% of the peak contrast (3.91 ms was the average threshold for 92% surround contrast condition, cf. Fig. 4A, leftmost point).

Analysis

To quantify the temporal aspects of center-surround interactions, we separately analyzed temporal sequences of surround motion that occurred during correct and during incorrect trials. For both types of trials, the specific goal was to look for patterns in the temporal sequence of surround motions that were different than expected by a random process. To perform such an analysis, the sequence of surround motions on each trial was coded relative to the center motion. Specifically, when any given 5 ms motion step in the surround was the same as the center motion, it was coded as 1. When it was opposite to the center motion, it was coded as 0. For every trial, this resulted in a temporal sequence of 0’s and 1’s with the origin (i.e. 0 ms point) aligned with the peak of the center motion. Correct and incorrect trial sequences were then averaged separately and smoothed with a moving Gaussian window. The standard
deviation ($\sigma$) of the smoothing Gaussian was 7.5 ms; this $\sigma$ removed most of the noise but did not affect the overall shape of the temporal profile. Figure 1C shows an example of raw data and the result of smoothing. All of the analyses were done on smoothed data.

A basic assumption behind this method is that if surround motion has no influence on the discriminability of the center motion, then after many trials the result at each 5 ms time interval would approach 0.5 (i.e. equal proportion of the same and opposite directions in the surround). If, for example, the occurrence of the same direction of motion at a specific 5 ms interval increases the likelihood of making a mistake, then the result for the incorrect trials at that time interval would be greater than 0.5. Note that in a 2AFC design, the incorrect trials are more informative than the correct trials because a correct response is often a correct guess. Hence, to increase the number of incorrect trials, a relatively high task difficulty was maintained (yielding 70% correct performance).

The method yields meaningful results only after a large number of trials; i.e., when the random noise is ‘averaged out’. Thus, all observers ran 2,500 trials per condition, with the first 500 trials discarded as practice. Observers typically ran 1,000 trials per session. The total number of trials in this experiment was 30,000 (the data presented in Figure 5 required an additional 20,000 trials). To quantify the variability expected by the random process alone, we ran 10,000 Monte Carlo simulations of the experiment assuming that surround motions have no influence on the discriminability of center motion. The results of each simulation were smoothed with a moving Gaussian window ($\sigma = 7.5$ ms), as shown in Figure 1C. This yielded 10,000 incorrect trial curves and 10,000 correct trial curves. Two standard deviation boundaries were estimated from these two sets of curves.
This method is designed to yield a temporal profile of the surround influence on the center motion. This temporal profile was characterized by five parameters: (1) direction of influence (main peak/dip greater or less than 0.5), (2) strength of influence (deviation of the peak influence from 0.5), (3) peak time (the time of the peak influence relative to the center motion), (4) start time (the earliest time at which significant influence is observed), and (5) duration of influence (time between the start time and the stop time).

Of particular interest is the determination of whether any of these parameters change with variations in surround contrast, as contrast will likely affect the timing of surround signals. In fact, the present method is optimized to estimate the relative latencies of surrounds with different contrasts, and is not very sensitive to the absolute delay between center and surround signals. That is because the zero (0 ms) point in our graphs denotes the physical occurrence of the center motion. A “real” zero point would be shifted rightward by the amount equal to the center stimulus latency — a number unknown to us. Given that the center stimulus appears gradually within a temporal Gaussian envelope, attains its peak contrast only in one frame, and its occurrence is random within 150 ms, we speculate that its neural latency may be rather long. Moreover, relatively long center latency may explain surround influence peaks occurring slightly ahead of the occurrence of the center motion (e.g., Fig. 1C), even if actual surround influence is delayed (cf., Allman et al., 1985b; Borghuis et al., 2003).

Low-contrast center experiment

We attempted to repeat the above described reverse correlation experiment with low-contrast center motion, but the results did not differ from chance. A likely problem was that the duration threshold for the low-contrast center motion was typically an order of magnitude higher than with high-contrast center motion. This longer exposure
duration is critical because the success of the reverse correlation experiment depends on having a very brief target motion. To get around this problem we repeated the experiment at low contrast with the following changes: (1) Duration thresholds for the low-contrast center were lowered by replacing the Gaussian temporal envelope with a trapezoid-like temporal envelope. This new profile was created by truncating the top half of the Gaussian profile and adding 0.5 (i.e., 50% contrast) to the truncated profile. For example, an 8.8 ms threshold (average threshold for the data shown in Fig. 5) would be shown in eleven 5-ms frames with contrasts that are 52%, 57%, 73%, 100%, 100%, 100%, 100%, 73%, 57%, and 52% of the peak center contrast. This was still a relatively long stimulus presentation, but it was much shorter than the threshold stimulus duration when the standard Gaussian envelope was used. (2) To reduce the number of different surround directions that may have an influence on the discriminability of the center motion during each trial, a new direction of surround motion was randomly chosen every 10 ms or, in a separate condition, every 15 ms. This maneuver meant that a given direction of motion in the surround continued for a longer duration, thereby reducing the number of motion direction changes in a given time period. (3) Center contrast was chosen to be relatively low, but still high enough to yield moderately low thresholds. Based on the results of pilot explorations, a 5.25% center contrast was used in the 10 ms surround motion condition and a 6% contrast was used in the 15 ms surround condition.

RESULTS

The discriminability of the center motion was substantially affected by the rapidly jittering surround pattern (Fig. 2). For all observers, surround temporal profiles estimated from incorrect trials significantly differed from what was expected by chance alone. Moreover, all temporal profiles are positioned largely above 0.5, indicating that
the presence of same direction of motion in the surround increased the probability of making a mistake. To derive an overall estimate of the temporal characteristics of the surround influence, the individual results were averaged (Fig. 3A). Quantitative estimates of these temporal characteristics are presented in Table 1. Peak time, start time (marked with arrows in Fig. 3A) and the duration of influence all showed a systematic dependence on surround contrast: the temporal profile of surround influence was longer, started earlier and peaked earlier as the surround contrast was decreased. These results may be a result of longer and more variable neural response latencies at low contrast (Lennie, 1981; Maunsell et al., 1999; Reich et al., 2001).

The strength of the surround’s effect on the discriminability of center motion depended on the contrast of the surround (Table 1), with the 6.5% contrast surround having the strongest and “longest” effect on the center motion. If our estimates of the duration and the strength of influence indeed indicate the potency of the surround effect and if the effect of surround is suppressive, than the center motion would be harder to perceive in conditions with stronger and longer surround influence. To test this hypothesis, we compared the potency of surround influence in different conditions with the observers’ thresholds in those conditions. For the quantitative part of this analysis, we excluded the data for the 1.7% surround contrast condition (shown as gray circles in Fig. 4), because this very low contrast surround pattern partially filled-in the region where the center would appear, likely affecting observers’ performance. Analysis of the remaining three surround conditions (Fig. 4A) showed a positive correlation between duration thresholds and the duration of influence \( p = .038 \), and there was a trend toward positive correlation with the strength of influence \( p = .13 \), Fig. 4E). Positive correlations between duration thresholds and the estimates of surround influence were also observed when the data for individual subjects were analyzed (Fig. 4B-D, F-H). This indicates that the task was harder in the conditions with stronger and longer
surround influence on the center motion, as indexed by both the strength and the duration of influence. This, in turn, suggests that the center-surround interactions recovered through reverse correlation are suppressive. Such an interpretation is in agreement with the psychophysical work revealing strong suppressive interactions in motion perception (Tadin et al., 2003) and a lack of significant opposite-direction facilitation in macaque MT (Raiguel et al., 1995).

Significant deviations from randomness were also found when correct trials were analyzed (even though the present reverse correlation experiment was designed to maximize the usability of incorrect trials – i.e., the “correct” trials also include trials on which the observer guessed correctly). The temporal profiles are now below 0.5 (Fig. 3B), indicating that observers were less likely to correctly identify motion direction when there was same direction motion in the surround. This is in accord with the results extracted from incorrect trials. The relative properties of the temporal profiles for different contrast surrounds (e.g., relative ordering of peak time, start time and the duration of the influence) are comparable to those estimated from the incorrect trials.

One interesting feature of our results is the “dip” appearing about 35 ms before the peak in 92% surround contrast condition (Fig. 3A). This dip is significant (more than 3σ below baseline) and indicates that at those times the presence of the opposite direction surround increased the probability of making a mistake. However, 20 to 50 ms later, it is the same direction surround motion that increases the likelihood of making an incorrect response. This temporal profile is reminiscent of the response of bi-phasic MT neurons (Bair & Movshon, 2004; Pergé et al., 2005), which are best activated by an anti-preferred direction followed by a preferred direction 40 ms later.

To further investigate this feature of our results, we asked whether different combinations of surround motion directions occurred more often than expected — a question that can be answered by a second-order analysis of the data. The probability
of each of four possible motion direction pairs (same-same, opposite-opposite, same-opposite and opposite-same) was computed for incorrect trials. Probabilities were calculated for all motion direction pairs — i.e., the analysis was not limited to sequential motion directions. The results for all surround contrasts (not shown) did not differ from what was expected given baseline (first-order) probabilities of each surround direction in a pair. (Expected probability is simply the product of independent probabilities for each motion direction in the pair that is being examined). A second-order analysis looking at the pairs of motion directions within correct trials also did not show any systematic deviations from chance. Such null results are hard to interpret because the smaller number of usable trials (each direction combination occurs only in about 1/4 of the trials) may make likely smaller second-order effects hard to detect. In addition, second-order effects are compared to already noisy baseline probabilities, hence further decreasing our chances of detecting them. Thus, we are uncertain whether the co-presence of the dip and the peak in 92% contrast data indicates two independent effects or whether that result is due to an opposite-same interaction analogous to that observed in bi-phasic MT neurons (Pergé et al., 2005; Bair & Movshon, 2004).

Presented data (Figs. 2, 3 & 4) suggest that the surround influence is suppressive regardless of surround contrast. This is somewhat puzzling because of the evidence demonstrating that surround influence is facilitatory when the entire stimulus is low contrast (Tadin et al., 2003; Pack et al., 2005). One possible resolution of this puzzle is that the contrast of the center and not the surround determines the directionality of center-surround interactions. We tested this possibility by modifying our experimental design to enable the use of low-contrast center stimulus (see Methods). The resulting reverse correlation temporal profiles were much broader than in the high-contrast center experiment (Fig. 5). This broadening is likely due to the longer center motion presentation and lengthening of surround motion impulses (to 10 & 15 ms) — our initial
pilot work with high-contrast center motion with longer surround motions (10 & 15 ms) also yielded broad surround temporal profiles. Also, note that temporal profiles were broader when 15 ms surround impulses were used (Fig. 5B), again linking the changes in surround motion with observed broadening of the results.

The most important aspect of the low-contrast center result is that the temporal profiles derived from incorrect responses are inverted compared to profiles produced by the high-contrast center (compare Fig. 5 with Fig. 3A). Moreover, by examining psychophysical thresholds in different conditions (shown as numbers near different curves in Fig. 5), it is apparent that the motion discrimination task was harder in conditions with stronger surround influence on the center motion. Given the directionality of the surround’s effect (i.e., the inversion), this indicates that there were fewer same-direction (and more opposite-direction) surround motions in incorrect trials. That is, same direction motion in the surround was associated the decreased probability of making a mistake, consistent with the same-direction facilitation hypothesis. Evidently, then, the center contrast does indeed determine the directionality of center-surround interactions — i.e., whether the interaction between the center and the surround is suppressive or facilitatory does not depend on surround contrast. The broad temporal influence functions for low-contrast center motion preclude accurate estimation of their temporal characteristics. Nevertheless, the peaks (i.e., dips) of the functions appear to have roughly the same dependence on surround contrast as the high-contrast center: progressively earlier peak times with decreasing contrast (Fig. 5).

**DISCUSSION**

These experiments reveal interactions between center and surround motions and their dependency on relative direction, contrast and timing. Same-direction surround motion reduced the discriminability of high-contrast center motion and improved the
discriminability of low-contrast center motion, regardless of surround contrast. The timing of the observed center-surround interactions depended on surround contrast; as the contrast of the surround decreased, surround motion needed to occur earlier relative to the center motion to have an effect on observers' performance.

These results were revealed using the temporal reverse correlation method, which allowed us to estimate the time course of center-surround interactions with relatively high precision, especially for very brief high-contrast center motion. It is worth reiterating that these results were obtained from surround motions that were perceived simply as a very fast up-down jitter. When queried, observers admitted that it was impossible to discern what surround motion sequence occurred just before and during center motion presentation – this aspect of the stimulus was invisible to perceptual awareness. Nonetheless, analysis of the raw data revealed strong and reliable patterns of surround influence on the discriminability of the center motion.

Our results imply that neurons coding visual motion adequately represent rapidly changing motions that comprise surround stimuli used in the present study. Analyses of retinal responses to moving stimuli show that the direction of fast moving stimuli can be encoded at a very small time scale (Chichilnisky & Kalmar, 2003; Frechette et al., 2005; B. G. Borghuis, D. Tadin, M. J. M. Lankheet, J. S. Lappin, W. A. van de Grind, unpublished observations). Optimal encoding of a ~20°/s stimulus requires integration (i.e., low-pass filtering) of ganglion cell responses for about 10 ms, but sufficient information about motion direction is obtained even if the retinal responses are integrated for just over 1 ms. This suggest that cortical motion mechanism might be able to represent motion direction of very brief motion impulses. Cortical direction-selective neurons indeed respond very well to stimuli randomly changing direction at 60 Hz (Buracas et al., 1998), 100 Hz (Bair et al., 2002; Bair & Movshon, 2004) or 120 Hz (Borghuis et al., 2003; Perge et al., 2005). In fact, MT neurons respond with less
variability and transfer information with higher efficiency when the stimulus rapidly changes direction (Buracas et al., 1998). In such cases, the spike timing precision to a repeated random sequence of directions can be as high as 2-3 ms. Thus, while there are no studies of motion neurons with the 200 Hz change rate used here, direction selective neurons respond with high fidelity to this general type of stimulation.

The longer neural latency associated with weaker visual stimuli (Maunsell et al., 1999; Reich et al., 2001) may explain differences in the start and peak time of the temporal profile for different contrast surrounds (Fig. 3A, Table 1). A “slow” low-contrast surround signal must be initiated well before the center signal to arrive in time to interact with the center signal. A “fast” high-contrast surround should be initiated only slightly before the center signal for the interaction to occur. Latencies of cortical neurons tend to increase by 30-40 ms as the contrast decreases (Reich et al., 2001). Coincidentally or not, the peak of the surround temporal profile in our data shifted about 35 ms back in time as the surround contrast decreased. In addition to the peak shift, we also observed broadening of temporal influence functions for low contrast surrounds. This result may be explained by increased variability in the latency of low-contrast stimuli (Maunsell et al., 1999). Specifically, the increased range of surround latencies at low contrast extends the range of time points within which surround motion can occur and still interact with the center motion. On the other hand, less variable latency of high-contrast stimuli restricts the range of relative temporal offsets for which the center and surround will interact.

We also found that the contrast of the center determines whether the spatial interactions in motion are suppressive or facilitatory (Fig. 5 vs. Fig. 3A). This makes functional sense if one views surround modulation as a mechanism whose main purpose is to enhance processing of the visual input stimulating the receptive field center. Thus, weak center responses are reinforced by center-surround interactions
regardless of surround contrast. When the center response is strong, the surround influence becomes suppressive — presumably allowing such neurons to perform more complex computations. This is an important observation that extends the initial psychophysical description of surround suppression (Tadin et al., 2003). Tadin et al. (2003) did not vary the contrasts of the center and surround separately, precluding any conclusions about whether the center or the surround contrast determines the sign of their interaction. The present finding is consistent with modeling work in which the activity level of the classical receptive field (i.e., center) determines the nature of center-surround interactions. Specifically, surround suppression is hypothesized to occur at high levels of center activity, while surround facilitation should be more pronounced at low levels of center activity (Stemmler, Usher & Niebur, 1995; Somers et al., 1998). It should be noted, however, that models based on increased spatial summation at low contrast (cf., Sceniak et al., 1999), might also be consistent with the aforementioned results, although it is unclear how such models would respond to a low-contrast stimulus encircled by a high-contrast surround.

As a final note, an important motivator for using the reverse correlation in neurophysiology is its time-efficiency — reverse correlation can be computed for every spike. In contrast, the psychophysical reverse correlation described here is extremely time-inefficient. Instead of using frequent spikes as the basis of the computation, we rely on infrequent observers’ responses. Nevertheless, the potential benefits of this technique can be well worth the extra effort. The psychophysical temporal reverse correlation may be adapted to investigate other visual mechanisms where different components of the response are likely to have different temporal profiles such as iso-orientation suppression (Bair, Cavanaugh & Movshon, 2003), figure-ground discrimination (Lamme, 1995) and illusory contour processing (Ramsden, Hung & Roe, 2001).
REFERENCES


dynamics of direction tuning in motion-sensitive macaque area MT. J Neurophysiol
93:2104-2116.

Reichardt W (1961) Autocorrelation, a principle for the evaluation of sensory information
by the central nervous system. In: Sensory communication (Rosenblith WA, ed), pp303-

Raiguel SE, Van Hulle MM, Xiao DK, Marcar VL, Orban GA (1995) Shape and spatial
distribution of receptive fields and antagonistic motion surround in the middle temporal
area (V5) of the macaque. Eur J Neurosci 7:2064-2082.

Raiguel SE, Xiao DK, Marcar VL, Orban GA (1999) Response latency of macaque area
MT/V5 neurons and its relationship to stimulus parameters. J Neurophysiol 82:1944-
1956.

Reich DS, Mechler F, Victor JD (2001) Temporal coding of contrast in primary visual

Ramsden BM, Hung CP, Roe AW (2001) Real and illusory contour processing in area

summation by macaque V1 neurons. Nature Neurosci 2:733-739.

approach to understanding integration of long-range inputs in primary visual cortex.
Cereb Cortex 8:204-217.


FIGURE LEGENDS

Figure 1. A, An illustration of the sequence of events occurring in the center and surround regions of the stimulus. Each arrow depicts a 5ms motion impulse. All upward surround motions (i.e., those in the same direction as center motion) are coded as 1, while all downward motions are coded as 0. The Gaussian envelope over the center motion depicts contrast modulation of the center motion in time. B, Single-frame snapshot of the surround pattern. The random-dot texture moved either up or down, with the direction randomly chosen every 5 ms. Such motion sequences were typically perceived as very fast up-down jitter. The edge of the central hole, the location where the center motion appeared, was always stationary. Scale bar is 1°. C, Illustration of the raw data and the Gaussian smoothing of the data. The data sample is for the incorrect trials in the high-surround condition (92%). Short-dash lines indicate ±2 s.d. boundaries for the raw data, while long-dash lines indicate ±2 s.d. boundaries for the smoothed result.

Figure 2. Temporal reverse correlation functions depicting incorrect trial results for three observers. Each curve represents data for a different surround contrast. Data were smoothed as illustrated in Figure 1C. Dashed horizontal lines are ±2 s.d.

Figure 3. A, Temporal reverse correlation functions depicting incorrect trial results averaged over three observers. For each surround contrast, arrows indicate the peak surround influence (top arrows) and the times at which surround influence reaches significance (arrows along the dashed line). B, Temporal reverse correlation functions depicting correct trial results averaged over three observers. For each surround contrast, arrows indicate the time point with the strongest surround influence (bottom arrows) and the times at which surround influence reaches significance (arrows along the dashed line). Dashed horizontal lines in both panels are ±2 s.d. boundaries.
Figure 4. The relationship between psychophysical thresholds and two estimates of the potency of center-surround interactions: (A-D) the duration of the surround influence and (E-H) the strength of the surround influence. Panels A and E show the average data, while the remaining panels show results for individual observers. Straight lines are linear fits to the data. Gray circles depict results for the 1.7% surround contrast condition. No such data is shown for observer EA, because his results for 1.7% surround contrast condition did not differ from chance (Fig. 2). His duration threshold in that condition was 6.7 ms. All error bars are s.e.m.

Figure 5. Temporal reverse correlation functions depicting incorrect trial results for observer EA in the low-contrast center condition, with surround motion directions constrained to move in one direction for 10 ms (A) and 15 ms (B). The numbers located near different curves indicate the psychophysical duration thresholds (in milliseconds) for each surround condition. The curves show smoothed raw data (smoothing was done with a moving Gaussian window (σ = 22.5 ms). Separate Monte Carlo simulations were performed to estimate two standard deviation boundaries (shown as dashed lines). The details of the simulations were as described in the Methods except that surround motion parameters were adjusted to match the stimulus changes we made in this experiment.
Table 1. Quantitative description of the temporal profiles shown in Figure 3A. Measures presented in the table are defined in the Methods. Strength of influence is also expressed in terms of standard deviations away from 0.5 (in parenthesis). Peak time and start time are also shown as relative to 92% surround contrast estimates (in parenthesis). To obtain a more precise estimate of peak and start times, we calculated a weighted average of data within ±10 ms of the temporal point where the surround influence was strongest, or, for the start point calculation, the point where the significant influence was first observed.

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<td>(12.9 σ)</td>
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<td>-2.0 ms</td>
<td>-27.0 ms</td>
</tr>
<tr>
<td></td>
<td>(0 ms)</td>
<td>(-5 ms)</td>
<td>(-10 ms)</td>
<td>(-35 ms)</td>
</tr>
<tr>
<td>Start time</td>
<td>-9.1 ms</td>
<td>-30.8 ms</td>
<td>-69.6 ms</td>
<td>-46.9 ms</td>
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<tr>
<td></td>
<td>(0 ms)</td>
<td>(-22 ms)</td>
<td>(-62 ms)</td>
<td>(-38 ms)</td>
</tr>
<tr>
<td>Duration of influence</td>
<td>41 ms</td>
<td>80 ms</td>
<td>123 ms</td>
<td>71 ms</td>
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Figure 1. A, An illustration of the sequence of events occurring in the center and surround regions of the stimulus. Each arrow depicts a 5ms motion impulse. All upward surround motions (i.e., those in the same direction as center motion) are coded as 1, while all downward motions are coded as 0. The Gaussian envelope over the center motion depicts contrast modulation of the center motion in time. B, Single-frame snapshot of the surround pattern. The random-dot texture moved either up or down, with the direction randomly chosen every 5 ms. Such motion sequences were typically perceived as very fast up-down jitter. The edge of the central hole, the location where the center motion appeared, was always stationary. Scale bar is 1°. C, Illustration of the raw data and the Gaussian smoothing of the data. The data sample is for the incorrect trials in the high-surround condition (92%). Short-dash lines indicate ±2 s.d. boundaries for the raw data, while long-dash lines indicate ±2 s.d. boundaries for the smoothed result.
Figure 2. Temporal reverse correlation functions depicting incorrect trial results for three observers. Each curve represents data for a different surround contrast. Data were smoothed as illustrated in Figure 1C. Dashed horizontal lines are ±2 s.d.
Figure 3. A, Temporal reverse correlation functions depicting incorrect trial results averaged over three observers. For each surround contrast, arrows indicate the peak surround influence (top arrows) and the times at which surround influence reaches significance (arrows along the dashed line). B, Temporal reverse correlation functions depicting correct trial results averaged over three observers. For each surround contrast, arrows indicate the time point with the strongest surround influence (bottom arrows) and the times at which surround influence reaches significance (arrows along the dashed line). Dashed horizontal lines in both panels are ±2 s.d. boundaries.
Figure 4. The relationship between psychophysical thresholds and two estimates of the potency of center-surround interactions: (A-D) the duration of the surround influence and (E-H) the strength of the surround influence. Panels A and E show the average data, while the remaining panels show results for individual observers. Straight lines are linear fits to the data. Gray circles depict results for the 1.7% surround contrast condition. No such data is shown for observer EA, because his results for 1.7% surround contrast condition did not differ from chance (Fig. 2). His duration threshold in that condition was 6.7 ms. All error bars are s.e.m.
Figure 5. Temporal reverse correlation functions depicting incorrect trial results for observer EA in the low-contrast center condition, with surround motion directions constrained to move in one direction for 10 ms (A) and 15 ms (B). The numbers located near different curves indicate the psychophysical duration thresholds (in milliseconds) for each surround condition. The curves show smoothed raw data (smoothing was done with a moving Gaussian window ($\sigma = 22.5$ ms). Separate Monte Carlo simulations were performed to estimate two standard deviation boundaries (shown as dashed lines). The details of the simulations were as described in the Methods except that surround motion parameters were adjusted to match the stimulus changes we made in this experiment.