A FIXED CORTICAL DISTANCE GOVERNS PERCEPTUAL INTEGRATION OF LOCAL MOTION AND POSITION

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1. Introduction

The ability to detect moving objects is an essential function of the visual system. Accurate motion perception is essential for visually guided movement; complex behaviors such as chasing prey or catching a thrown ball require that an organism be able to rapidly determine the position and velocity of a moving object, and to anticipate its trajectory through space.

Psychological research on motion perception has established that separate mechanisms are involved, an idea that dates back to Wertheimer's phenomenological distinction between fast 'phi' and slower 'beta' motion [Steinman et al., 2000]. One mechanism responds to the motion of visual features that are defined by luminance, or by motion energy in the Fourier domain [Adelson and Bergen, 1985], at short temporal and spatial scales. These stimuli contain what is variously known as local, first-order or short range motion. Another class of stimuli (long-range, higher-order or global motion) results in a perception of motion without requiring features to differ in mean luminance from the background, and without containing motion energy in the Fourier domain. Some examples of global motion stimuli are contrast modulation or texture flicker stimuli; the forms of global motion are varied, but in general involve the moving modulation (i.e. a change in position) of some visual feature over time [Lu and Sperling, 1995].

Typically, studies of visual motion have either not tried to distinguish local from global motion, or have used stimuli intended to drive one system without driving the other. But objects moving realistically change position as well as possess local motion energy, so that they activate all motion systems concurrently in varying ways. It may be the case that there are not cleanly separated streams of local and global motion processing, but that one form of processing influences the other, so that the interaction between local motion and position signals would be key to understanding global motion. Indeed there is evidence that a system responding to a consistent change in position of a stimulus interacts with the output of local motion detectors. In a field of dots undergoing random Brownian movement, a single dot that changes its position in a consistent direction is more easily detected than local motion energy detectors can account for [Verghese et al., 1999]. The enhancement in detectability seems to occur only after 100 ms of movement, possibly due to a process that responds to an initial cue from local motion detectors by reducing the number of detectors monitored to those in the vicinity of the initial motion signal, in particular those in the object's predicted path [Verghese and McKee, 2002]. An interaction between local motion and position sensors thus appears necessary to account for performance at motion discrimination.

To investigate the interaction between local motion and position signals, we constructed stimuli that combined a local motion with global position shift. By setting the local motion and position shift in opposition, we produced a striking illusion. Here (Movie 1) we show a display with two wheels, each containing five spots. The spots are composed of Cauchy wavelets designed to drive local motion sensors, with no change in mean luminance of feature against background [Klein and Levi, 1985]. Independent of its local motion, each spot is given a global apparent motion, by presenting it at successive locations at intervals of 100 ms. On the left side of the display, the local motion and position change are in the same direction; on the right side the local motion and position change are in opposite directions. Full details of the construction of this display are given in Methods.

[MOVIE 1]

In this display the rotation of the spots around the fixation point on the left side of the display appears constant regardless of viewing angle, but the motion of the spots in the right side appears to change direction based on retinal eccentricity. When fixating in the center of the right circle, the spots appear to travel clockwise around the circle; when viewed parafoveally, the spots appear to move counterclockwise. When making an eye movement that shifts the right circle from a parafoveal to a foveal location, or vice versa, it appears to suddenly reverse its direction.

An eccentricity-dependent reversal in perceived direction has been previously reported for some reverse-phi stimuli [Mather et al., 1985, Chubb and Sperling, 1989]; a display similar to ours, arranging discrete elements in circles, has also been independently developed by Shapiro et al. [2008]. Chubb and Sperling [1989] proposed that the global motion in reverse-phi displays was detected by rectification of the output of some feature detectors, after which a more normal motion-energy filtering process followed, and that the resolution of this rectification and detection was weaker in the periphery. Because our display assigns local and global motion to the same features, it was natural to ask whether the eccentricity-driven reversal of apparent motion direction happened with only one spot moving around the fixation point. It did not; when all but one of the spots in the circle were eliminated, the remaining spot appeared to move consistent with its global position shift, regardless of eccentricity. Because the targets were the same size in both conditions, a motion energy detector operating on rectified input should have performed as well in both cases. Instead this illusion suggested that a long range interference between the distinct elements was responsible for the failure of global apparent motion in parafoveal viewing. In other words, a form of crowding limits the detection of shifts in global position.

Crowding is a phenomenon wherein identification or discrimination of an object presented in the visual periphery is impaired by the presence of nearby, but non-overlapping flanking objects. A finding characteristic of crowding is that critical spacing (usually a measure of the distance between target and flanker which achieves a particular elevation of threshold for recognition) scales linearly with retinal eccentricity [Bouma, 1970, Toet and Levi, 1992]. Although most studies of crowding focus on its effect of impairing the recognition of shapes (e.g. letters) in parafoveal vision, it has become apparent that crowding is a more general phenomenon, extending to many different types of visual features (e.g. (van den Berg et al. 2007; for review, see Levi 2008) It is thought that crowding is characteristic of some cortical mechanism that integrates signals from low-level feature detectors, a so-called "integration field" [Pelli et al., 2004]. Because the scaling of critical distance with spacing mirrors the variation of cortical magnification with eccentricity, the integration field is thought to be a process that subsumes a constant distance on the cortical surface [Pelli, 2008].

Pelli et al. [2004] proposed that the crucial diagnostic test for crowding as opposed to masking or other forms of spatial interference is that the critical spacing scales with eccentricity and is relatively unaffected by signal size. Accordingly, we set out to determine which target spacing and motion parameters are necessary to drive the reversal of apparent motion as various eccentricities. In Experiment 1 below, we determine the relationship between critical spacing and target spacing, which satisfies Bouma's law. In Experiment 2 we show that the critical distance and scaling property is robust to the size of the stimuli. We also test its robustness to variations in temporal frequency, step size, and step interval. In Experiment 3 we show that the critical spacing is unaffected by the presence of an occluder which covers 2/3 of the visible circle, meaning that it is the spacing which is relevant and not the number of visible targets.

While most studies of crowding involve stationary stimuli, motion stimuli add a temporal component. In Experiments 1 through 3 we consistently find that for stimuli near the crowding distance, the trials for which the subject took longer in responding were more likely to correctly reflect the global direction of motion. In Experiment 4 we use an auditory cue to vary the subjects' response time to investigate this effect in more detail. Our results reinforce the idea that global motion processing is the result of an integration of the output of low-level feature detectors, and that in fact the process subserving detection of global motion might be identical to the processes underlying object recognition and target selection. We discuss the implications for possible mechanisms of higher order motion perception and speculate on their possible physiological implementations.

2. General Methods

2.1. **Subjects.** Five subjects took part in this series of experiments. The subjects and the experiments they took part in are listed in Table 1. Subject P.M. is an author. Subject S.K. was made aware of the purpose of the experiments only after completing Experiment 1. Subjects S.M., D.T., and G.B. were paid and were naive to the purpose of the experiments.

It would be cute to pull this out from data but I have more pressing concerns.

2.2. **Equipment.** Stimuli were presented on a flat CRT video monitor (ViewSonic PF790; 800×600 pixels; display area 341×256 mm; 120Hz refresh rate) Experiments were programmed in MATLAB using the Psychtoolbox [Brainard, 1997] and Eyelink toolbox extensions [Cornelissen et al., 2002], along with custom OpenGL code. All stimuli were presented on a 50% gray background whose luminance was $33.10 cd/m^2$. The display had a black level of $0.10 cd/m^2$ and a white of $66.05 cd/m^2$ measured against the gray background.

Subjects sat behind a blackout curtain so that ambient illumination was mostly due to the monitor and viewed the screen binocularly using a chin and forehead rest with the eyes 60 cm from the screen. Eye position was monitored using a video-based eye tracker (EyeLink 1000; SR Research) using a sample rate of 250 Hz. Eye movements were recorded but are not reported in this paper. Subjects gave responses by turning a knob (PowerMate; Griffin Technologies) with their preferred hand.

Include this.

2.3. **Stimuli.** Example stimuli are shown in Movie 1 and are illustrated in an (x, t) plot in Figure 1c (x here being a slice around a circle centered on the fixation point and passing through the center of each motion element.) The stimuli consisted of discrete local motion elements presented at regular temporal and spatial intervals as in apparent motion. Each local motion element had a luminance profile along the circle given by a Cauchy filter function [Klein and Levi, 1985] with peak spatial frequency f. The luminance profile shifts phase with a constant temporal frequency ω and is temporally modulated by a Gaussian envelope with standard deviation $d/2$. In the radial direction, each local motion element had a Gaussian envelope with standard deviation $w/2$. The equation describing the luminance profile of a patch as a function of position and time is then:

Is the equation totally necessary? Is the use of x,y to describe a circular stimulus confusing here?

$$C(x, y, t) = \cos^n(\tan^{-1}(fx/n))\cos(n \cdot \tan^{-1}(fx/n) + \omega t)e^{-(t/2d)^2-(y/2d)^2}$$

with the direction of motion along x. The spatial bandwidth parameter n was set to 4 for all stimuli.

In each trial, a number of identical elements were arranged in a circle around the fixation point, each oriented with the direction of motion tangential to the circle. Each element was presented repeatedly at intervals of Δt, each successive appearance displaced a fixed distance Δx around the circle. The examples in Movie 2 have the following settings, the same as used in Experiment 1 : $\Delta t = 100$ ms, $\omega = 10$ cyc/s, $d = 0.033$ s, and if ϕ denotes eccentricity, then $f = 8.9 cyc/\phi$, $\Delta x = 0.05 \cdot \phi$, and $w = 0.066 \cdot \phi$. The contrast of the local motion elements was 100% for trials using counterphase stimuli, and 70.7% for other trials (so as to keep the motion-energy of the display constant.)

Double check these figures

For Experiments 1, 2, and 3, subjects were required to respond within a fixed temporal window. If the latency from motion onset to response was outside the window, the fixation point changed color (red for late responses, blue for early responses) for 1 second as feedback and the trial was reshuffled into the stimulus set to be repeated later in the session.

Subjects performed the task in sessions of at most 1 hour, divided into 4 or 5 blocks of 150 to 200 trials each, and were prompted to take a break between blocks. Subjects could also rest at any point by simply delaying fixation. At the beginning of each block, the eye tracking system was automatically recalibrated by asking the subject to make saccades to a sequence of targets at randomly chosen locations on the screen.

For all experiments reported here, three stimulus types were used with equal probability. In one third of trials the direction of local motion was congruent with that of global motion. In the second third, the direction of local motion was opposite to the direction of global motion. In the remaining trials, elements with counterphase local motion were used. Counterphase elements were constructed by superposing two local motion elements with equal and opposite directions of local motion.; i.e. the counterphase stimuli have the same spatial and temporal frequency content as the congruent and incongruent elements, but their motion energy is equivocal between opposite directions. The third stimulus in Movie 2 shows counterphase local motion.

3. Experiment 1. Scaling of critical spacing with eccentricity.

3.1. Methods. We presented stimuli at eccentricities of 10, 6.67, 4.44, and 2.96 degrees, using the parameters described above for Movie 1 but scaling all spatial parameters (Δx, w, $1/f$) of the elements along with the eccentricity; i.e. at eccentricity of 6.67 degree, Δx and w decreased to 2/3 the value used at 10 degrees and f increased to 3/2 its value. The global apparent motion was shown over 4 stations at intervals of $\Delta t = 100$ ms.

At each eccentricity, we varied the number of elements ~~in~~ the circle (and consequently the inter-element spacing) ~~in the circle~~ using the method of constant stimuli, using values chosen for each subject based on preliminary sessions.

The sigmoids need to be refit with a constant slope (since that is how we will approach the variations and occlusions data; QUEST data doesn't well support calculating slope and it adds noise to the PSE calculation. Also, look at different choices of scaling in element spacing to see what is the best fit? Maybe plot on log but fit linearly? Does that scale?

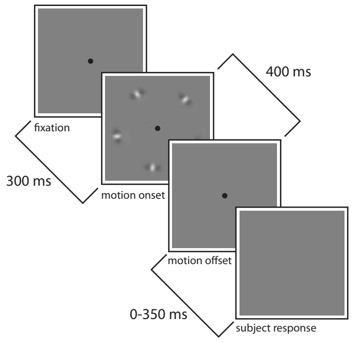
3.2. Results.

Using the third of trials where global motion opposed local, we obtained a psychometric function relating the target spacing to the probability that the stimulus is seen to rotate in the direction of the global motion. The data were fit to a cumulative logistic function using a maximum likelihood estimator. We found the spacing where the logistic curve intersected 50%.

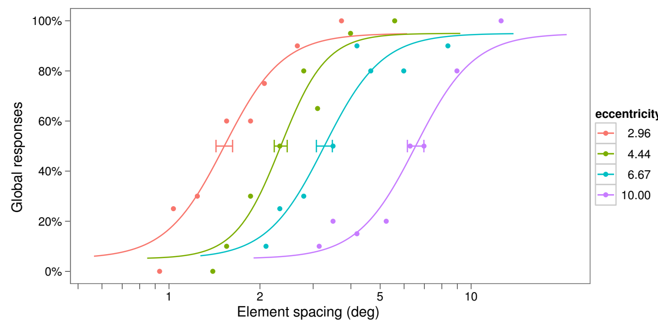
We fit the subject's responses at each eccentricity to a logistic function, as illustrated for subject D.T. by the curves in Figure 1b. A separate curve was fit for each eccentricity, with a guessing rate that was fit for each subject [Wichmann and Hill, 2001] . From these fits we estimated the point at which subject responses would be equally split between local and global directions of motion. This point of subjective equivalence (PSE) is indicated by the horizontal error bars in Figure 1b, and are plotted using vertical error bars in Figure 1d for all subjects. This spacing at the PSE appears to scale with the eccentricity of the stimulus. We made another fit to a model where the size of the PSE was proportional to the stimulus eccentricity; this model fit is shown as lines and shaded regions in Figure 1d. When

tually do this

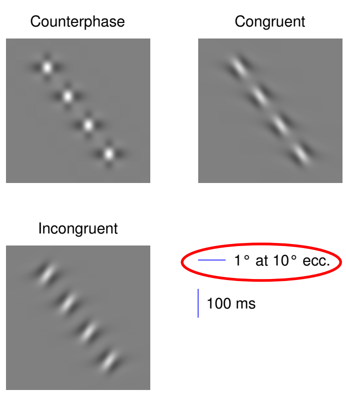
I'm not happy abut calling this 'subjective equivalence' because I'm not sure what the stimuli are 'equivalent' to, they're not metamers. Perhaps a point of equivocation?



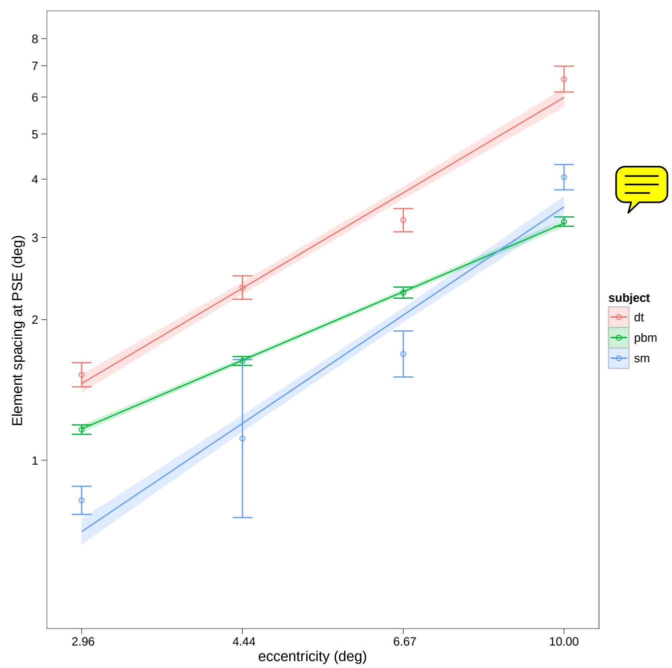
(A) Task illustration. Subjects first fixate and after a brief delay a motion stimulus of constant duration appears. Subjects judge the apparent direction of motion and respond by turning a knob before the time window has expired. Subject receives feedback about whether their response falls inside the time window.



(B) Example data. The responses of observer DT to incongruent stimuli are plotted as a function of between-element spacing, for four values of eccentricity. The values plotted are the proportion of responses that agree with the global motion direction. Curved lines are fit to the data by a cumulative logistic with a constant guess rate. The point of subjective equality (PSE) is indicated on each fit.



(C) Example stimuli in space-time form, where time progresses down along the vertical axis. Stimuli were 'congruent', 'conterphase' or incongruent, based on whether the global direction of motion agreed with the local. Counterphase stimuli are a superposition of congruent and incongruent stimuli.



(D) Points of subjective equality (target separation subserving 50% response probability) for each eccentricity for all subjects. Intervals show standard errors. Lines show a power-law fit between eccentricity and critical target separation. Shaded region shows standard error of the power-law fit.

FIGURE 1

compared to estimates taken at each individual eccentricity, we saw XXXX significant differences at YYYY conditions.

OK, so what's the appropriate test? Fit a model plus one data point, at each data point, and see if the added coefficient was a significant change? (ONLY X conditions, significant marked with a star; were these differences explainable?)

The scalar dependence on critical separation is broadly similar to the phenomenon of crowding, in which recognition or discrimination of a target object is impaired by the presence of flanking objects. It is also suggestive of a cortical mechanism. There are several areas of cortex that are organized into retinotopic maps. The foveated scaling of space within these maps has the property that network interactions that span a constant distance in cortex, including V1, will correspond to interactions in visual space whose distance approximately scales with retinal eccentricity.

does this need a cite? "Who defined crowding" is a hard thing to cite.

cite?

I can cite papers for MT and V4 that make the claim that those maps are just simple linear scalings of the V1 map.

4. Experiment 2. Occlusion.

The results of Experiment 1 suggest that the perceived direction of incongruent motion stimuli follows the global translation when stimuli are widely spaced, but follows the local motion direction when stimuli are packed more closely together. The between-element spacing at which the percept changes from global-dominated to local-dominated appears to be roughly proportional to the stimulus eccentricity. As a result the stimulus at PSE has approximately the same number of elements, independent of eccentricity. This leaves open an alternate explanation: observers' correct perception of global motion may be limited by the number of simultaneously visible elements rather than their closeness. Such might be the case if subjects were determined the direction by individuating and tracking distinct elements in the display. Humans appear to have a limited capacity for individuating and tracking multiple targets within a scene [Pylyshyn and Storm, 1988], which might be overwhelmed by displays with large numbers of targets.

The data from Experiment 1 do not distinguish target number from spacing; there is not a consistent trend for the number of targets at PSE to change as a function of eccentricity. If target tracking capacity may be different for different portions of the visual field, as for example it appears to differ between the lower and upper visual field [He et al., 1996], then Experiment 1 cannot even in principle differentiate an explanation based on target number from one based on density. To distinguish the effect of target number from that of density, we repeated the measurement of critical spacing with and without an occluder that obscured most of the targets, reducing their number without changing their spacing.

In retrospect, seeing where this analysis is taking me, a much better approach would be to (1) not bother testing at different eccentricities and (2) test varying sizes of the (visible) window!

4.1. Methods.

Trial structure and timing were as in Experiment 1, but with the addition of an occluder that was present or absent on either side of the screen. The occluder was a 'C' shape with an opening subtending 120° on either the left or right of the screen and covering all eccentricities that a target might appear at. The stimuli are shown schematically in the legend of Figure 2a, but for the data reported here the occluder was not visible (i.e. it had the same luminance as the background.)

(and this inflation was partially recovered by using a visible occluder that cued the side that targets were to appear on. – supplementary figure?)

We decided to test stimuli in the left and right hemifields over separate sessions. If subjects used attentional resources to individuate and track the motion elements, then their spatial allocation of attention may impact performance. Mixing left-visible and right-visible stimuli in the same trial blocks would require subjects to alternately allocate attention to left and right sides, perhaps unnecessarily limiting their performance; preliminary data suggested that a fully interleaved design inflated the critical spacing measurement for occluded conditions. Therefore we measured critical spacing for right and left hemifields in separate sessions. In each session, half of trials contained an occluder and half did not. Note that spatial allocation of attention may also impact subjects' performance in the case that individuation of elements turns out not to be necessary to perform their task.

Instead of the method of constant stimuli we used the QUEST procedure [Watson and Pelli, 1983] to select the target density for each trial. A separate QUEST sequence was used to seek the PSE at each eccentricity and for both fully visible and occluded stimuli (so 8 interleaved QUEST sequences for each session) with trials from all sequences being randomly interleaved. As before, there were three trial types, with local motion congruent with global motion, incongruent with global motion, or in counterphase. The online QUEST estimates was used to select target spacing for all trials, but only incongruent trials with responses given during the response window were used to update the online estimates.

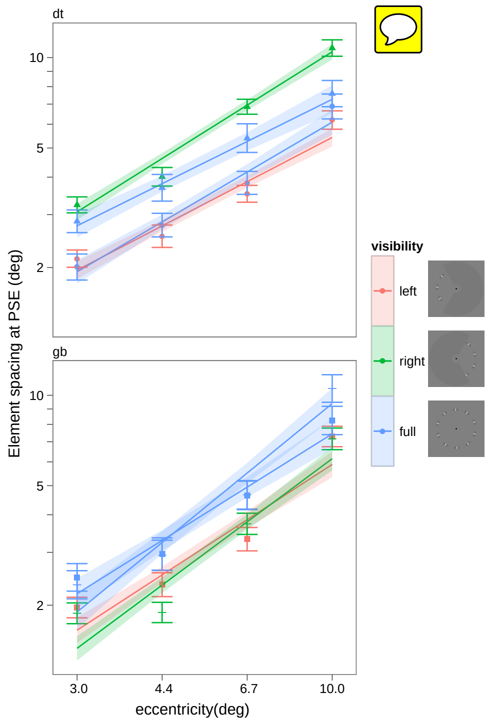
I have not actually done this yet; currently it's just a fixed 5% guess rate.

In modeling subjects' responses we employed a generalized linear regression using binomial errors and a modified logistic link function with variable upper and lower asymptotes, corresponding to a guess rate and a lapse rate [Wichmann and Hill, 2001]; these rates were allowed to vary between subjects and were iteratively fit to maximize likelihood. Comparisons between nested models were done by likelihood ratio test using a χ^2 distribution with the appropriate number of degrees of freedom depending on the models, as well as by comparisons of Akiake's information criterion (AIC) between models. Before comparing models, guess and lapse rates were first fit to maximize the joint likelihood of both models. For statistics such as the PSE that are not linear functions of the regression coefficients, standard errors and comparisons were computed by parametric bootstrap.

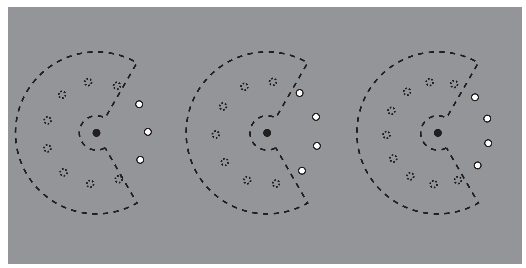
ref?

4.2. **Results.** The measured PSEs are shown in Figure 2a. The online estimates from QUEST are disregarded and the PSEs are calculated by fitting a logistic response function with slope, guess and lapse rates varying per subject, as in section 3.

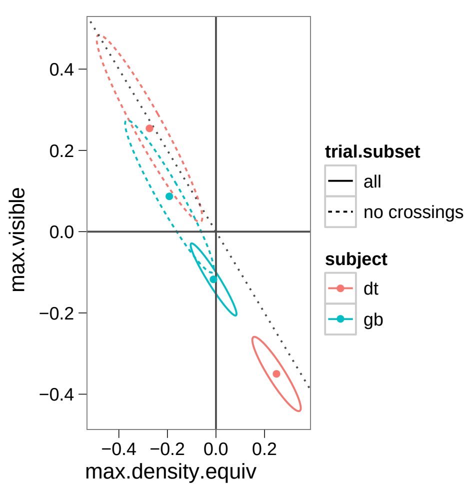
If the perceived motion direction were driven by element number rather than element spacing, we might first expect the measured critical spacing to decrease when most targets are occluded. For Subject DT the smallest spacing at PSE were observed in the session where the unoccluded window was in the left hemifeld. In the left hemifield spacing at PSE did not reliably differ between occluded and unoccluded conditions (parametric bootstrap, $p = .16$) In the right hemifield, the spacing at PSE increased for the occluded conditions



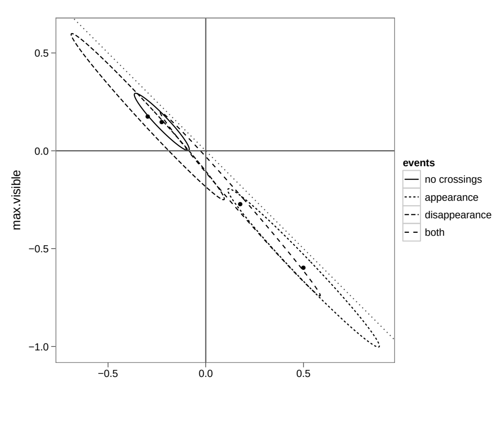
(A) PSE values, measured as in Figure 1. Colors indicate visibility condition (left-visible, right-visible, fully-visible). Shape of data points indicates sessions data were taken on; each measurement in a partially occluded condition is matched with a fully-visible condition taken during the same session.



(B) Adding an occluder helps to disentangle target number from target density. Left: out of 11 targets spaced evenly around a circle surrounding the fixation point, two are visible in the non-occluded window. Middle: With a different starting position, four targets are visible with the same target density. Right: Again four targets are visible, but at a higher density (13 targets in the full circle). Thus target density and the number of visible targets are not strictly dependent on each other.



(C) Confidence ellipse of the coefficients resulting from logistic regression analysis for each subject. The horizontal axis shows the coefficient β_d for target density while the vertical shows the coefficient of β_n for target number The graph is scaled to equalize the importance of each variable. Solid ellipses show the results for when all occluded trials are considered; dashed ellipses consider only trials where an element did not cross



(D) With subject data pooled, confidence ellipses for the different trial groups according to whether trials contained appearances or this is apparently the case for most data but I need to re-run using the final set of stimulus parameters

($p = .001$). [Author PBM did not show a significant difference in critical spacing between occluded and unoccluded stimuli.]

this standard error includes both the estimation uncertainty and the scatter between different conditions, all in one pool. Is that confusing?

On the other hand, GB showed a significant decrease in critical spacing for occluded stimuli shown on both sides of the screen ($p < .001$, left; $p < .001$, right.) Over all eccentricities and both hemifields, the average PSE for occluded conditions was $76\% \pm 14\%$ that of unoccluded conditions. This reduction is considerable, but nonetheless there are more elements visible in one hemifield during unoccluded stimuli at PSE than there are in the occluded condition at PSE. In other words the reduction in PSE is not great enough to be accounted for solely by target number.

Nonetheless, in this first measurement, introducing an occluder has mixed effects on the resulting PSE measurement. This may reflect different strategies taken by each subject, or other differences between subjects. Unpacking the components of the display in the occluded condition may reveal an underlying explanation or the different effects, as well as shedding further light on the question of whether it is target number or spacing that is responsible or the reversed direction of perceived motion at high densities.

This section wanted to start with addressing the d
but after plotting the confidence ellipsoids it seems
all. All it does is lead to a nonsensical result that
and disappearances to untangle.

4.3. **Is density a better predictor than number?**

It is the case that multiple values of target density can result in the same number of elements being present. Contrariwise, the same target density in two different trials can result in different numbers of targets being visible, depending on the randomly selected initial position of the targets (Figure 2b). This fact may give us leverage to answer the question of whether it is element density or number that determines the perceived direction of motion, since multiple values of target density have been tested with the same number of visible targets and vice versa.

In order to even discuss this simplified first stab at the question I need to explain why use n_{max} versus some other count of visible elements. I don't really see a way around it.

As expanded on below, because elements in the display move behind an occluder, the number of targets visible can change during the stimulus. So the notion of 'number of elements visible' for each trial can have different definitions. We considered several measures of element number: the number of targets visible at the onset of motion stimulus (n_{on}); the number of targets visible at the offset of the stimulus (n_{off}); the maximum number of targets visible at any point during the stimulus (n_{max}); the minimum number of targets visible at any point during the stimulus (n_{min}); and the average number of targets visible integrated over the duration of the stimulus (n_{mean}). Of these variables, by far the best fit to subjects' responses was obtained using n_{max}; the difference in AIC score from the next best contender was 26. Therefore we use $n_{\max}$ for this and subsequent analyses in this section.

Note that if you add appearances and disappearances to the model, all these variables span the same space, so once there's appearances and disappearances, there's no real distinction between any of these variables other than which ones soak up how much variance from certain appearances and disappearances. So am I shooting myself in the foot here, by picking a "number" alternative that already has some of the effect of appearances and disappearances built in?

We reconstructed the positions of the elements for each trial and calculated $n_{\max}$. Then we regressed subjects' responses against two variables, $n_{\max}$ and the corresponding element density $d_{\max}$. The equivalent element density was defined as the expected maximum number of elements visible in a trial with a given density, taking the expectation over the randomized starting position of the elements. Therefore, $d_{\max}$ is purely a function of the spacing between targets, and trial-by-trial differences between $d_{\max}$ and $n_{\max}$ are due to the randomized starting position of the elements. Regression coefficients of the two variables should thus be directly comparable.

The estimated values of the two regression coefficients are plotted in Figure 2c for each subject, along with standard errors drawn as solid ellipses. As expected, since n_{max} and d_{max} are largely correlated, the ellipses are elongated along an axis with slope -1, indicating that the two coefficients trade off against each other. The estimated coefficients lie below the diagonal line with slope -1, confirming that either added targets, or added density, tended to produce fewer correct answers. However we do not appear to have a consistent answer as to whether density or number of targets produces a better prediction. For instance, in the case of subject DT, the estimated regression coefficients would have an increased number of targets strongly associated with incorrect answers, while increased density strongly promotes correct answers, a situation which is somewhat nonsensical, unless there is a confounding property of the stimulus that correlates with changes of density and number. Therefore we turn our attention to other visual cues that are present in the stimulus.

"Additionally the residual deviance is probably larger than expected due to overdispersion, indicating that other factors influencing subject's responses have not been accounted for." – quantify?

4.4. **Appearances and disappearances as confounding cues.** Introducing an occluder unavoidably introduces ancillary visual cues that can give away the global direction of motion even if crowding obscures the direction of motion of flanked elements. Appearance and disappearance events may provide one cue. As illustrated in (Figure 3a), if elements cross the boundary of the trial window, their appearances or disappearances can provide a significant clue to the direction of global motion, since it is global and not local motion direction that determines where appearances and disappearances happen.

Subjects may also be able to exploit the fact that the elements nearest the boundary of the occluder are only flanked on one side; the effect of crowding is much reduced on targets with only one flanker versus targets with flankers on either side [Bouma, 1970], so that even if the elements in the midst of the window cannot be spatially distinguished, the 'endpoints' of a moving mass of elements might still be successfully tracked thereby giving away the global motion direction. In this scenario, appearance and disappearance events would be deleterious, as they cause the 'endpoints' to shift opposite the direction of global motion.

R tells me that there is still a difference between subjects on appearances, but not on the other three groups

In Figure 2c the dashed ellipses show the results of the regression when only trials that do not contain a boundary crossing (appearance or disappearance) are considered. The ellipses are larger due to the reduced sample size, but the data shows that for both subjects, the reversal of apparent motion direction is more likely to be driven by target density than by number. Moreover, when subjects' behavior is stratified by the presence of boundary crossings in the visual stimulus, the differences between subjects' behavior appears to be more consistent with each other, up to a change in intercept. Therefore data from both subjects are pooled in Figure 2d. We see that in aggregate, the data from trials containing no crossings is more consistent with apparent motion reversal being driven by target density than by target number; when all trials are considered, it is the appearances in particular that disguise this fact. We proceeded to try to account for the effect of appearances and disappearances in the regression model.

This is where the model exploration used to start, before the business with the ellipses. Move the data in this para up or eliminate it?

4.5. **The effect of appearances and disappearances.** Of the trials with an occluder reported on in Figure 2a, 21% of trials contained an element appearance, 21% of trials contained an element disappearance, 10% of trials contained both, and 68% contained neither. No trials contained more than one appearance or disappearance event.

We first added the predictor n_{max} which was the the maximum number of targets visible during the stimulus presentation. n_{max} was a significant predictor of subjects' responses (Likelihood ratio test, $p < 10^{-4}$). Furthermore, n_{max} was a significant predector among each subset of trials delineated by subject and occlusion condition; (dtleft, $p < 10^{-4}$; dtright, $p = .013$; gbleft, $p = .0013$; gbright, $p < 10^{-4}$). However adding interaction terms for subject and hemifield did not improve the fit, so we did not block n_{max} by those factors.

is this the right phrasing? adding interaction coeficients between subject and appearances significantly improved model fit.

We then considered the effect of targets appearing from behind the occluder, adding the regressor n_{app}, the number of appearance events during each trial. The coefficient for n_{app} was negative ($\beta_{n_{app}} = -1.5 \pm .21$), indicating that appearances increased the rate at which the subjects answered incorrectly (i.e. in agreement with the local direction of motion.) Furthermore, there was a significant interaction between number of appearances and subject identity ($p = .0019$), indicating that appearance events affected different subjects' responses differently. The effect of appearances was considerable compared to the effect of adding targets to the display; for subject GB, the coefficient associated with n_{app} was $.66 \pm .56$ times the coefficient of n_{max}; for subject DT the ratio was $1.5 \pm .63$. In other words shifting the initial target position so that an appearance occurs midway through the trial had more effect than adding two or three targets to the unoccluded portion of the display. Differences in the effect of appearances may be due to differing strategies employed by the subjects, and may help to explain the differing effects of occlusion on the PSE values measured for Figure 2a.

As for disappearances, these also had an effect, although less strongly than appearances. Interestingly, the pattern of effects for disappearances was nearly the inverse of that for appearances: a disappearance generally increased the likelihood of subjects' answering correctly. Moreover, the improvement was significant for subject GB ($B_{dis,GB} = .2 \pm .28$, $p = .48$) but did not reach significance for subject DT ($B_{dis,GB} = -0.32 \pm .35$, p $= p = .35$) Overall, including disappearances significantly improved the model fit ($p = .0098$) and the fit was not further improved by stratifying by subject ($p = .22$).

I could reference something from MOT literature, like Scholl and Pylyshyn, in assonance with this.

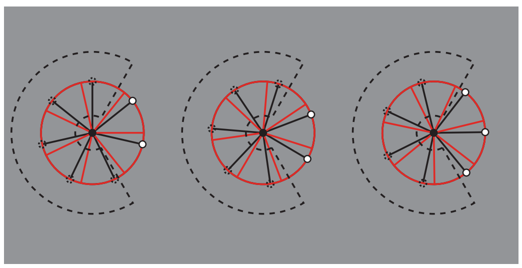
There's a "significant" interaction with GB, left/right side and disappearances; but it's silly to get that specific esp. to get that specific for one subject and not another

I start to think that the small number of trials with both an appearance and a disappearance are so wacky that they throw a lot of fits off, and we might benefit from leaving them out altogether. But what's a good way to quantify that?
Another thing to think about: I described how appearances could plausibly have either direction of effect (inference of global direction vs. movement of the endpoints.) If in fact both effects are present, that may complicate things and a symptom would be excessive residual deviance in the appearance trials.

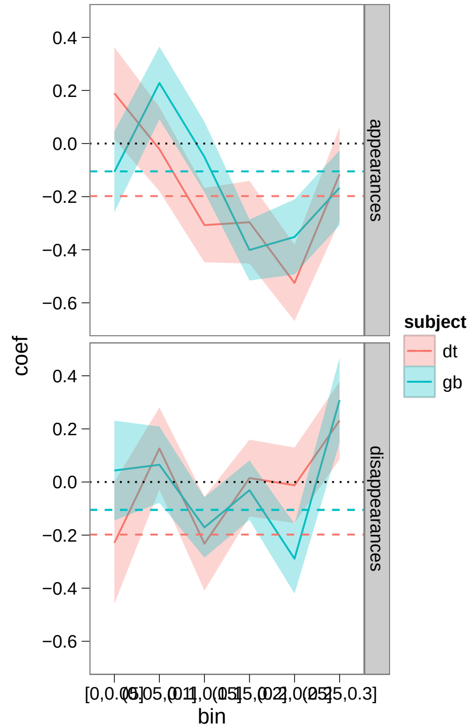
Since appearances have such a marked effect on subjects' responses, we next looked at the timing of appearances within each stimulus presentation. Appearances that occur immediately following stimulus onset or immediately preceding stimulus offset ought not to have much effect on subjects' responses, since the visual stimulus is virtually identical to one that contains no appearance events. On the other hand, appearances that occur during the middle of the stimulus presentation should have a greater effect. To examine the effect of occlusion events as a function of time we stratified the appearance times into equally sized bins. The effect of appearances and disappearances as a function of time is shown in Figure 3b; for both subjects, the effect of appearances starts near zero and grows significantly negative (associated with responses in the direction of local motion) in the second half of the stimulus presentation. In contrast, the effect of disappearances is smaller, not significantly deviating from zero in these time bins except possibly at the end of the trial.

finally, adding density to the equation; show that it obliterates the need for n_{max}.

I got stuck on how-to-get-to-this-figure for a bit, since . But then I discovered that a stepwise regression starting with a kitchen-sink of the various factors ends up spitting out a model that drops target-number and keeps target-density as the most significant explanatory variable. Stepwise regression doesn't know anything about the problem domain and proceeds dumbly by significance value ignoring effect size, so I'd like to not use it and have a more traditional discussion, but since a dumb algorithm gets to the right place, that lets me synthesize the key figure.



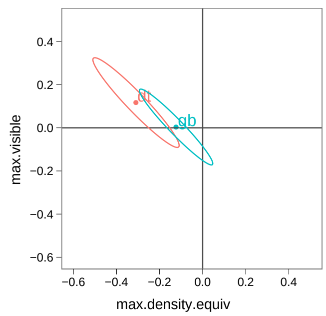
(A) Appearances and disappearances provide additional cues for the direction of motion. The initial position of the targets is shown and the path of their travel is shown as red arrows. Left: a target appears from behind the occluder while the stimulus is visible. Middle: neither an appearance or disappearance occurs during the limited duration of the stimulus. Right: a target disappears behind the occluder while the stimulus is visible. The target density is the same for all three stimuli.



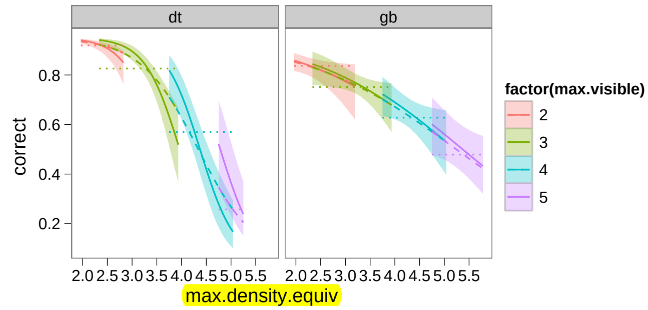
(B) The effect of appearances on subjects' response rate as a function of time. The horizontal axis divides the stimulus duration into bins. The vertical axis plots the change, in log odds of subjects' rate of answering according to global motion direction, as compared to stimuli that do not contain an appearance or disappearance. Bars indicate standard error of the estimated effect.

FIGURE 3. Effect of appearance and disappearance events in partially occluded stimuli.

Overall, then, in our model which attempts to account for the side effects of occlusion, it appears that element density explains the apparent reversal of motion direction better than element number. We visualize this in two ways. One is to replot the ellipsoids of Figure 2c; in Figure 4a, these ellipsoids now draw on data from all occluder trials and account for occlusion side effects, and are more consistent with a main effect of target density than one of number (graphically speaking they place more density on the x-axis than on the y-axis). Another is to draw the predicted psychometric functions resulting from the model, showing



(A) Confidence ellipses as in Figure 2c for the occlusion model, showing the values of both β_d for target density while the vertical shows the coefficient of β_n for target number. Both subjects' fits are more consistent with target density than with target number.



(B) Relation between target spacing, target number and subjects' responses. Here data for DT in the left hemifield, and GB in the right hemifield, is used to generate model fits. Each connected line segment represents varying target spacing while holding the number of targets visible in the window. Different colors correspond to different numbers of targets visible in the window, while the equivalent target spacing is plotted along the horizontal axis. Dotted lines indicate predictions made using only element number, and dashed lines show a fit that uses only target spacing. Solid lines and shaded confidence regions are fit allowing a mixture of density and number. The mixture models' results are more compatible with those of the target spacing than those of target number.

Figure 4

how these functions vary in terms of both target number and target density, and what the uncertainty in the prediction is. We do this in Figure 4b. Here we compare model fits obtained under three conditions: one in which the subjects' response depends on number (dotted lines), and a model allowing a mixture of the mixture. The same set of interaction variables are used in all fits. In Figure 4 we only show the data from each subject's better hemifield (left for DT, right for GB.) We observe in that in Figure 4a, for both subjects, the measured coefficients are more consistent with the illusion being driven by element density rather than number. In Figure 4b we see that when allowing a mixture of number and density to be used in fitting the psychometric function, the result (solid lines) follows more closely a function based only on density density (dashed lines) than one based only on element number (dotted lines). Thus we assert that the apparent reversal of motion direction is driven by element density.

and as a conclusion, now I really ought to update Figure 2a for the more detailed model.

Figure 5. Effect of target properties on critical spacing. A. Each plot shows critical spacing versus eccentricity for three different stimulus conditions. in one subject. B. Normalized logistic regression coefficient for each stimulus condition in each subject. * indicates significance ($p < 0.5$)

5. Robustness of scaling to stimulus properties.

A noted property of crowding in parafoveal vision is that the range of spatial interaction between nearby targets is not dependent on the size of the stimuli **?**. To determine whither the motion reversal illusion shared this property we collected thresholds for each eccentricity under altered stimulus configurations. In separate sessions we varied spatial frequency (using values of ϕ scaled by 66%, 100% and 150% compared to section 3), temporal frequency (using values of 6.6, 10, and 15 Hz), spatial step size (scaling values of Δx by 66%, 100% and 150% compared to section 3), and temporal step interval (using Δt values of 66, 100, and 150 ms, and d values of 44, 66, and 100 ms, respectively). For these experiments we used the QUEST procedure Watson and Pelli [1983] to select the the number of targets at each trial. As before, there were three types of trials, with local motion congruent, incongruent, or ambivalent to the global translation. The QUEST algorithm selected the target spacing for all trial types, but the subject's response was used to update the QUEST estimate only for trials with local motion incongruent to global. Separare, randomly interleaved estimations were performed for each stimulus configuration and eccentricity. The QUEST algorithm was only used to efficiently select stimulus values and not to obtain final threshold estimates; we re-fit the data using maximum likelihood logistic regression, as in section 3.

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