Peripheral Influences on Motion Integration in Foveal Vision Are Modulated by Central Local Ambiguity and Center-Surround Congruence

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PURPOSE. To study how central visual motion integration and segmentation processes are influenced by the congruence or incongruence of peripheral contextual moving surroundings and to determine their clinical relevance.

METHODS. Nine subjects participated in experiments 1 and 2 (12-second blocks containing 2-second static fixation and 10-second surface plaid movement) and 15 in experiment 3 (72-second blocks, with 12-second fixation, and 60-second motion). Observers reported whether they perceived nontransparent (corresponding to visual integration of motion cues into one surface) or transparent (segmentation of two surfaces from motion cues) plaid motion within a 5° central circular region. Surround stimuli were 20° transparent or nontransparent moving plaids.

RESULTS. Contextual effects required the presence of both local and global ambiguity. If central local motion became unambiguous, then surrounds became ineffective. Under local and global ambiguity, transparent surrounds invariably induced central congruence while also strongly suppressing incongruent percepts. Nontransparent surrounds produced similar but less consistent congruent bias, especially for longer viewing times. In the latter case, however, suppression of incongruent central interpretations became barely detectable compared to the observed significant facilitation of congruent percepts.

CONCLUSIONS. Local ambiguity is critical in contextual modulation, and the peripheral enhancement or suppression of central motion integration depends both on transparency bias and center-surround congruence. The importance of local ambiguity in contextual modulation is clinically relevant, because it implies that contextual effects will be stronger in disorders with impaired central vision, such as macular degeneration.

Moreover, the increased efficacy of global context under conditions of increased local ambiguity may be useful in future rehabilitation approaches. (Invest Ophthalmol Vis Sci. 2009; 50:980–988) DOI:10.1167/iovs.08-2094

The study of center-surround interactions in visual perception is of great relevance in health and disease, in particular for understanding different forms of visual impairment in which central and peripheral vision are differentially affected, such as macular degeneration¹–³ and scotomas of cortical origin.³ Previous literature has shown that what patients can see is not necessarily correctly anticipated from their visual fields or neurophysiological data.³–⁵ Indeed, we have reported previously that patients with acquired or neurodevelopmental disorders could integrate coherent motion representations despite the presence of local disruption of magnocellular information processing; thus, we hypothesized that such patients were integrating contextual information over space to solve for local ambiguity.³–⁵ Our own work on Stargardt and Best disease has in fact elucidated that local impairment is strongly dependent on how much spatial information can be integrated over space (explaining why magnocellular impairment is more confined to central vision than parvocellular impairment).¹,² In this study, we explored the well-known concept that visual context can influence the perception of local stimuli,³–⁵ an effect that is observed even if the experimental subject is not aware of the presence of a modulatory stimulus.¹¹ The most commonly explored and discussed types of center-surround interactions are the contextual sensitivity of human contrast, orientation discrimination, and vernier thresholds, because they can be directly related to neurophysiological studies in monkey V1 and also because the role of primary visual cortex in contour integration is relatively well understood. It is known that contrast detection can be improved up to 40% by suprathreshold contextual information, the effect being modulated by low-level properties such as relative orientation and collinearity.¹² Moreover, it is well established that responses of visual neurons may be markedly modulated by stimuli outside the classic receptive field (i.e., stimuli that do not themselves evoke responses of such neurons), and such modulation is dependent on the relative orientation, direction of motion, and contrast of stimuli presented in surrounding regions.¹³–¹⁶ Accordingly, there is also evidence that relative-motion stimuli represent important contextual influences.¹⁷ Most of these interactions can be explained by models that postulate contour integration mechanisms through long-range horizontal connections¹⁸,¹⁹ or competition processes based on surround suppression and/or binocular rivalry.²⁰–²² However, the rules governing peripheral contextual influences on the interpretation of ambiguous central motion stimuli remain largely unexplored. Comprehending the local and global rules that constrain the facilitatory effects of visual context in solving visual integration problems is equally relevant in the understanding of normal and pathologic vision, since ambiguity in perception is a common denominator in diseases causing visual impairment. A better insight on these
mechanisms can lead to an improved understanding of disease pathophysiology and also to the development of new rehabilitation strategies.

In this study, we have explored peripheral contextual influences on the perceptual competition between moving surface segmentation and integration processes. The effects of context were studied using ambiguous bi-stable stimuli: Subjects were to report their interpretation of two superimposed gratings moving in different directions (plaid stimuli, see Fig. 1 for experimental design and stimulus conditions, and the Methods section for further details). Plaids may be perceived either as two surfaces, one being transparent and sliding on top of the other (transparent or component motion) or as a single, coherent pattern whose direction of motion is intermediate to the component vectors (nontransparent or pattern motion).

The degree of perceived transparency depends on the luminance of the grating intersections, the angle between movement directions, and the speed of the components.25–25 Our question was whether the type of perceptual congruence of peripheral contextual surrounds could modulate suppression and enhancement of center surface motion signals, and whether local and global ambiguity had distinct roles in this process.

METHODS

Participants

Nine subjects participated in experiments 1 and 2, and 15 in experiment 3, all with normal or corrected-to-normal visual acuity, and good fixation abilities (described later). The experiments were undertaken with written informed consent of each subject, in compliance with the Declaration of Helsinki and Guidelines of the Ethics Committee of the Faculty of Medicine of the University of Coimbra.

Experimental Setup and Stimuli

Stimuli were generated by our own custom-developed scripts (running in a commercial software environment, MatLab, The MathWorks, Natick, MA; using the Cogent 2000 Software Toolbox; http://www.vislab.ucl.ac.uk/cogent.php/ provided in the public domain by the Laboratory of Neurobiology, University College London, UK) and presented on a gamma-corrected 21-inch CRT monitor (Sony, Tokyo, Japan, equipped with Trinitron phosphors) with an 800 × 600-pixel resolution and a refresh rate of 60 Hz. The monitor was the only light source in the room during the experiment. The 60-cm viewing distance and the head position of observers were stabilized with a chin/forehead rest. Stimuli were presented in subject-initiated blocks containing an initial cue for fixation followed by a moving plaid display (Fig. 1) under three distinct overall luminance/contrast sets (Table A1, in the appendix, for details on stimuli physical parameters): high-luminance, high-contrast (HLHC); high-luminance, low-contrast (HLLC); and low luminance (LL). Observers were asked to give continuous report whether they perceived nontransparent or transparent plaid motion within the 5° central circular region of the 20° diameter plaid display. Behavioral responses (perceptual decisions) were continuously recorded during the motion period by means of mouse button presses. The recorded button-press data yielded the percentage of nontransparent, transparent, and ambiguous perceptual states during the period of moving stimulus presentation. A 0.15°-diameter fixation dot was present and a 0.25°-wide red annulus ensured physical separation between center and surround regions within the moving plaid display (Fig. 1).

Experiment 1: Surround Modulation under Short Viewing Times. Stimuli were presented in subject-initiated, 12-second blocks containing 2 seconds of fixation and 10 seconds of plaid movement (Fig. 1a). We defined 11 center conditions for all luminance/contrast sets with graded levels of perceptual coherence: eight were obtained by varying the luminance of grating intersections (for details, see Table A1 in the Appendix) and three by applying local dynamic texture on the gratings (Figs. 1c, 1d). Surround conditions were defined as either no surround (to establish perceptual ambiguity of the central stimuli per se) or as a 20° diameter moving plaid patch surrounding the central patch, having similar spatiotemporal properties as the central stimulus, thus differing only in terms of intersection luminance and/or local texture (Fig. 1d), yielding categories of surround stimuli biased toward either nontransparent or transparent mo-
tion. Center and surround regions were separated by a 0.25° wide red annulus of fixed size, so that they were not adjacent.

The spatiotemporal parameters of plaid movement were kept constant throughout the experiments: movement with 30% duty-cycle gratings, 1 cyc/deg spatial resolution, 1 dps velocity, and 120° difference in movement direction with upward coherent motion direction in experiments 1 and 2; and coherent movement in all the cardinal directions in experiment 3. Only luminance parameters, texture, and the presence or absence of the surround patch were varied across conditions.

The direction of motion of dots forming the textures was the following (when referring to the upward motion used in experiment 1): three directions (one vertical, two horizontal) for ambiguous textures (Txd ambiguous), two directions (both horizontal) for textures unambiguously biased for transparency (Txd component), and 1 direction (vertical) for textures unambiguously biased for (pattern) coherence (Txd patt). Note, that ambiguous textures were constructed such that 50% of the superimposed dots provided bias towards transparency and 50% towards nontransparency.

Experimental blocks were organized into three repeated runs for each of the three luminance conditions, each run containing 66 blocks in randomized presentation order.

Experiment 2: Ruling Out Patch Size as the Explanation of the Main Effect. In the second experiment, we analyzed the effect of stimulus size on coherency decisions by varying the size of plaid stimuli (Fig. 1e). We included five luminance- and/or texture-defined plaids from the first experiment in all the previously described three overall luminance and contrast sets while varying the size of the moving plaid patches in five steps. The spatiotemporal characteristics of plaid movement and the perceptual task were the same as in experiment 1.

Experiment 3: Surround Modulation under Longer Viewing Times. In the third experiment, we investigated the modulation of highly ambiguous center stimuli during relatively long stimulus presentation periods. Since the three overall luminance and contrast sets defined in experiment 1 yielded similar results, we used only stimuli from the HLHC set for this follow-up investigation. The stimulus arrangement and spatiotemporal characteristics were similar to that of the first two experiments; however, stimulus blocks were presented for 72 seconds, with 12 seconds of static fixation and 60 seconds of plaid movement (Fig. 1b). The behavioral task was similar to those in experiments 1 and 2.

Every subject underwent two sessions of experimental runs: In the first session, we presented center-only stimuli with varying luminance of the intersections, to find the region of ambiguity of each subject and to minimize possible floor and ceiling effects. In the second run, we presented the central patch found to be the most ambiguous either with no contextual surround or with textured component and pattern biased surrounds. We decided to present textured unambiguous surrounds only, because this way we could prevent any possible bias induced by switches in the surround percepts.

In addition, coherent plaid motion directions were randomized across the four cardinal directions to further generalize our results for long exposure times.36

Defining Regions of Maximum Perceptual Ambiguity

Before experiment 1, we first searched for regions of perceptual ambiguity for the different stimulus conditions, to determine the best parameter range for contextual modulations. We have observed the previously described inverted U-shaped curve (peak corresponding to frequently perceived transparency) for all overall luminance and contrast sets for stimuli in which no modulatory surround was present (see Supplementary Figs. S1, S2, online at http://www.iovs.org/cgi/content/full/50/2/980/DC1). This procedure was replicated before experiment 3.

Selection of Contextual Surround Stimuli

For providing reliable surround modulation, we needed to select contextual modulatory stimuli with stable perceptual effects and, possibly, with low ambiguity. Therefore, we decided to use texturred stimuli along with luminance-defined stimuli. Textured surrounds indeed proved to be more stable (0% transparency for Txd patt and 90% transparency for Txd comp stimuli) than luminance-defined surrounds (~0% transparency for pattern and ~45% transparency for component stimuli), regardless of the overall luminance/contrast conditions (Fig. 2a). The reason for the perceptual stability of textured stimuli is their local (single dot) and global (populations of dots moving vertical for pattern and horizontally for component) unambiguosity. In sum, textured surrounds and luminance-defined pattern stimuli showed the most stable perceptual effects and efficacy for contextual modulation (see details in the Results section), and an intermediate stability and efficacy were observed for luminance-defined component (transparent) stimuli. The observed low level of ambiguity and strong perceptual stability of textured surround stimuli confirms the prediction that local dot motion provides physical disambiguation and reduces uncertainty.27

Eye Movement Control Experiments

All subjects were experienced observers and were selected on the basis of fixation ability on concurrent eye movement experiments. We nevertheless ran further control eye movements experiments using plaid stimuli in eight subjects (iViewX High-speed Eye-Tracker; SMI, Munich, Germany) which allowed for data collection at 240 Hz. Data time series were searched for fixation, blinks, and saccadic events (Begaze Software; SMI) and subsequently exported to one of two standard statistical packages (SPSS, SPSS, Chicago, IL; StatView; SAS) for analysis.
Institute, Cary, NC). Analysis of the recorded data showed that fixation could be stably held across all conditions, with very rare saccades, and reduced the number and duration of blinks, which was similar across conditions. Under the conditions of the experiment, we could therefore ascertain that the subjects did not foveate the surround region.

Statistical Analysis

The continuous recording of responses allowed us to estimate the overall duration of single-percept types (transparent or nontransparent), the relative ratio of these perceptual states during the presentation periods, and the number of perceptual switches as a possible measure of perceptual stability. Note that the total amount of time in a given state is dependent both on the number of switches to that state and single-state durations.

In describing the overall perceptual state duration during the presentation period, we provide statistics based on the percentage of “transparent” responses, because these statistics are complementary to those based on the percentage of nontransparent responses (taking into account that % transparent + % nontransparent + % unsure = 100%), and the percentage of unsure responses, in which subjects pressed either both buttons or none of them, because their uncertainty in describing the percepts was low and stable across all conditions (see Supplementary Fig. S1, http://www.iovs.org/cgi/content/full/50/2/980/DC1). The latter observation proved that the perceptual response patterns were indeed not influenced by the level of subject uncertainty.

We have applied ANOVA statistics (except as otherwise stated) after excluding potential violations of its statistical assumptions (including Kolmogorov-Smirnov normality verification, and Levene homogeneity tests).

In the case of experiment 3, we performed GLM (general linear model)/ANOVA repeated measures and random-effects analyses (given a relatively large number of subjects), using the subjects as the random variable. Effects were tested by using both between-subjects (with subjects entered as random effects) and within-subject comparisons. Fisher PLSD correction for post hoc comparisons was applied. The same dichotomy of contextual influence was found using within-subjects GLM and nonparametric statistical models (Friedman and Wilcoxon tests, for within-subject comparisons), thereby proving the robustness of our results and their independence of the statistical model used. In the special case of assessment of the number of percept switches as an indicator of perceptual stability we have used the Kruskal-Wallis test given the gross violations of ANOVA assumptions even after variable transformations.

Assessing the Stability of Single Percepts

Although our main analyses focused on the overall time spent in each perceptual state, it is also important to specifically analyze the stability of a single percept. In this part of the analysis, we therefore departed from considering the total amount of time spent in a given perceptual state and used the duration of single perceptual states. This approach helps in differentiating between the inherent perceptual bias and the ambiguity (in the sense of stability) of a given stimulus, thus providing an independent measure of percept stability or stimulus ambiguity. Note that a highly ambiguous stimulus with a given perceptual bias can solely differ from a similarly biased but less ambiguous stimulus in the number of perceptual switches. Accordingly, a given surround type may lengthen specific single-percept-duration events without a change in the overall summed duration, depending on the number of switches during that condition. This notion may also be clinically relevant in the study of visual impairment and ageing processes.

Moreover, response type (pattern or component) ordering of single-percept durations provides means for describing the effects of surround modulation in terms of enhancement or suppression depending on perceptual congruency and incongruency between centers and surrounds compared to the no-surround condition. In this kind of analysis, there is a signature of enhancement of congruent percepts if the average single-percept duration for the perceptually congruent surround condition is longer than that of the no-surround condition. Similarly, active suppression is verified if the average single-percept duration for the perceptually incongruent surround condition is shorter than that of the no-surround condition.

RESULTS

Experiment 1: Surround Modulation with Short Viewing Times

We found that reported central percepts significantly depended on the types of contextual surrounds used (one-way ANOVA, \( P < 0.0001 \) for the main effect of surround, for post hoc analyses; see below). It is worth pointing out that we explored contextual surround modulations using both luminance- and texture-defined moving plaids (for details on stimulus parameters, see Table A1 in the Appendix), since it was critical that the chosen modulatory surrounds yielded perceptually stable reports across all luminance and contrast sets. Note that textured pattern (Txd Patt) and textured component (Txd Comp) stimuli are best suited as efficient surround conditions (being perceived with 0% or ~90% probability as transparent or nontransparent, respectively). Still, all the used surrounds yielded stable percepts across all predefined luminance/contrast sets (see the discussion of Fig. 2a in the Methods section).

We observed a clear and statistically significant surround modulation of perceptual decisions of luminance-defined (nontextured) central plaid patches, regardless of their inherent perceptual ambiguity, stronger modulations being nevertheless observed for more ambiguous centers. Figure 2b shows data concerning the modulation effects for only the three most ambiguous center conditions, and Figure 2c shows data pooled across all investigated luminance-defined central plaid patches (significance of pair-wise post hoc comparisons is also highlighted in Fig. 2c). Note, that the inclusion of less ambiguous center conditions (putatively more prone to ceiling/floor effects) does not change the pattern of results.

Post hoc analyses of contextual effects, with data being split across the most ambiguous center conditions, showed that component surrounds yielded the most powerful modulations, with textured component surrounds having the greatest impact (Fig 2b). The following effects (comparisons in italics had a significance of \( P < 0.0001 \), otherwise \( P < 0.05 \)) were observed on post hoc pair-wise comparisons between surround conditions: no surround (No S) versus luminance-defined component (Comp), Txd Comp versus No Surround, Txd Comp versus Txd Patt, Comp versus luminance-defined pattern (Patt), Txd Comp versus Patt, Txd Patt versus Comp.

One-way ANOVA showed significant modulation, even on data collapsed across all center conditions (Fig. 2c, \( P < 0.0001 \)) with the following significant post hoc effects on paired comparisons: Comp versus No Surround, \( P = 0.0006 \); Txd Comp versus No Surround, \( P < 0.0001 \); Comp versus Txd Patt, \( P = 0.0055 \); Txd Comp versus Txd Patt, \( P < 0.0001 \); Comp versus Patt, \( P = 0.0005 \); Txd Comp versus Patt, \( P < 0.0001 \); and Txd Comp versus Patt, \( P < 0.0001 \) (significant differences in the post hoc results are highlighted in Fig. 2c).

In summary, comparison of context types revealed an asymmetric dependence on the type of surround perceptual bias: component surrounds (transparent) being either textured or luminance-defined evoked significant modulatory effects, while pattern (nontransparent) surrounds did not yield significant effects when compared to absent surrounds. This effect was present across all center conditions on all the luminance and contrast sets. It is also important to note that textured component surrounds yielded a stronger effect than luminance-defined component surrounds.
The stronger modulations evoked by textured component surrounds were probably because of their being inherently more biased for transparent motion due to the disambiguation provided by local dots, also resulting in higher perceptual surround stability. A complete disambiguation by local texture should predict that these stimuli should not be prone to modulation by surround. This is indeed what we observed for central textured component and pattern stimuli (Fig. 3a). The absence of a modulatory effect was probably due to low uncertainty levels: Textured pattern stimuli are virtually always perceived as one surface (∼100% probability) and textured component stimuli as two surfaces (∼90% probability). We predicted that the generation of textured ambiguous stimuli, which have identical probability of being perceived as pattern or component (by having 50% of the dots moving vertically and 50% horizontally), would render this type of stimulus more susceptible to contextual modulation. Surprisingly, no contextual effects were observed even in the presence of such global ambiguity. This finding suggests that local disambiguation by texture is sufficient to prevent contextual modulation.

In other words, textured stimuli had a strong contextual modulatory influence on other stimuli but were, in contrast, not susceptible to significant surround modulation by themselves and were perceptually stable regardless of the type of surround applied (ANOVA, ns). This novel and intriguing finding suggests that if local motion becomes fully disambiguated by local texture, it is sufficient to render contextual modulation ineffective. Indeed, the amount of perceived transparency of textured centers was quite stable over time, even for the textured ambiguous plaids where texture lead to a locally disambiguated (bimodal motion directions) but globally ambiguous (due to the bimodality) interpretation. This global ambiguity was, as already stated, because in the case of ambiguous textures, 50% of the dots provided bias towards transparency and 50% towards nontransparency. Figure 3a shows that the overall level of perceived transparency was constant for central textured stimuli, regardless of surround manipulations. In contrast to textured centers, as stated, luminance-manipulated centers showed a significant dependence on surround manipulations (Fig. 3b, data plotted for the HLHC stimulus set; see Fig. 2c for statistics).

In summary, the above-described data suggest that transparent surrounds have a more powerful modulatory effect than nontransparent surrounds, with added local texture enhancing the effect. However, given the relatively short viewing time and a slight nontransparency bias for most baseline conditions, there remained a slight possibility that floor effects might explain the observed surround asymmetry. Still, we found this interpretation unlikely, because there were conditions clearly unaffected by floor effects while still showing a prominent modulatory influence (e.g., 40% transparency for the no-surround condition of the HLHC set). In fact, the effect was strongest for the most ambiguous conditions (Fig. 2). Nevertheless, to fully exclude the possibility that floor effects would confound the asymmetry of pattern/component contextual modulations, we performed a follow-up experiment with more ambiguous stimuli and longer viewing times (see experiment 3).

**Experiment 2: Ruling Out Patch Size as the Explanation of the Main Effect**

By assessing the effect of size on perceived stimulus transparency as a further control, we replicated previous findings suggesting that an increase in the size of the moving plaids augments perceptual coherence (pattern percepts) by increasing the number or visible intersections or blobs.27 Slopes of the curves relating perceived percentage transparency with stimulus size were approximately constant across all investigated conditions, implying that size does not interact with any particular condition or baseline perceptual bias of the stimuli (Supplementary Fig. S3, http://www.iovs.org/cgi/content/full/50/2/980/DC1). Furthermore, since increasing the size consistently decreased the transparency of the presented moving plaids, size effects cannot explain the surround modulations induced by component stimuli.

**Experiment 3: Surround Modulation with Longer Viewing Times**

Our previous findings showing that shifts in the central percept are heavily influenced by the type of the perceptual bias of the modulatory surround are further supported by the results obtained using longer presentation times and center plaids closer to the point of maximum ambiguity (see Fig. 4 for all 15 subjects’ data, collapsed across multiple plaid directions).

These results generalize the finding obtained under short viewing conditions and further substantiate the observation that the pattern of center-surround interactions was replicated with longer presentation times. In individual data from experiment 3, interaction bar plots depict single subject (n = 15) data collapsed across all four cardinal plaid directions. Component surrounds increased the perceived central congruent percepts for all subjects, unlike pattern surrounds, which occasionally even had an opposite paradoxical effect (i.e., increasing incongruent percepts) Error bars, 1 SEM.
that transparent and nontransparent biased surrounds act differently: component surrounds had a highly effective and congruent modulatory effect across all 15 subjects in contrast to pattern (nontransparent) surrounds which, in general, had a more variable effect (ANOVA/GLM with subjects entered as random factor, \( P < 0.0001 \) for component surrounds; NS for pattern surrounds, after correction for multiple comparisons, summary data shown on Fig. 5a). Moreover, we found that the described contextual effects are independent of the direction of the coherent plaid motion (data on Fig. 4 are collapsed across all directions). Nontransparent surrounds may nevertheless also have a significant effect at least in some subjects, which led us to study the subtle dynamics of single-percept durations and perceptual switch frequencies. We therefore also investigated the effect of context on stability of single percepts.

Transparent-biased surrounds induced more switches and coherence-biased surrounds induced fewer switches than that observed without surround modulation (\( P < 0.0001 \), Kruskal-Wallis test, Fig. 5b, post hoc analysis confirmed a more significant effect for pattern surrounds). This finding suggests that nontransparent surrounds may also induce strong contextual effects, but these effects are mainly represented as changes in perceptual switch frequency.

In any case, the average contextual modulation effect was significantly stronger for component surrounds. This finding was confirmed by analyzing effects induced when stimuli with at least 25% baseline ambiguity were considered in the effect size calculations, to prevent possible bias caused by floor effects (see effect size plot in Fig. 5c). Textured component surrounds have a significantly higher modulatory effect on the percentage of component motion duration than textured pattern surrounds (\( P = 0.013 \), ANOVA, repeated measures).

To find the mechanisms of contextual modulation at the single-percept level, we investigated whether the observed surround modulation is caused by the suppression of single incongruent center percepts or the enhancement of single congruent percepts. We found that both suppression and enhancement effects were present for component surrounds (ANOVA; \( P < 0.0001 \) and \( P = 0.0005 \), respectively), but only an enhancement effect was observed for pattern surrounds (ANOVA; facilitation effects, \( P = 0.004 \), suppression, NS), showing a clear facilitation of congruent percepts (see Fig. 5d).

In other words, although component surrounds enhance the duration of single congruent percepts and reduce the duration of incongruent percepts, pattern surrounds have a marked facilitatory effect on congruent percepts and no significant suppression or even slight facilitatory effect on incongruent percepts. The lack of a clear effect on incongruent states may be due to an overall stabilization of perceptual states (decreased switch frequency, thus increased percept stability) caused by the nontransparent surrounds.

It is worth pointing out that the total percept stability, as indexed by the total number of switches between perceptual states in a given surround condition and the durations of single percepts have to be treated independently in the estimation of overall perceptual effect. This is best achieved by weighting the single-percept durations with the total number of perceptual switches (Fig. 5e). The effect of component surrounds of increasing congruent transparency percepts in the center becomes even more evident with this weighting procedure. A phenomenologically distinct process is observed for pattern surrounds: facilitation of congruent effects is present, but the suppressive effects of incongruent pattern surrounds are still at an insignificant level after this transformation. The type of context thereby influences dominance and suppression durations in a distinct manner.

**Figure 5.** Contextual effects with longer viewing times. (a) Component surrounds evoked significant overall contextual modulation effects compared with pattern surrounds in the increased presentation time trials of experiment 3. (b) Pattern and component surrounds introduced significant modulation in switch frequency. (c) The modulatory effect size of component surrounds was higher than that of the pattern surrounds. (d) Pattern and component surrounds caused differential modulation in single-percept (split according to pattern or component) duration. (e) The overall impact of enhancement and suppression effects after weighting with the number of switches (i.e., percept stability). Data from upward moving plaids are shown on all plots. Txd, textured; C, congruent; I, incongruent. Error bars, 1 SEM.
Taken together, average surround modulation effects were significantly stronger for component surrounds and invariably consistent across subjects.

To exclude that the initial perceptual bias influenced the observed pattern of results, we performed an additional control analysis, by excluding the first perceptual epochs from the data. The asymmetric modulatory effect of different surround types was preserved after this manipulation (ANOVA, $P = 0.0042$ for component surrounds, NS for pattern surrounds, Fig 6). These results confirm that the initial perceptual bias is not relevant in the explanation of overall results.

**DISCUSSION**

We investigated the influence of peripheral visual context on the perception of central motion. We found that contextual effects are strongly dependent on the presence of both local and global ambiguity. These findings have strong implications in the understanding of normal and impaired vision, because in the latter ambiguity is increased in general.

Natural scenes present concomitant challenges to central and peripheral vision, and it is widely known that this is of particular relevance in normal vision, as well as in neurodevelopmental disorders and diseases related to aging.\(^3\)–\(^5\),\(^30\) Central–peripheral interactions, in particular those concerning magnocellular and motion processing, are of strong importance both in different eye diseases and aging, where temporal sensitivity is often decreased, and center-surround visual motion antagonism reduced.\(^20\)

Our findings show that what subjects can perceive in the foveomacular regions is strongly influenced by the level of congruence/incongruence of peripheral visual information. These results extend our previous findings in patients,\(^3\)–\(^5\) showing that contextual information may be integrated over space to solve for local ambiguity even in normal vision.

We found that the dynamics of central motion integration significantly depended both on the type of motion perception in the contextual peripheral surround and on the presence of central local motion disambiguation cues. Transparently perceived surrounds (two perceived peripheral moving surfaces) evoked more consistent effects (enhancement of congruent percepts and suppression of incongruent percepts) compared with nontransparent (just one perceived peripheral surface) surrounds (which only showed a clear enhancement effect of congruent percepts, at the level of single-percept durations). This influence was stronger with textured surrounds, in line with the fact that they are inherently unambiguous. Indeed, unambiguous feature motion provided by overlaid random dots completely determines the perceived direction of local contours, and thereby provides a solution to the aperture problem.\(^27\) This rendered textured peripheries to have a powerful contextual influence.

A remarkable property of central textured stimuli was their own resistance to contextual modulation. This is probably because their unambiguousness renders them less susceptible to be influenced by the surround. We were surprised, however, to find that even when central textured stimuli were designed to be globally ambiguous (e.g., containing bimodally disambiguated local motion: 50% of the dots providing bias toward one percept type, and 50% toward the other), surround modulation was not effective. This surprising effect is explained by the absence of local ambiguity despite the presence of global ambiguity. Indeed, whenever local motion became unambiguous, the effect of surround modulation diminished regardless of the overall luminance/contrast.

These observations have strong basic and clinical research implications. First, they suggest that the shifting balance between the coherent and transparent (two-surface) percepts are attributed to processing stages before any integration or combination of local motion signals, in agreement with previous work.\(^51\) Second, these findings are also clinically relevant because motion may often become ambiguous in different visual disorders. Furthermore, in patients with macular diseases, central ambiguity occurs more frequently, which implies that the surround has a more powerful effect, which may be used clinically in rehabilitation approaches.

Contextual effects were similar both for short (10 seconds) and long (60 seconds) stimulus presentations, which shows that they generalize across levels of motion adaptation and were independent of pattern motion directions.

A possible locus of the described contextual modulation effects would be MT, a pattern selective region playing a key role in surface motion integration,\(^25\) with well-described center-surround modulation properties.\(^16\),\(^22\) However, an earlier point of interaction could be attained via an MT-V1 feedback, analogous to the one suggested by the model of Bayerl and Neumann,\(^32\) in which localized V1 motion signals are the target of feedback modulation, by means of velocity-matching operations. Since component (local) motion selective neurons represent the overwhelming majority in V1 and V2,\(^33\)–\(^37\) the proposed feedback route would produce an imbalance of early response distributions producing more robust shifts toward transparent (component) than coherent interpretations on the population level. This model would thus explain the differential contextual modulation of surface integration processes for pattern (nontransparent) and component (transparent) motion conditions.

This notion is consistent with results in previous work,\(^38\) emphasizing that integration of local motion signals across space is a relevant mechanism in vision that might be implemented by the existence of a cooperative network linking neurons sensitive to different directions/speeds and different spatial locations. Furthermore, this view is not inconsistent with the issue of spatial integration/segregation within a visual

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**FIGURE 6.** Excluding the first perceptual epoch in all trials did not change the pattern of surround effects. Error bars, 1 SEM.
area (in fact pattern and component neurons also coexist in MT).

As stated earlier, the fact that locally disambiguated but globally ambiguous (due to local bimodal motion distributions) textured stimuli could escape surround influences—possibly posed either by top-down feedback or by collinear facilitation mechanisms that were probably enabled by our experimental conditions—does in any case provide strong evidence for an early neural locus underlying surround modulation.

Given the notion that contextual effects may occur even if the experimental subject is not aware of the presence of the modulatory stimulus, which is also the case when stimuli are placed peripherally, future studies should determine the role of high level top-down mechanisms in modulating such peripheral effects.

We were able to measure how congruent and incongruent context influences central visual dominance and suppression durations. In this way, we have found further evidence of distinct mechanisms underlying pattern and component surround modulation. Component surrounds lead to a higher frequency of perceptual switches (indicating higher perceptual instability, with consequentially shorter single-percept durations), enhanced dominance of congruent stimuli, and enhanced suppression of incongruent stimuli. Pattern surrounds are associated with fewer switches (i.e., increased percept stability), and although they enhance the individual duration of congruent stimuli, they are less effective in suppressing incongruent percepts (possibly because their main effect is to increase stability of all percept types). We conclude that context may distinctly influence both dominance and suppression of single-percept durations, in parallel or not with percept stability, depending on the type of surround. Moreover, we found that the switch dynamics in our center-surround plaid displays were different from those found without contextual modulation (in particular, the first percept was not always pattern).

This notion of percept stability is also relevant for future studies seeking clinical applications for patients with scotomas. These studies should also elucidate how surround effects can be integrated into reciprocal inhibition based perceptual switch models similar to the ones suggested for binocular rivalry, which are relevant in strabismus and amblyopia research. Such a unified framework may also be useful to explain why nontransparent surrounds (resulting from perceptual integration) show such different dynamics compared with transparent surrounds (resulting from perceptual segmentation).

We do believe that these results will help develop new rehabilitation strategies that take advantage of improved knowledge of the rules governing peripheral modulation of visual foveomacular signals. Center-surround interactions may for example be stronger in diseases such as macular degenerations where central ambiguity is increased, but effective surrounds can still be processed in the visual periphery and influence center processing.

Taken together, the results in our study extend the knowledge on low-level contextual influences on the perception of local visual stimuli and integration of form and depth information in extracting surface representations in early visual areas, by demonstrating a role of peripheral perceptual bias in global surface segmentation/segregation processes and the role of enhancement and suppression mechanisms in this process. Finally, our study also clarifies the relative influence of local and global disambiguation, showing that peripheral influences on motion integration in foveal vision are strongly modulated by local/global ambiguity, a knowledge that can be applied in novel approaches to low-vision rehabilitation.

References


**APPENDIX**

**Table A1. Exact Luminance Values for the Three Overall Luminance/Contrast Sets**

<table>
<thead>
<tr>
<th>Element</th>
<th>HLHC</th>
<th>HLLC</th>
<th>LL</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Background</strong></td>
<td>45</td>
<td>58.5</td>
<td>0.27</td>
</tr>
<tr>
<td><strong>Gratings</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Baseline (G1 &amp; G2)</td>
<td>75</td>
<td>61.5</td>
<td>0.71</td>
</tr>
<tr>
<td>Pattern bias (G1 &amp; G2)</td>
<td>75</td>
<td>61.5</td>
<td>0.71</td>
</tr>
<tr>
<td>Component bias (G1)</td>
<td>80</td>
<td>63</td>
<td>0.71</td>
</tr>
<tr>
<td>Component bias (G2)</td>
<td>70</td>
<td>60</td>
<td>0.57</td>
</tr>
<tr>
<td><strong>Intersections</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pattern bias</td>
<td>37</td>
<td>50</td>
<td>0.4</td>
</tr>
<tr>
<td>Component bias</td>
<td>80</td>
<td>63</td>
<td>0.71</td>
</tr>
<tr>
<td>Lum_1</td>
<td>60</td>
<td>59.75</td>
<td>0.57</td>
</tr>
<tr>
<td>Lum_2</td>
<td>68</td>
<td>60.97</td>
<td>0.66</td>
</tr>
<tr>
<td>Lum_3</td>
<td>76</td>
<td>62.19</td>
<td>0.74</td>
</tr>
<tr>
<td>Lum_4</td>
<td>84</td>
<td>65.41</td>
<td>0.82</td>
</tr>
<tr>
<td>Lum_5</td>
<td>92</td>
<td>64.65</td>
<td>0.91</td>
</tr>
<tr>
<td>Lum_6</td>
<td>100</td>
<td>65.85</td>
<td>1.0</td>
</tr>
<tr>
<td>Dots</td>
<td>1.6</td>
<td>4.2</td>
<td>1.6</td>
</tr>
<tr>
<td>Average Michelson contrast of gratings (%)</td>
<td>24.9</td>
<td>2.48</td>
<td>41.23</td>
</tr>
</tbody>
</table>

The three luminance sets differ in the luminance and contrast relations of their elements: HLHC, high luminance and high contrast; HLLC, high luminance and low contrast; LL, low luminance. Elements composing the stimuli can be gratings, grating intersections, or dots. Pattern bias (G1 & G2) is the luminance of the gratings leading to pattern biased stimuli, regardless of the presence of dots. These patterns are symmetrical; hence, the G1 & G2 indication. For component biased stimuli without dots, grating luminance parameters differ; thus, they are shown separately.