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Abstract

Center-periphery interactions in visual processing of dynamic stimuli have been considered as an example of surround modulatory effects on receptive field properties. Such effects have been observed in different areas of the visual system and their functional role has been related to figure-ground segregation, noise reduction, sparse coding or metabolic efficiency. We investigated the effects of surround motion direction, speed, and orientation of elongated moving elements on fine motion direction discrimination. The moving elements were Gabor patches with an orientation along the motion direction in the surround and at an angle of 0°, 45°, 90° or 135° from the motion direction of the central stimulus. Two different sizes of the center stimulus were used. The surround motion direction varied from 0° to 315° with a step of 45°. The direction of the central stimulus was changed with adaptive staircase procedure. The Subject's task was to discriminate whether the central motion was to the left or to the right from the vertical downward. The results show higher bias and reduced sensitivity when the center and surround motions were orthogonal and when the orientation of the elements and motion direction differed. The contribution of V1 and MT in the observed context modulatory effects is discussed.

Keywords: Visual perception, motion, center-surround interactions

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Introduction

Surround modulation is a repetitive motif in the sensory systems. It is observed at different levels of the visual system and is expressed as a shift in the balance of the excitatory and inhibitory processes depending on the type and the strength of the signal. Most often the surround modulation is suppressive meaning that when the stimuli in the vicinity and in the center of the neuron's receptive field are similar, the activity of the neuron is reduced. Surround modulation is supposed to have different functional roles in visual processing like figure-ground segregation, noise reduction, redundancy reduction or metabolic efficiency (Krause and Pack, 2014). As surround modulation is observed at different stages of information processing, it could have an additional function related to the transformation of the stimulus information at each stage.

In motion processing the surround modulation is supposed to have as a psychophysical correlate the effect of stimulus size on sensitivity to motion direction (Tadin et al., 2003; Tadin et al., 2007; Tadin et al., 2011; Tadin and Lappin, 2005). This effect consists in decreasing in the temporal threshold for correct discrimination of the direction of two opposing motions up to a certain stimulus size and a decrease in performance afterward. The transition from performance improvement to a decline occurs at stimulus sizes matching the typical receptive field size in MT – the first visual area specialized for motion processing. When the stimulus strength is low like at low contrasts, the effect is greatly reduced. The size effect is also diminished for populations known to have a decrease in the inhibitory processes in the brain like elderly, people in deep depression or with schizophrenia. In short, surround modulation in the size effect occurs in transient conditions and is revealed as a sensitivity change.

Other behavioral phenomena related to surround modulation and involving dynamic visual information are the induced motion, where a stationary stimulus appeared to move in direction opposite to the surround motion (Murakami and Shimojo, 1993, 1996; Takemura and Murakami, 2010), the overestimation of the speed of two opposing motions (Baker and Graf, 2008, 2010; Van der Smagt et al., 2010) or motion direction repulsion (Curran et al., 2009; Marshak and Sekuler, 1979; Wilson and Kim, 1994). Direction repulsion occurs for two superimposed motions occupying the same spatial region as in transparent conditions or in configurations where a motion stimulus is surrounding a central stimulus. In all of these conditions surround modulation is observed at long stimulus durations and is mostly related to changes in the precision of motion estimation and not to changes in sensitivity. These phenomena are also typically related to processes in area MT.

In the present study, we tried to evaluate the changes in both the precision and sensitivity to central motion when the direction of the surrounding stimulus varied. We used elongated moving elements in both regions of the stimulus configuration and varied their orientation with respect to the motion direction. We tested whether the orientation and motion direction were independent in order to evaluate the contribution of the different stages of motion information processing on the observed effects and to describe their potential functional role in motion estimation.

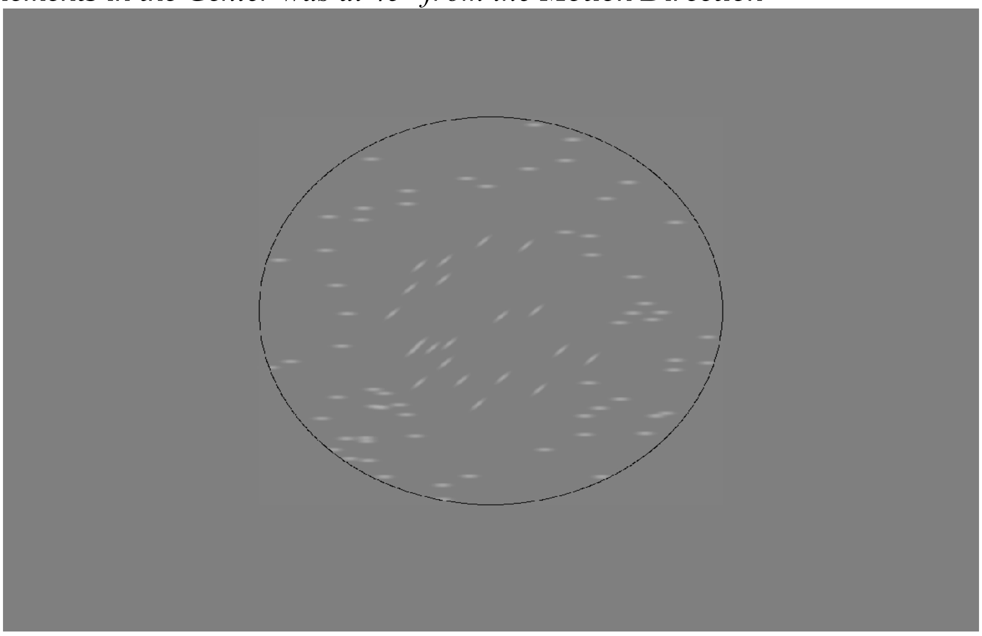
General Methods

Stimuli

The moving elements were Gabor patches with aspect ratio 4:1 and a length of 1.0 deg of visual angle. They were restricted to move in two regions – a circular region with a diameter of either 2.6 or 5.25 deg of visual angle and an annulus region with an inner diameter equal to the diameter of the circular region and an outer diameter of 10.5 deg of visual angle. The elements in the annular (surround) region were always oriented with their longer axis along the motion direction, while in the circular (central) region the long axis of the elements could deviate from the motion direction by an angle of 0°, 45°, 90° or 135°. The speed of motion of the elements in the central and surround region was always equal and could be either 2 deg/sec or 6 deg/sec. The density of the elements in the two regions was the same and was equal to 1 element/deg^2. If an element reached the border of its region, it was replaced by a new element at a random position inside it.

The stimuli were presented on a gray background with a mean luminance of 25 cd/m^2. The contrast of the stimuli was set to 50%. They were generated and presented with Dell computer running MATLAB (Mathworks) with the help of PsychToolbox (Brainard 1997; Pelli 1997). Figure 1 shows an example of the stimuli.

Figure 1. *An Example of the Stimulus Configuration. The Surround Moves to the Right while the Central Motion was Downward. The Orientation of the Elements in the Center was at 45° from the Motion Direction*



Procedure

The observers performed a single-stimulus two-alternative forced choice task. They had to indicate whether the central motion was to the left or to the right of the vertically downward direction. After each trial, an adaptive algorithm estimated the size of the angular deviation of the mean direction from the vertical to be presented on the next trial. The direction of the surround motion was randomly selected.

Each subject participated in two experiments. In Experiment 1 all 4 angular deviations between the central motion and the orientation of the elements were used and the speed of motion was 2 deg/sec. In Experiment 2 the orientation of the elements in the central region was either along the motion direction or orthogonal to it and the speed of motion was 6 deg/sec. The different experimental conditions: size of the central region and orientation of the elements were presented in separate blocks that involved eight separate, but interleaved adaptive QUEST (Watson and Pelli, 1983) staircases of 40 trials for each surround motion direction. The experimental sessions lasted less than 20 minutes. Two sessions separated by a break were performed on a single day. The order of the experimental blocks was counterbalanced across the subjects.

The subjects sat at a distance of 114 cm from a computer screen (20.1″ NEC MultiSync LCD monitor with Nvidia Quadro 900XGL graphic board) with their head fixed by a chinrest. The refresh rate of the monitor was 60 Hz, and the resolution was set to 1280×1024 pixels. The observation was binocular. The subjects used the mouse buttons to indicate their responses.

Subjects

Ten subjects, aged 34-62 yrs. old participated in the experiments. All of them have normal or corrected to normal vision.

Statistical Analyses

Mixed-effects probit regression was fitted to the data to evaluate the overall effect of the experimental factors. The parameters of the psychometric functions were estimated from separate mixed-effects probit regressions for each size, speed, and orientation of the elements in the center region. The angular difference between the vertically downward direction that was varied by the adaptive QUEST procedure was considered as a continuous factor, while the rest of the experimental factors were regarded as categorical. The 95%-confidence intervals were estimated by using a nonparametric bootstrap procedure (Effron and Tibshirani 1993) with 200 samples. All statistical analyses of the study were performed using R (R Core Team 2014). Generalized linear probit regression was performed using lme4 package (Bates et al., 2015). The generalized mixed-effects model regression allows to take into account the individual differences between the observers and to test different random effects.

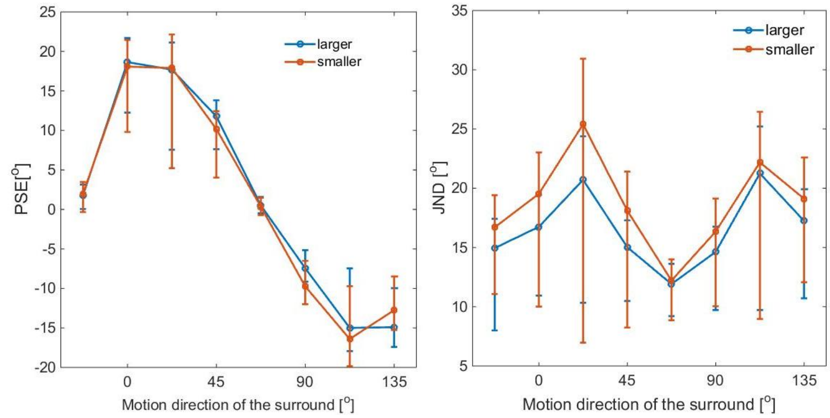
Results

The results of both experiments will be considered together. We will show only the graphs representing the interactions between the motion direction of the surround and the main experimental factors on the measures of sensitivity and precision to the central motion. As a measure of sensitivity, we used the Just-Noticeable-Difference (JND) obtained from the psychometric functions representing the performance of the observers evaluated by the generalized linear mixed-model probit regression, while as a measure of precision we used the Point of Subjective Equality (PSE) from the same analysis. To compare the effects of the experimental factors on PSE and JND we performed ANOVA on the bootstrapped values of PSE and JND. In this way, we took into account not only the central tendency of change due to the experimental factors but also the variability of the estimates that they introduced.

The results suggest a significant effect of the surround motion on both the precision ($F(7,12424)=1119.4$; $p<.05$) and the sensitivity ($F(7,12424)= 30.15$; $p<.05$) to the motion direction of the center. Overall, the lowest precision and sensitivity were observed when the motion in the center and the surround were orthogonal. The apparent motion direction of the center was repelled from the surround motion direction leading to positive shifts in the PSE for angles between the two motion directions less than 180° and negative shifts afterward. Our data also show the best performance in terms of precision and sensitivity for the case when the surround moved in a direction opposite to the center.

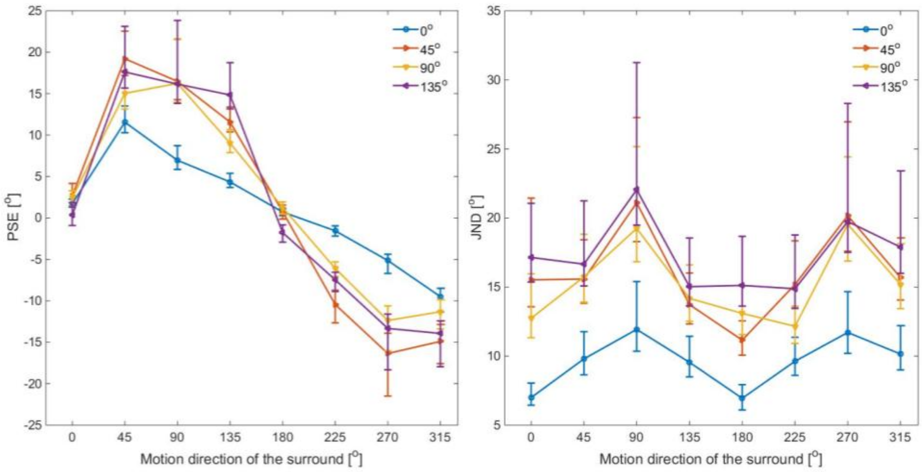
Figure 2 shows the interaction between the size of the central region and the motion direction of the surround. It shows no significant effect of size on the precision ($F(1,12424)=.7$; $p=.9$), and a lower sensitivity to the motion direction of the center when the size of the central region is smaller ($F(1,1224)=15.73$; $p<.05$). This result was obtained at high contrast and it differs from the known data for the changes in sensitivity to motion direction discrimination of two opposing motions at brief time durations (e.g. Tadin et al. 2003; Tadin and Lappin, 2005). One reason for this difference might be that in the present study the task requires fine motion discriminations.

Figure 2. *The Combined Effects of Surround Motion Direction and the Size of the Central Region on the Precision and Sensitivity to Motion Direction in the Center. The Error-bars Represent the 95% Confidence Intervals of the Estimates*



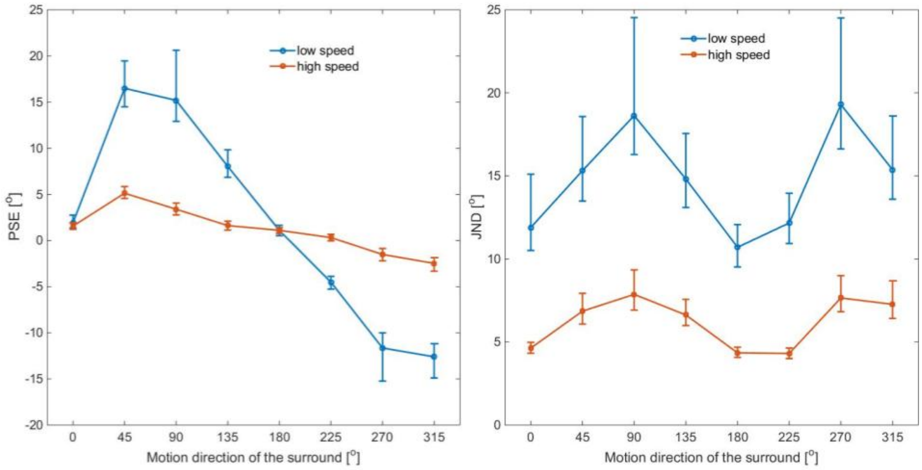
The orientation of the elongated elements with respect to the motion direction also significantly affected the performance ($F(3,12424)=19.73$ for PSE and $F(3,12424)=100.29$ for JND, $p<.05$). The precision and sensitivity were higher when the motion direction and the longer axis of the moving patterns coincided. In this situation, the effect of the surround on the performance was reduced. No systematic or significant differences in performance were obtained for the other angular deviations of the elements' orientation from the motion direction. These results are shown in Figure 3.

Figure 3. *The Combined Effects of Surround Motion Direction and the Orientation of the Elements in the Central Region on the Precision and Sensitivity to Motion Direction in the Center. The Error-bars Represent the 95% Confidence Intervals of the Estimates*



When the speed of motion was increased, the effect of the surround motion decreased. Figure 4 shows the interaction of the surround motion direction and the speed of the configuration.

Figure 4. *The Combined Effects of Surround Motion Direction and the Speed of the Configuration on the Precision and Sensitivity to Motion Direction in the Center. The Error-bars Represent the 95% Confidence Intervals of the Estimates*



There were significant interactions not only with the motion direction of the surround but also between the other experimental factors. For example, the sensitivity to motion direction was improved when the elements' orientation and the motion direction coincided for the smaller size of the center and worsened when the long axis of the elements deviated from it. The effect of size on PSE was negligible when the orientation of the elements was along or orthogonal to the motion direction. The effect of speed on the PSE varied depending on how the moving elements were orientated with respect to the motion direction. This interaction is a result of the larger improvement of precision for the case where the long axis of the moving elements was orthogonal to the motion direction (Experiment 2). The change in sensitivity and precision with speed differed depending on the motion direction of the surround and was greatest when the center and the surround moved in opposite directions.

Discussion

The results of the present experiments imply strong effect of the surround motion on the apparent motion direction in the central region. The significant interactions between the experimental factors and their different effects on sensitivity and precision in some conditions suggest a complicated picture that might be caused by the occurrence of the different effects at separate stages of motion information processing.

Could we relate the observed effects with surround modulation of the activity of neurons? It is more feasible to assume that the observed influence of surround motion is related to population encoding of the motion in the configuration. This possibility is related to the fact that in no case the surround modulation of the activity of single neurons (Born, 2000) leads to a shift in the direction preferences of the neurons, but only to changes in their activity i.e. in changes in the strength of the response and in the width of the neuron's tuning curve. When the surround motion has parameters that resemble those of the central motion, it could cause an asymmetric depression of these directions in the population encoding of the central motion and thus, it would bias the motion direction of the center away from the surrounding motion.

The results of the present study contradict the effect of size observed at high contrast and brief durations in other studies (e.g. Tadin et al. 2003; Tadin and Lappin, 2005). Our data show that the sensitivity changes are accompanied by changes in precision as well. Overall, the sensitivity is worse, not better for the smaller size of the central region. The size effect also differed depending on the orientation of the elements with respect to the motion direction. One reason for the insignificant effect of size on the precision of motion direction estimation and on the reverse or insignificant effect on sensitivity might be that at long durations the performance is dominated by neurons with no center-surround suppression i.e. wide-field neurons (Tsui and Pack, 2011).

Previous studies (e.g. Kim and Wilson, 1997; Chen et al., 2014), using different type of stimuli like gratings or dot patterns have shown larger biases in motion direction of the center in the range up to 45-60°, while in our data the largest shift is observed when the two directions are orthogonal. However, a careful examination of the data shows that when the motion direction and the axis of elongation of the moving elements coincided, the largest bias was observed at 45°, while when the axis of elongation and the motion direction were at different angles, the bias was largest for orthogonal surround and center motions. This outcome could be due to the involvement of neurons with asymmetric receptive fields in coding the motion direction and to unequal effects of the inhibition along the long axis of such neurons and orthogonal to it. This explanation could not account, however, for lowest sensitivity when the center and the surround moved in orthogonal directions and for the highest precision when the two motions were in opposite directions. It might be related to the changes in the apparent relative speed in the two regions of the configuration. The better performance for motions along the axis of orientation also could be due to the higher apparent speed as compared to motions at any other directions (e.g. Rider et al., 2014). The lower sensitivity to speed when the center and the surround moved in orthogonal directions might also represent the higher diversity (Cui et al., 2013) in the selectivity of the neurons showing suppression from motions in the orthogonal direction.

The effects of orientation, however, could be inherited from the encoding of motion information in V1 where the activation along the orthogonal axis is stronger at low speeds and along the axis of orientation at high speeds.

The single-unit studies (Born, 2000) show that surround modulation of neuronal activity in the preferred motion direction is independent of the motion speed in the surround. As neurons in area MT have preferences to higher speeds than the neurons in V1, one might expect to observe stronger suppression at higher motion speeds. Indeed, in a study on the effect of speed on surround suppression in motion direction discrimination, Lappin et al., (2009) showed that the performance deteriorates more with the increase of speed suggesting an increased suppression at higher speeds. As the surround suppression in motion processing is explained with the size of the receptive fields in area MT, this result would imply smaller receptive fields of neurons tuned to higher speeds. However, MT units tuned to higher speeds have larger receptive fields and their spacing is assumed to be sparser, with the distance between units proportional to the speed (e.g., Perrone and Listone, 2015). Our data also suggest that the surround modulation is greatly attenuated when the speed of the whole configuration is increased.

The possibility that changes in the apparent speed of motion induced by the surround motion or by the orientation of the moving elements affect the perceived motion direction in the center requires a relation between direction and speed in population coding of motion information. One such link between these two motion characteristics could be the correlated activity of neurons tuned to similar directions and speeds of motion and to similar retinal positions. These correlations could explain the observed center-surround interactions as they will depend on the similarity of the motions in the configuration, the size of the regions with similar motions as well as on the speed of the motion configuration. As reported by Huang & Lisberger (2009), the neuronal correlations between the activities of neurons in area MT are higher at lower speeds of motion. The correlations are higher when the retinal position of the receptive field centers are less than 7.5 deg. visual angle and this could explain the insignificant effect of size on the precision of motion direction estimation found in our study. While neuronal correlations decrease with the stimulus presentation, they do not disappear. Therefore, the surround modulation could be thought as a normalization of the population response by the activity of all neurons reacting to the motion stimuli and extracting from it reliable information for behavior. At short and long stimulus duration it could have different functional roles. At brief durations, its main function might be selecting an object for tracking, while at longer durations it might be involved in reducing the effects of lateral translations on the estimation of self-motion direction and in the transformation of the speed information for better used by the downstream brain areas.

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