## Short Report

Vigorous orientation signal propagates best from collinear motion

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#### Abstract

In the present study, the Poggendorff illusion was tested with four types of stimuli: A moving dot, a moving bar parallel to the inducing lines, a moving bar collinear to the motion trajectory, and static bars as in the classic illusion. Psychometric functions of the alignment task showed that the collinear bar, where orientation and motion trajectory matched, yielded the best alignment performance almost eliminating the illusion; the vertical bar, on the contrary, showed the worst alignment, finally the dot and the static bars led to intermediate alignments. These results demonstrate the interaction between orientation and motion trajectory that likely takes place in the primary visual cortex (V1) where these two signals might be modulated by top-down activity from higher order areas such as the middle temporal (MT). This vigorous orientation-motion trajectory interaction allows extremely accurate positional predictions of moving objects in the visual scene, in particular during occlusion.


Keywords: collinear context, Poggendorff illusion, visual motion, context modulation, orientation-motion trajectory interaction, V1-MT.

## 1 Introduction

Natural as well as manufactured objects do trace a path behind them while they move along a trajectory in space, e.g., a dolphin swimming in the sea, an aircraft at the cruising altitude or a rocket taking-off from the ground. These paths are evident in fast moving objects that leave smeared traces behind, usually referred to as "motion streaks" or "speed lines" useful to disambiguate the orientation of the trajectory, namely the direction of movement (Burr, 2000; Geisler, 1999). A moving object with elongated shape, e.g., a bar, in addition to follow a trajectory of motion, does have a proper orientation with respect to the trajectory of motion and to attenuate the inevitable friction of the medium, elongated objects usually move along a direction collinear to their longitudinal axis. Sensitivity to motion is evident in the visual system starting from direction selective simple and complex cells in different layers of the primary visual cortex: Area V1 (Hubel, 1988), to visual areas highly specialized to process motion, such as the middle temporal area (MT), whereby neurons are specialized to signal a particular direction and speed of motion (Albright, 1984; Maunsell \& Van Essen, 1983). A substantial amount of neurons in area MT, called Type II, do show a selectivity for bars collinear to their motion trajectory (Albright, 1984). A similar mechanism has been recently reported in cat's primary visual area "Area 17 ," whereby the population activity around 200 ms from the onset of a moving dot represents both the position of the stimulus and the orientation of the trajectory of motion (Jancke, 2000), as if a collinear bar instead of a dot was actually moving. A bar moving collinearly, thus, presumably activates a motion path along its direction of motion behind and, more importantly, ahead its actual position that is crucial to represent motion during occlusion. The collinearity of the motion trajectory with the longitudinal axis of the moving object is reminiscent, although in stationary condition, of a facilitatory effect, called "contextual effect" observed in orientation selective neurons in superficial layers of V1 connected via a plexus of long-range horizontal connections (LRHC), whereby the contrast threshold for target detection is lower with nearby stimuli collinearly aligned to the target with respect to stimuli orthogonal to the target or offset with respect to the collinear path (Gilbert, Das, Ito, Kapadia, \& Westheimer, 1996). This effect is explained as a direct connection, via LRHC, of columns with the same orientation selectivity and lying along the collinear path. Recent experimental evidence in primate V1, combined with psychophysical testing in human observers, suggests that the "contextual effect" might result, at least in part, from the collinear elongation of the V1 population responses in the retinotopic orientation representation (Michel, Chen, Geisler, \& Seidemann, 2013).

According to the temporal coherence theory, put forward by Grzywacz and coworkers, for visual motion detection: A moving object is likely to occupy in successive times a sequence of points in space lying on a straight path, i.e., it keeps moving in the same constant direction. Coherence in this theory is achieved by comparing past responses with present responses sequentially activated along such "delay lines" (Grzywacz, Watamaniuk, \& McKee, 1995, p. 3195) that spatially lie along a collinear path and the LHRC might be the best candidate to provide the neural basis of the temporal coherence theory for visual motion detection. Therefore, moving bars collinearly oriented to the motion trajectory should activate V1 orientation and motion selective neurons and Type II MT neurons along the motion path ahead and behind the actual position of the bar as if the moving bar filled a straight growing line like a railway track with respect to a locomotive moving along it.

### 1.1 Present study

The aim of this study was to provide evidence of the strength of the perceptual representation of a motion trajectory as predicted by a collinearly moving object. It was hypothesized that a moving object, such as a bar, with its longitudinal axis collinearly aligned with the motion trajectory would enhance the representation of the motion direction and allow to predict the trajectory ahead of time during occlusion. An orientation-less moving object, such as a dot, on the other hand, would not be as effective, and a moving bar orthogonal to or with a large angular separation between the longitudinal axis and the motion trajectory would be the less effective in predicting the motion trajectory since its orientation does not match the direction of motion. In order to test this hypothesis, the famous Poggendorff illusion was used: In the illusion, a line passing behind an occluder and oriented at $45^{\circ}$ with respect to the vertical edges of the occluder is misperceived as though the two visible strokes were misaligned. In the present study, in addition to the static bars as in the classic illusion, the following moving objects were used: A moving vertical bar, a moving dot, and a moving bar collinear to the motion trajectory (see Figure 3). It was predicted that the moving bar collinear to the motion trajectory would provide the smallest misalignment since it strengthens the orientation as well as the motion trajectory representations, the dot and the static bars would yield an intermediate misalignment and, finally, the vertical moving bar would yield the largest misalignment.

## 2 Results

A psychometric function was generated onto the percentage of the "above" response, with respect to the total of trials for each offset of the right segment of the motion trajectory or of the motionless right bar in the four stimulus type conditions: Vertical Bar, Dot, Collinear Bar, and Static (Figure 1).

Data fitting was obtained by a Probit analysis: This procedure enables to estimate the strength of a stimulus required to induce a certain proportion of responses. In particular, in this study, the amount of offset of the right segment of the trajectory leading to a chance performance ( $50 \%$ "above" response) was considered. This value was called point of subjective alignment (PSA) and it was obtained for each subject, run, and experimental condition. The mean values of PSA in the four experimental conditions across runs and observers are plotted in Figure 2.


Figure 1. Psychometric functions of alignment discrimination performance of observers (a) LM, (b) MG, and (c) DM, in the four experimental conditions: Vertical Bar (blue line); Dot (red line); Collinear Bar (green line); Static (black line). Each data point represents the sum of "above" responses in 40 trials. Error bars represent $\pm 1$ SD.


Figure 2. Point of Subjective Alignment (PSA) mean values referred to the $50 \%$ performance, in the four experimental conditions, from left to right: Vertical Bar (blue bar), Dot (red bar), Collinear Bar (green bar), and Static (black bar). Error bars represent $\pm 1 \mathrm{SE}$ of the mean. Each data point is the mean of 840 trials.

The PSA measurement for each subject and for the four runs entered a one-way analysis of variance (ANOVA) for repeated measures- $p$ values were corrected by applying the Greenhouse-Geisser epsilon for nonsphericity-with the unique factor Condition that represented the four levels of stimulus type: Vertical Bar, Dot, Collinear Bar, and Static. The main effect Condition was highly significant $(\mathrm{F}[3,33]=25.49 ; p<0.001 ; e=0.918)$. Post-hoc pairwise $t$-tests, corrected for multiple comparisons according to Bonferroni correction, confirmed that the Collinear Bar condition led to the best alignment perceived with respect to the $0^{\circ}$ offset. The Dot and the Static conditions led to intermediate alignment errors and did not differ from each other. An interesting result was showed by the Vertical Bar condition, which led to the worst alignment of the two segments of the motion trajectory, that is to the largest Poggendorff illusion (see Figure 2): Collinear Bar vs. Dot $(t(11)=-0.221 ; p<0.001$ ); Dot vs. Vertical $\operatorname{Bar}(t(11)=0.138 ; p=0.010)$; Collinear Bar vs. Vertical $\operatorname{Bar}(t(11)=-0.360 ; p<0.001)$; Collinear Bar vs. Static $(t(11)=-0.221 ; p<0.001)$; Dot vs. Static $(t(11)=-0.0001 ; p=0.999)$; Vertical Bar vs. Static $(t(11)=-0.139 ; p=0.009)$; Mean values of PSA: Vertical Bar $=-0.46^{\circ}$; Dot $=-0.32^{\circ}$; Collinear Bar $=-0.1^{\circ}$; Static $=-0.32^{\circ}$. Observers reported that in the Vertical Bar condition, in order to make their judgments about the alignment, they focused onto the upper end of the bar that was also the closest position to the lead of motion and appeared the best strategy to do the task.

## 3 Discussion

The novel result showed in this study is that a collinear moving object potentiates the effect of propagating an oriented motion signal during occlusion in that it is capable to almost eliminate the Poggendorff illusion. An intermediate performance, in the alignment error caused by this illusion, was yielded by the moving dot and static bars, while the worst performance was showed by the vertical moving bar; whereby in order for the observer to perceive an aligned transversal line, the second segment on the upper right side of the occluder had to be displaced as much as $0.46^{\circ}$ of visual angle. Importantly, the powerful orientation signal propagating from the collinear motion was a real change of response bias in the observer's psychometric function (rightward shift of the curve and similar slope of the curve except at the asymptotes) rather than a change in sensitivity to the signal (Morgan, 1999; Morgan, Dillenburger, Raphael, \& Solomon, 2012) as confirmed by the high d-primes values yielded by the observers in the four experimental conditions (Table 1). In recent work (Watamaniuk, 2005), moving dots were thought to diminish the Poggendorff illusion because, when in motion, they show little orientation energy (but see Westheimer \& Wehrhahn, 1994), in the present study they were undistinguishable from the static bars of the classic illusion. Moving collinear objects are better than moving dots in propagating the motion signal during occlusion because, being oriented objects, they potentiate the orientation signal developing 190-200 ms after motion dot onset in V1 (Jancke, 2000). Temporal discontinuity produced by dynamic objects favors figure-ground segregation between the transverse element and the occluder and reduces the Poggendorff illusion (Mori, 1981), thus avoiding the orientation interaction at the intersection point along the side of the obtuse angle whereby the confound between the transverse element and the inducing line of the occluder is the highest (Weintraub, Krantz, \& Olson, 1980). This is confirmed here by the vertical bar condition in which the motion trajectory was at $45^{\circ}$ but the moving element was parallel to the vertical inducing lines of the occluder

Table 1. d-primes of the three observers LM, MG, and DM (rows) in the four experimental conditions: Vertical Bar, Dot, Collinear Bar, and Static (columns).

| Observers/Conditions | Vertical Bar | Dot | Collinear Bar | Static |
| :--- | :---: | :---: | :---: | :---: |
| LM | 1.51 | 1.92 | 2.23 | 2.11 |
| MG | 1.37 | 1.73 | 2.52 | 1.73 |
| DM | 1.89 | 2.26 | 2.33 | 2.52 |

and the brief interval when the moving bar and the leftmost inducing line coincided led to the worst alignment error $\left(0.46^{\circ}\right.$ of visual angle) as if the vertical element continued to move along the vertical component of motion. The dynamic collinear stimulus, on the contrary, likely avoided a confusing signal in particular at the obtuse angle formed with the vertical inducing line of the occluder during the brief contact with it, yielding the smallest alignment error ( $0.1^{\circ}$ of visual angle). Linear motion paths are the more consistent trajectories in the visual field as they represent best the "correspondence problem" in motion whereby successive instances in time and space of an object do represent the same object in motion. Consistent motion paths can bias apparent motion of simple dots providing that they are aligned along a linear path in the effect called: Visual inertia (Anstis \& Ramachandran, 1987). Thus, collinear moving objects might exert a stronger bias on nearby moving objects in this type of visual effect since they evoke identical orientation as well as motion trajectory signals propagating along a linear path and anticipating the representation of positions occupied along the path that appears to begin as early as in the retina (Berry, Brivanlou, Jordan, \& Meister, 1999).

## 4 Conclusions

This study showed that a visual stimulus moving collinearly with respect to its longitudinal axis propagates a vigorous signal of orientation overlapping its motion trajectory along the motion path during occlusion. This combined positional in time and orientation signal allows a better representation of a transverse element partially occluded, as in the Poggendorff illusion, preventing alignment errors.


Figure 3. Stimuli: On the bottom left are indicated the stimulus types used in the experimental conditions: Vertical Bar, Dot, Collinear Bar, and Static. On the top right are indicated the seven trajectories followed by the stimuli after occlusion with the relative offsets. Dimensions are indicated in degrees of visual angle. (Note, the static bars in the experimental trials where positioned in the middle of the two vertical lines serving as the occluder like the moving stimuli).

Positional in time and orientation signals interaction might be accomplished by the combined bottomup and top-down interplay between V1 and MT and by local LRHC in V1.

## 5 Methods

### 5.1 Observers

Three observers performed in the experiment (mean age $=31$ ): One was the author and two were completely naive. They were all right-handed, neurologically intact, and had normal or corrected to normal vision. They signed a consent form to participate in the experiment and their rights were protected according to the Declaration of Helsinki.

### 5.2 Stimuli

The stimuli were displayed onto a CRT-60Hz 17 " Philips monitor at a distance of 114 cm . A chin-rest was used to limit head movements. To guarantee eye fixation at the center of the screen, a small fixation point was presented at the beginning of a trial and vanished after 2 s . Two vertical white lines, flanking the position previously occupied by the fixation point, $2^{\circ}$ apart, $7.5^{\circ}$ long and $0.2^{\circ}$ thick were presented against a dark gray background $\left(0.4 \mathrm{~cd} / \mathrm{m}^{2}\right)$, and remained on the screen during the whole session representing the occluder of the Poggendorff illusion. Four different types of stimuli were used and presented in white at a luminance of $90 \mathrm{~cd} / \mathrm{m}^{2}$ : Vertical Bar ( $1^{\circ}$ long; $0.1^{\circ}$ thick) parallel to the inducing lines of the occluder, Dot (diameter $=0.1^{\circ}$ ), Collinear Bar ( $1^{\circ}$ long; $0.1^{\circ}$ thick) aligned with the motion trajectory, and two Static bars ( $2^{\circ}$ long; $0.1^{\circ}$ thick) on both sides of the occluder as in the classic illusion. All stimuli, except for the static bars, moved from the left bottom position, with respect to the inducing lines, to the right top position at the speed of $5^{\circ} /$ s along a trajectory at $45^{\circ}$ with respect to the inducing lines. The stimuli travelled for $2^{\circ}$ before disappearing behind the occluder. When they reappeared at the higher right position with respect to the vanishing position, they travelled for additional $2^{\circ}$ before going completely off. The reappearing position could be perfectly aligned with respect to the trajectory segment before disappearance ( $0^{\circ}$ offset) or reemerged with offsets of: $0.25^{\circ}$; $0.5^{\circ}$; and $0.75^{\circ}$, either above or below the aligned trajectory with $0^{\circ}$ offset. From now on all the offsets will be refer to as: $+0.75 ;+0.5 ;+0.25 ; 0.0$ (aligned trajectory); $-0.25 ;-0.5 ;-0.75$ from the highest to the lowest. In the Static condition, the two motionless bars were extended for the same space ( $2^{\circ}$ ) covered by the moving stimuli and the right bar offset was varied according to the values indicated above for the moving stimuli (Figure 3).

### 5.3 Procedure

The observers were required to discriminate if the stimulus reappearing at the top right position was on a trajectory "above" (middle finger) or "below" (index finger) the aligned trajectory ( $0^{\circ}$ offset) in a 2AFC task by using two buttons on a response device. Two observers used the right hand and one used the left hand. Each type of stimulus: Vertical Bar, Dot, Collinear Bar, and Static was presented in four different blocks, 10 times for each offset for four successive runs ( 40 total repetitions per offset), according to the constant stimuli method. The order of the stimulus type was counterbalanced among the three observers. Short breaks in between runs where allowed to the observers in order to rest. The whole sequence: Motion segment on the left side of the occluder, disappearance of the stimulus behind the occluder, and reappearance of the stimulus on the right side of the occluder in the second motion segment, lasted for 1400 ms (certainly the collinear bar took 200 ms more to completely disappear behind the occluder with respect to the vertical bar and the dot which disappeared instantly, but it took also 200 ms on the right upper position of the occluder in order to have full sight of the collinear bar whereas the vertical bar and the dot appeared instantly) and the following trial began after 1000 ms . In the Static condition, the stimulus duration was kept constant ( 1400 ms ) as in the conditions with moving stimuli.

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