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Systematic Directional Error in Peripheral Vision

Master thesis

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Systematic Directional Error in Peripheral Vision

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Abstract

This study investigated the pattern of systematic directional error (DE) in peripheral vision This pattern manifests as a perceived expansion of space in the vicinity of cardinal directions (0°/90°/180°/270°) and a contraction of space in the vicinity of diagonal directions (45°/135°/225°/315°). Alongside this pattern, the phenomenon of radial bias was also investigated. A total of 20 subjects were asked to fixate their gaze and then to align an arrow to a target using only their peripheral vision. The arrow and the target would appear in 4 different peripheral locations in comparison to the center of fixation (at an angle of 0°, 22.5°, 157.5°, or 180°). The mean difference between the subjects' answers and the target's actual direction was used to demonstrate the existence of the systematic DE, which was similar in pattern but differed in magnitude between cardinal peripheral locations and the oblique peripheral locations. No evidence of a radial bias was found.

Keywords: Systematic directional error, mean directional error, oblique effect, radial bias, space categorization, space representation

Introduction

Oblique effect is a phenomenon which is mainly encountered in the literature of vision. It has been described first in the German (Mach, 1861) and later in the English literature (Jastrow, 1893). In those experiments, subjects had to either answer whether separate lines were parallel or not, had to reproduce visually presented lines, or had to align lines to specific directions. It was observed that subjects were both more accurate and faster with vertical or horizontal lines compared to oblique ones. This superiority in performance when visual stimuli are vertical or horizontal as opposed to oblique was then reproduced in many different studies and was later given the name oblique effect (Appelle, 1972). The oblique effect has been demonstrated in primates (Boltz, Harweth, & Smith, 1979), but also in more (evolutionary) distant organisms like cats (Sutherland, 1963), rats (Lashley, 1938) and octopuses (Sutheland, 1958). It seems that the oblique effect is a result of neural processing (Campbell, Kulikowski, & Levinson, 1966) however the exact substrate has not been found. Cell recordings in cats have shown that more neurons in the V1 region of the visual cortex have a greater affinity for the cardinal as opposed to the oblique directions (Li, Peterson, & Freeman, 2003), while the same findings have been demonstrated in macaques but in area V2 (Shen, Tao, Zhang, Smith, & Chino, 2014). Studies utilizing fMRI has found greater activation patterns both for the cardinal (Furmanski & Engel, 2000) as well as for the oblique directions (Shen, Tao, Zhang, Smith, & Chino, 2014). Meanwhile, extrastriate visual areas like the middle temporal area (Xiagmin, Collins, Khaytin, Kaas, & Casagrande, 2006) and parahippocampal place area (Nasr & Tootell, 2012) have been linked to the generation of the oblique effect. It has been proposed that the conflicting findings are a result of differences between the protocols of the different studies (Li, Peterson, & Freeman, 2003) (Shen, Tao, Zhang, Smith, & Chino, 2014).

The existence of two classes of oblique effect has been proposed (Essock, 1980). Class 1 oblique effect is a purely visual one, is related to lower-level neural processing, and emerges in tasks involving visual acuity and sensitivity to contrast. On the other hand, Class 2 oblique effect is related to higher-order processing like orientation discrimination and retrieval of directional information and it also emerges not only in the visual modality but also in the haptic and kinaesthetic ones (Essock, 1980) (Luyat & Gentaz, 2002).

An example of a Class 2 Oblique effect will be the major focus of this study. That is the systematic directional error (DE) (also referred to as “Cognitive Oblique Effect” (Balikou , et al., 2015) (Kaspiris-Rousellis, Siettos, Evdokimids, & Smyrnis, 2017)), a pattern that emerges in a variety of tasks, in which subjects have to reproduce the orientation of a previously presented stimulus. Specifically, when reproducing oblique orientations, the subject's answers tend to move away from the cardinal axes (0°/90°/180°/270°) and towards the closest diagonal (45°/135°/225°/315°). This pattern has been also described as an equivalent of an expansion of the directional space near the cardinal axes and a contraction around the diagonal ones (Krukowski & Stone, 2005) (Smyrnis, Mantas , & Evdokimidis, 2007). It has been described in mnemonic tasks, where the subjects had to memorize the position of a dot on a circle and then reproduce it (1991) or had to realign an array based on a previous presentation (Balikou , et al., 2015), in tasks which required hand movement to a specific direction in 2D (de Graaf, Sitting, & van der Gon, 1994) (Mantas, Evdokimidis, & Smyrnis, 2008) or 3D space (Kaspiris-Rousellis, Siettos, Evdokimids, & Smyrnis, 2017), in an arrow pointing task, in an antisaccade task (Koehn, Roy, & Barton, 2008) and in a smooth pursuit task (Krukowski & Stone, 2005). It should be noted that the emergence of the systematic DE is not limited to visually presented stimuli but it has been also demonstrated in tasks involved kinaesthetic (de Graaf, Sitting, & van der Gon, 1994) (Baud-Bovy & Viviani, 2004) or haptic stimuli (Baud-Bovy & Gentaz, 2012).

In order to explain the pattern of systematic DE, a model of space categorization has been proposed (Huttenlocher, Hedges, & Duncan, 1991) (Huttenlocher J. , Hedges, Corrigan, & Crawford, 2004). In this model, the direction of a stimulus has two distinct representations: a veridical one, based on the sensory information gained from the respective sensory modality, and a categorical one, in which the direction of the stimulus is coded to belong in one of four categories. These categories are centered on the four diagonal directions (45°/135°/225°/315°), while the cardinal directions are used as boundaries (the usage of the cardinal directions as boundaries may be attributed to the better precision around those directions, which will result in less category classification errors). The representation of the stimulus can be given by the following equation (Baud-Bovy & Gentaz, 2012):

$$R = \lambda * M + (1 - \lambda) * P$$

where M is the veridical (or fine-grained) representation, P is the categorical one and λ is the weight of the veridical representation. When the amount of available sensory information decreases, the weight λ decreases accordingly and as a result, the magnitude of the categorical representation is compensatory increased. This leads to the emergence of the systematic DE as it can be seen in studies where a memory delay was introduced (Balikou , et al., 2015) or where conditions with less information available were introduced (Smyrnis , Mantas, & Evdokimidis, 2014). An updated version of this model was made to include four more categories, this time centered on the cardinal directions, in addition to the original four centered on the diagonal directions (Baud-Bovy & Gentaz, 2012).

When it comes to the visual modality, all the studies mentioned so far have been performed with the subjects utilizing their central vision. When the peripheral vision is used, a preference for stimuli that are oriented collinearly with a line that intersects the center of attention, irrespective of whether the stimuli are oriented cardinally or oblique, emerges which is called the radial bias (Rovamo, Virsu, Laurinen, & Hyvdrinen, 1982) (Berkley, Kitterle, & Watkins , 1974) (Westheimer, 20003). Also named the meridional effect, this phenomenon “competes” with the oblique effect as the stimuli are moved away from the center of fixation; the exact magnitude of its effect and the rate of its change are however not known. It has been reported that the oblique effect seems to disappear at eccentricities of 8 to 18 degrees away from the fixation point (Berkley, Kitterle, & Watkins , 1974) (Rovamo, Virsu, Laurinen, & Hyvdrinen, 1982). It has been also reported that at eccentricities larger than 20 degrees the oblique effect is fully substituted by the radial bias (Rovamo, Virsu, Laurinen, & Hyvdrinen, 1982). As in the case of the oblique effect, radial bias is thought to be a production of neural processing (Westheimer, 20003), albeit no exact neuronal substrate has been found. However, it has been correlated with activation of the V1, V2, V3, V3A/B, and hV4 regions (Mannion, McDonald, & Clifford, 2010).

So far the pattern of systematic DE has not been studied in the peripheral vision. The aim of this study is first and foremost to investigate the existence of the pattern. Secondly, the existence of radial bias will be also investigated. Finally, any possible interaction between those two phenomena will be also be investigated. Should a radial bias is found, then the axes around which precision is greater are expected to change and therefore a modification of the pattern of systematic DE could occur.

Methodology

Subjects

A total of twenty one (21) participants, aged 22 to 32 (M = 26.8, SD = 2.4), were recruited for this experiment (12 females, 10 males). The subjects were all either under- or postgraduate university students. All of them were screened by the examiner for any history of neurological and/or psychiatric conditions as well as for the status of their vison (normal or corrected). Of the initial subjects recruited one was rejected on the grounds of non-corrected astigmatism (1 female) bringing the final number of subjects down to twenty (20). Seventeen (17) participants were right-handed and three (3) were left-handed and all of them performed the task using their preferred hand. All participants gave written informed consent for participation in the study after a detailed explanation to them, of the experimental procedure. The experimental protocol was approved by the Scientific and Ethics committee of the University Mental Health, Neurosciences, and Precision Medicine Research Institute.

Materials

The experimental procedure was depicted in a Dell S2417DG computer monitor (23.8", 2560*1440 pixels) and the participants' responses were given using a Microsoft Basic optical mouse. The program that was used for the task was created using the Delphi Programming Language. All the necessary procedures were performed in the Laboratory of Cognitive Neuroscience and Sensorimotor Control of the University Mental Health, Neurosciences, and Precision Medicine Research Institute.

Set up and procedure

Subjects were seated comfortably in front of the computer monitor at a distance of approximately 60 cm. The task contained two conditions: the central and the peripheral one.

The central condition was a partial replication of the task done by (Smyrnis , Mantas, & Evdokimidis, Two independent sources of anisotropy in the visual representation of direction in 2-D space., 2014). Each trial started with a filled red disk (3 mm diameter) appearing at the center of the screen. After a period of 1 s, a second white filled disk (3 mm diameter) appeared in the circumference of an imaginary circle of 3 cm radius in one of 16 directions (22,5° intervals) and a white arrow (10 mm length) appeared originating at the center target. The arrow pointed a varied amount of degrees away from the peripheral target clockwise or counterclockwise chosen at random. Using the mouse the subject could move the arrow in either direction and was instructed to align the arrow to the direction of the peripheral target.

The subject's answer was finalized by pressing the left mouse button and then a new trial began. The direction of each trial was chosen randomly.

In the peripheral condition, each trial started with a filled red disk (3 mm diameter) appearing at the center of the screen. Subjects were instructed to fixate on this central target and not to stray their gaze at any point during the trial. After a period of 1 s, a second white filled disk (3 mm diameter) and a white arrow (10 mm length) originating 40 mm from the disk and pointing away from it in either a clockwise or counterclockwise direction (chosen randomly each time) appeared. Those stimuli would appear in one of four (4) different possible peripheral locations (chosen randomly each time). Those locations were in an angle (0°, 22.5°, 157.5°, 180°) compared with the central target and at a distance of 10 cm. Using the mouse to move the arrow in either direction the subjects were instructed to align the arrow to the direction of the peripheral target utilizing only their peripheral vision. The subject's answer was finalized by pressing the left mouse button and then a new trial began. Both the location and the direction of each trial were chosen randomly.

In order to ensure the subjects' gaze remained fixated throughout each trial a combination of three measures (apart from the strict instructions in the beginning) was implemented. Firstly throughout each block of trials, a number of "Catch" trials were introduced. In those, at random time intervals after the beginning of a new trial, the center of the central red target would turn white and the subjects were required to disregard the arrow's alignment and press the left mouse button within 1 second. There would be 24 "Catch" trials, scattered randomly within each block. Secondly, the subjects were instructed to inform the examiner every time that they looked towards the peripheral target. The trial number was noted and the trial was afterward manually discarded. Finally, the examiner was observing the subjects during the block, recording eye movements away from the fixation point.

Each block in the central condition contained 32 trials (16 directions done twice each) while each block in the peripheral condition contained 152 trials (16 directions done twice each in each of the 4 locations plus 24 "Catch" trials). The blocks were done in pairs of two (one central block, followed by a peripheral block) with small time breaks between each pair. Each subject was required to complete seven blocks for each condition and all were performed during one experimental session. Of the 20 subjects, one completed only five blocks for each condition.

Data and Analysis

The parameter of interest used throughout the analysis was the Directional Error (DE). That was the polar angular difference (in degrees) between the direction of the peripheral target and the direction of the arrow at each trial. A counter-clockwise deviation from the peripheral target was defined as positive DE. Absolute values of DE greater than 15° were excluded from the analysis.

For each subject, each location and each target direction the mean DE (as a measure of the systematic DE) and its standard deviation (SD) were computed. In the case of the central condition, each measure was used as the depended variable in a one-way ANOVA with target direction as the independent variable, while in the peripheral condition each was the depended variable in a two-way ANOVA with target direction and location as the independent variables.

In one more analysis of the peripheral condition, further manipulation of the dataset was performed. The values of DE for each of the 16 possible target directions were pooled together into 4 different groups: one group with the cardinal directions (0°/90°/180°/270°), one group with the diagonal directions (45°/135°/225°/315°) and two groups with the in-between oblique directions (22.5°/112.5°/202.5°/292.5° and 67.5°/157.5°/247.5°/337.5°). For each subject, each location and each of these directions groups the mean DE and its SD were once again computed. The rationale behind this grouping was, in the case of the mean error, to cluster together the directions where the mean DE is expected to either be close to zero (0°/90°/180°/270° and 45°/135°/225°/315°) or to be maximized (22.5°/112.5°/202.5°/292.5° and 67.5°/157.5°/247.5°/337.5°). Similar logic was applied in the case of variable error since the groups were created based on whether the SD was expected to be minimum (0°, 90°, 180°, 270°), maximum (45°/135°/225°/315°) or in-between (22.5°/112.5°/202.5°/292.5° and 67.5°/157.5°/247.5°/337.5°).

The last variable computed was the gain which is a measure of the contraction or expansion of directional space in the vicinity of a target (Krukowski & Stone, 2005) (Smyrnis, Mantas , & Evdokimidis, 2007). It is defined as the slope of the best fitting regression line for mean arrow directions at target x and its two neighbor targets $x-1$ and $x+1$. A gain of 1 shows no distortion of the directional space while a gain greater than 1 and less than 1 shows contraction and expansion respectively. Gain was used as the depended variable in a two-way ANOVA with target direction and location as the independent variables. In the analysis of the gain, the aforementioned pooling was used once more.

A total of 4416 trials for the central and 17519 for the peripheral condition were performed. In the latter case, 342 trials were removed as extreme values and another 211 were rejected through monitoring bringing the number of those available for analysis down to 16966 (96.84 % of the original). All statistical analyses were performed using the SPSS (IBM Corp, Released 2017) software.

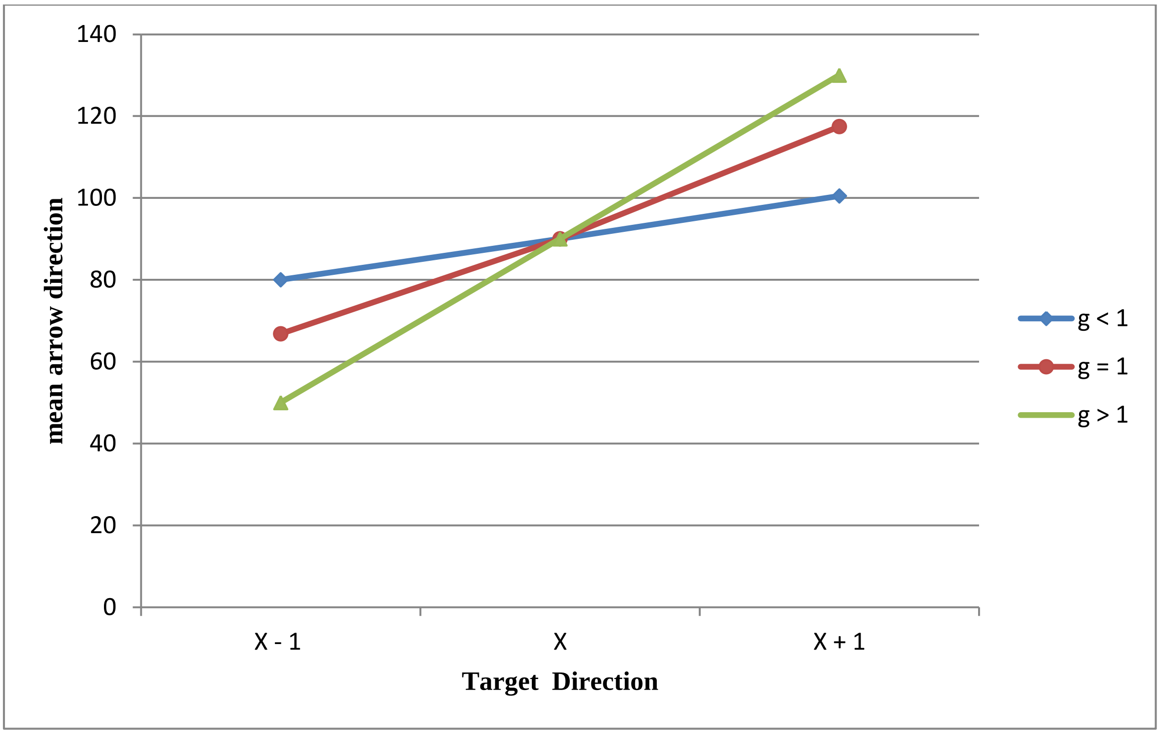

Figure 1 Sample computation of gain for target direction *x*, using the mean direction of arrow endpoints at neighboring directions *x*, *x – 1*, and *x + 1* and comparison for different gain values

Results

Central condition

This experiment repeats the results of previous studies by showing the mean of the DE to be significantly affected by the target direction (*F(15,285) = 19.77, p <.001,* η^2_p *= 0.51*). Furthermore as seen also in Figure (2A), the established pattern emerges, with mean direction being pushed away from the cardinal directions and towards the diagonals. Concurrently the SD of DE is also modulated by the target direction (*F(15,285) = 7.34, p <.001,* η^2_p *= 0.28*) and a clear oblique effect emerges, with a gradual increase of the SD as the direction moves away from the cardinal positions (Figure (2B)).

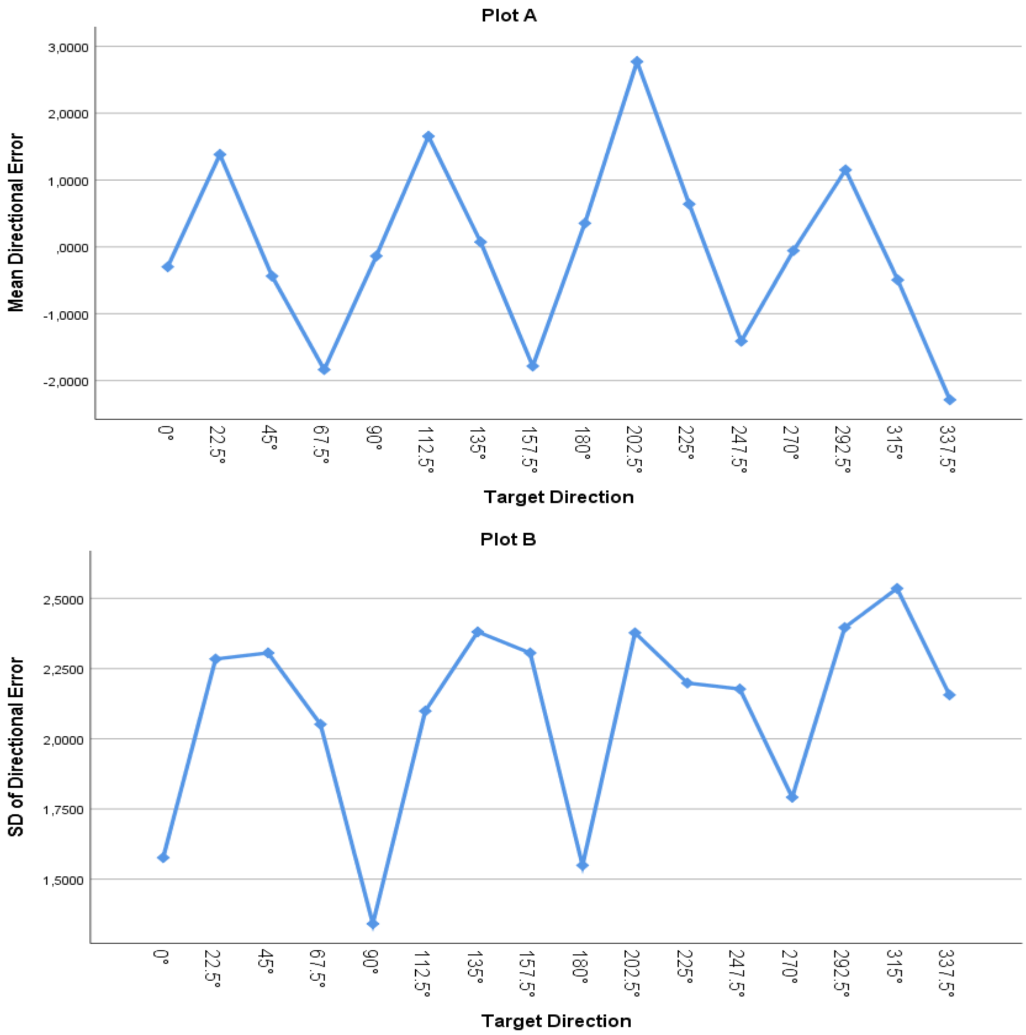

Figure 2 A: Plot of mean DE for arrow endpoints for all subjects for each target direction. B: Plot of SD of DE for arrow endpoints for all subjects for each target direction.

Peripheral Condition

Figure (3) shows the modulation of mean DE by target direction for each of the four locations. There is a significant effect of both the target direction (*F(15,285) = 14.51, p <.001*, η^2_p *= 0.29*) and the location (*F(3,57)= 7.83, p <.001*, η^2_p *= 0.43*) on the mean DE, while the interaction between those two is also significant (*F(45,855)= 12.72, p <.001* η^2_p *=0.40)*. The same figure also shows the modulation of the SD of DE by target direction for each of the four locations. There is a significant effect of both the target direction (*F(15,285) = 3.41, p <.001*, η^2_p *= 0.15*) and the location (*F(3,57)= 5.90, p =.001* η^2_p *= 0.24*) on the SD of DE, while the interaction between those two is not significant (*F(45,855)= 1.57, p =0.14).*

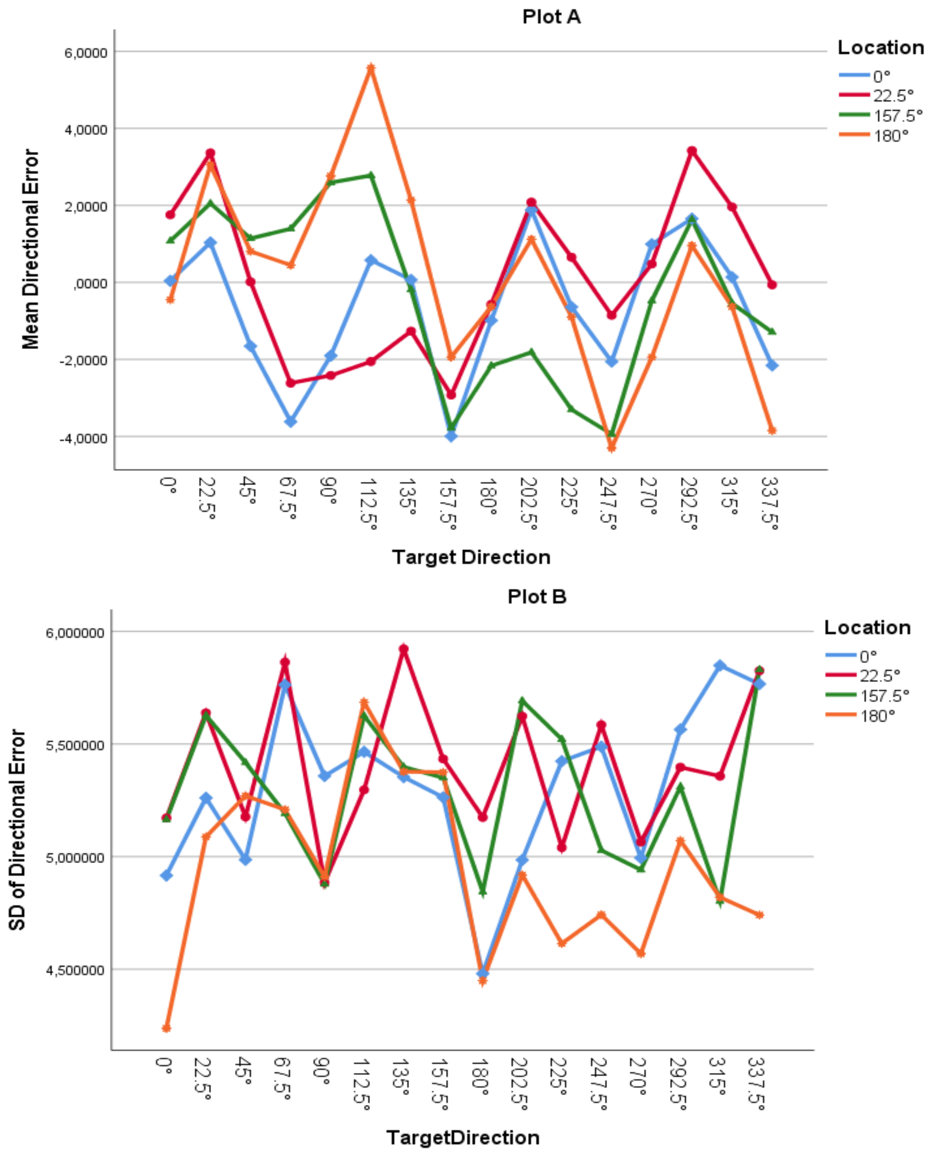

Figure 3 A: Plot of mean DE for arrow endpoints for all subjects for each target direction. B: Plot of SD of DE for arrow endpoints for all subjects for each target direction.

Using the grouping of directions as described in the Methods section and running the same analysis, once again there is a significant effect of both the target direction ($F(3,57)= 125.79$, $p <.001$, $\eta^2_p = 0.87$) and the location ($F(3,57)= 7.83$, $p =.001$, $\eta^2_p = 0.29$) on the mean DE, while the interaction between those two is also significant ($F(9,171)= 7.08$, $p <.001$, $\eta^2_p = 0.27$). This time, Figure (4A) demonstrates a familiar pattern emerging across all locations, in which mean DE tends towards zero in the cardinal and diagonal directions whereas there is a positive and negative peak for the diagonal directions as expected from a push away from the cardinal and towards the diagonal directions.

Analyzing the interaction effects confirms the qualitative observation. No significant difference between the Mean DE of the cardinal and diagonal directions group was found whereas maximum absolute values where found in the in-between directions, with all other pairwise comparisons being statistically significant. Furthermore, it is shown that the 0° and 180° peripheral locations have greater absolute mean DE values in the in-between oblique directions (22.5°/112.5°/202.5°/292.5° and 67.5°/157.5°/247.5°/337.5°) when compared to the 22.5° and 157.5° locations. The only exception to this finding is the value of mean DE for the 0° peripheral location at the 22.5°/112.5°/202.5°/292.5° directions group which does not differ statistically compared with the respective values of the 22.5° and 157.5° locations.

Figure (4B) shows the modulation of the SD the DE by target direction for each of the four locations when the grouping of directions is used. Similarly to the ungrouped results there is a significant effect of both the target direction ($F(3,57)= 16.88$, $p <.001$, $\eta^2_p = 0.47$) and the location ($F(3,57)= 4.47$, $p =.007$, $\eta^2_p = 0.19$) on the variance of DE, while the interaction between those two is not significant ($F(9,171)= 0.80$, $p =0.61$).

Figure (4C) shows the modulation of the gain by target direction for each of the four locations when the grouping of directions is used. Specifically there is a significant effect of both the target direction ($F(3,57)= 51.99$, $p <.001$, $\eta^2_p = 0.73$) and the location ($F(3,57)= 5.07$, $p =.008$, $\eta^2_p = 0.21$) on the mean DE, while the interaction between those two is also significant ($F(9,171)= 5.38$, $p =.001$, $\eta^2_p = 0.22$). Analysis of the interaction effect shows that the gain is maximum (and larger than 1) in the cardinal and minimum (and lower than 1) in the diagonal directions for all peripheral locations showing compression and expansion of the directional space respectively. The only exception to this finding is the case of the 157.5° location where the value of gain for the 45°/135°/225°/315° directions group which does not differs significantly with the value of gain for the 22,5°/112,5°/202,5°/292,5° directions

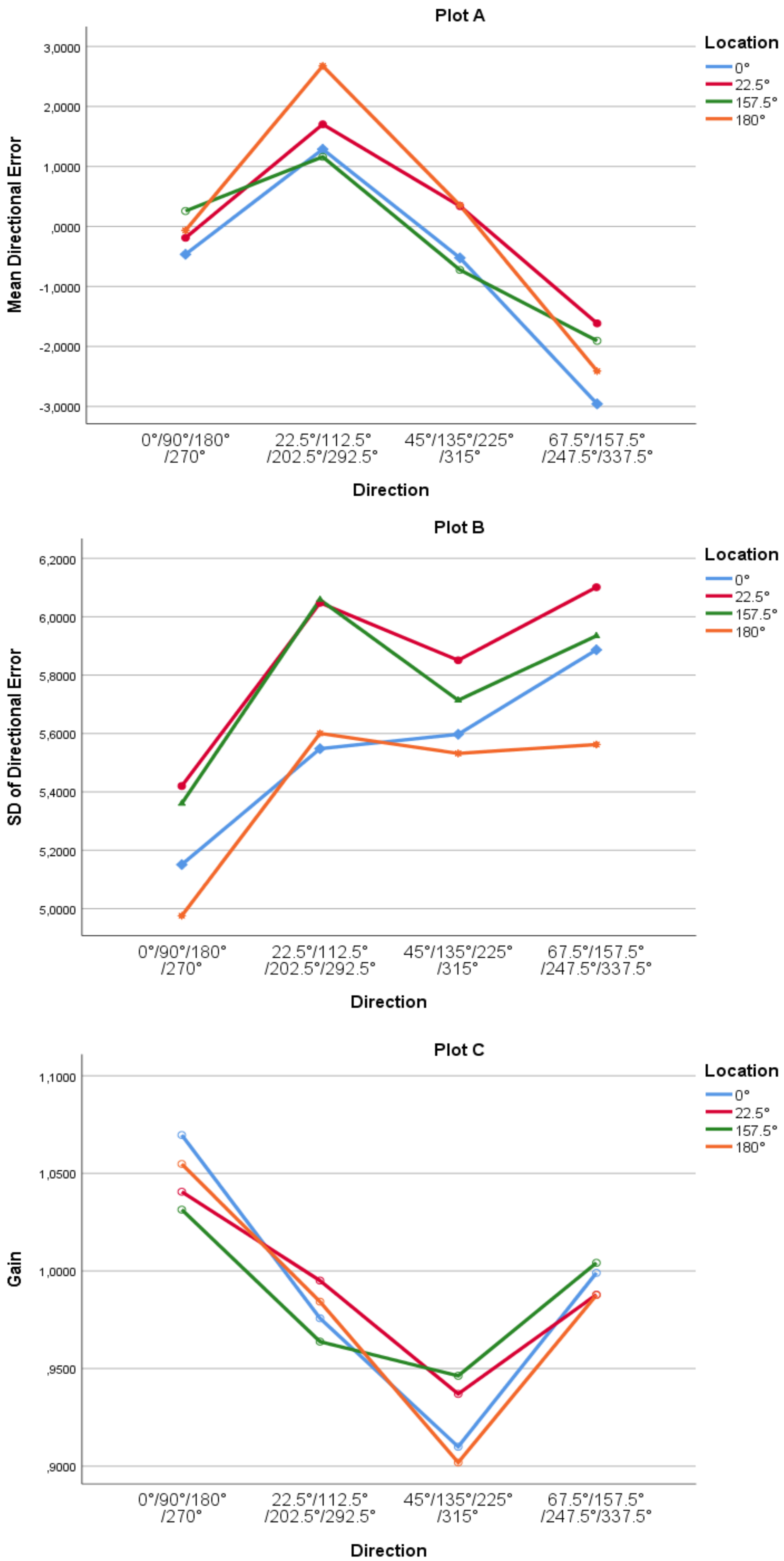

Figure 4 A: Plot of mean DE for arrow endpoints for all subjects for each directions group. B: Plot of SD of DE for arrow endpoints for all subjects for each directions group. C: Plot of Gain for all subjects for each directions group

group. Furthermore it is shown that the for the 0° and 180° locations the value of gain is greater in the 0°/90°/180°/270° and respectively lower in the 45°/135°/225°/315° directions group when compared with respective values of the 22.5° and 157.5° locations.

Figure (5) and Figure (6) show the results of two additional groupings that were performed after the evaluation of the previous results. In Figure (5) the values of the DE for the 0° location were grouped together with the values of the 22.5° location and the same was done for the values of the 157.5 ° and the 180° essentially creating a group with data for the right and the left side of the peripheral vision respectively. When compared against each other no differences were found.

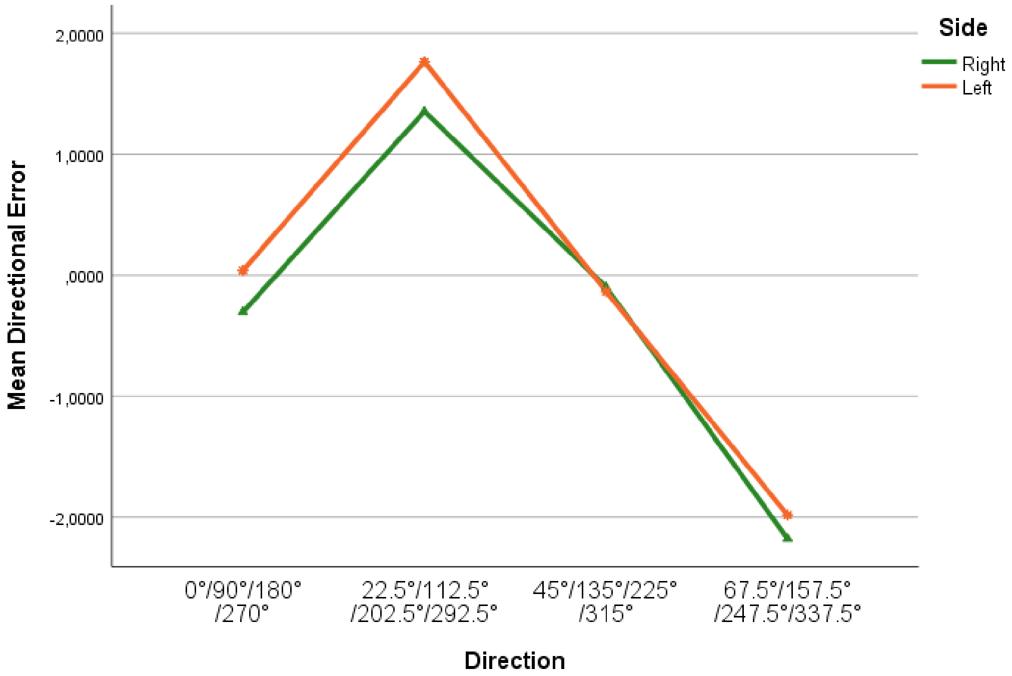

Figure 5 Plot of mean DE for arrow endpoints for all subjects for each directions group. Comparison between the right and left visual side.

The second grouping, shown in Figure (6) resulted in the creation of one group of values for the cardinal peripheral locations (0° and 180°) and one group for the values of the oblique peripheral locations (22.5° and 157.5°). It can be seen that even though the pattern of the systematic error is similar in both cases, the magnitude of it appears to be greater in the cardinal peripheral location. This is shown by the more flattened appearance of the lines of the peripheral oblique locations which is caused by having smaller deviations from the baseline of 0 in the case of the mean DE and the baseline of 1 in the case of the Gain.

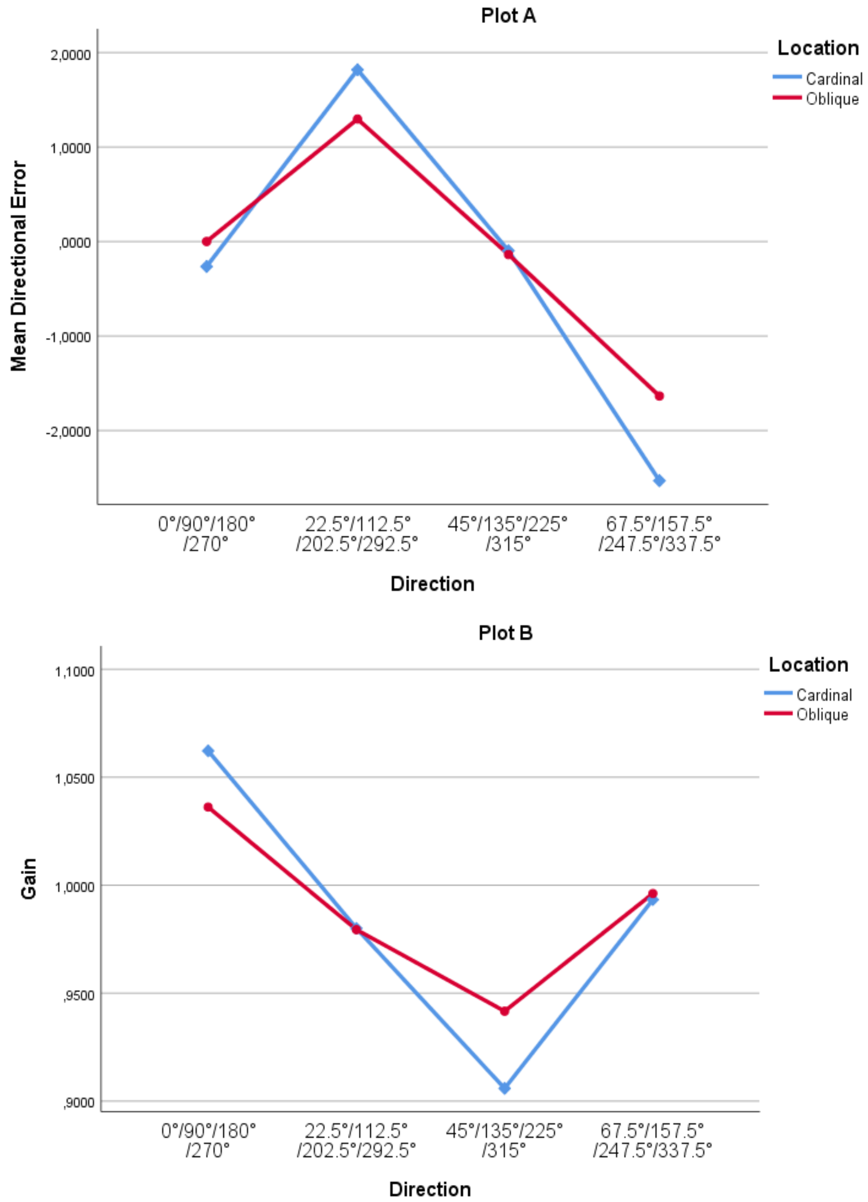

Figure 6 Comparison between the cardinal and the oblique peripheral locations. A: Plot of the Mean DE for the cardinal and oblique locations. B: Plot of the Gain for the cardinal and oblique locations.

Discussion

The present study utilized an arrow pointing paradigm (de Graaf, Sittig, & van der Gorn, 1991) (Smyrnis , Mantas, & Evdokimidis, 2014) in the periphery of vision in an attempt to investigate:

a) The existence of the systematic directional error in the peripheral vision, a pattern which it has been documented in many previous studies in the central vision (Huttenlocher, Hedges, & Duncan, 1991) (Huttenlocher J. , Hedges, Corrigan, & Crawford, 2004) (Smyrnis , Mantas, & Evdokimidis, 2014)

b) The existence of the radial bias.

c) The interaction between those two phenomena should both were to be demonstrated.

In this study, the Mean Directional Error and the Gain were used as measures of the systematic error and the Standard Deviation of the Directional Error was used as a measure of the radial bias.

Analysis of the Mean DE and the Gain showed a clear pattern of systematic DE emerging across all the tested locations. This pattern was manifested as a contraction of the directional space around the cardinal axes (the subjects' answers were pushed away from them) with a simultaneous expansion around the diagonal axes (the subjects' answers were pushed towards them). The interesting finding was that even though the pattern of the systematic DE was the same in all locations, there was a difference in the magnitude of the distortion of directional space. More specifically, expansion and contraction were lower in the case of the two oblique peripheral locations (22.5° and 157.5°) when compared with the two cardinal peripheral ones (0° and 180°).

A distortion in the pattern of systematic DE has been found in a study of arm movements in 2-D space (Gourtzelidis, Smyrnis , Evdokimidis, & Balogh, 2001). More specifically when a visual cue was introduced in the vicinity of some targets, a new pattern emerged in which minimal errors near the cue and a tendency for movement endpoints within the cue's quadrant to move away from the cue location were found.

In the present study however, no form of cue existed. According to theoretical models for the systematic error (Huttenlocher, Hedges, & Duncan, 1991) (Baud-Bovy & Gentaz, 2012), the cardinal axes are used as references in order to estimate the location of a stimulus when information about its true location is scarce. It could be the case that in the peripheral vision a new reference frame emerges that acts alongside the original one. This would consist of an axis that crosses through the centre of fixation and through the relevant peripheral stimuli and an axis perpendicular to it. In the case of the cardinal peripheral locations of this study, those axes essentially overlap with the cardinal ones and therefore no effect is expected. However, in the case of the oblique peripheral conditions those axes (the axis of 22.5° and 157.5° for both conditions in the present study) would create a separate reference frame which acting along the original one results in a "dilution" of its effects i.e. the relative flattening that is seen when the Mean DE or the Gain is plotted. A way to test whether such a hypothesis holds could be to repeat the experiment with more possible target directions (to see whether answers are pushed away or attracted by those axes) and in different distances compared to the centre of fixation (to see whether this effect is modulated by distance).

Regarding the second and third aims of this study, analysis of the SD of the DE showed a clear oblique effect, as the SD was significantly lower for cardinal directions in all test locations. No evidence of a radial bias was found. As it is not clear in which distance from the center of fixation the radial bias begins to take effect (Berkley, Kitterle, & Watkins , 1974) (Rovamo, Virsu, Laurinen, & Hyvdrinen, 1982), a possible explanation could be that the stimuli were too close to the center. A repeat of this experiment in greater distances could perhaps demonstrate a radial bias.

In conclusion, this study demonstrated the existence of the systematic DE in the peripheral vision. Its pattern is similar across all tested locations, but its magnitude was found to be lesser in the case of the oblique peripheral locations (22.5° and 157.5°). Simultaneously no evidence of radial bias was found.

References

Appelle, S. (1972). Perception and discrimination as a function of stimulus orientation:the "oblique effect" in man and animals. *Psychological bulletin*,. 266-278.

Balikou , P., Gourtzelidis, P., Mantas, A., Moutoussis, K., Evdokimidis, I., & Smyrnis, N. (2015, July). Independent sources of anisotropy in visual orientation representation: a visual and a cognitive oblique effect. *Exp Brain Res*.

Baud-Bovy, G., & Gentaz, E. (2012). The perception and representation of orientations: a study in the haptic modality. . *Acta Psychol*.

Baud-Bovy, G., & Viviani, P. (2004). Amplitude and direction errors in kinesthetic pointing. *Exp. Brain. Res.*

Berkley, M., Kitterle, F., & Watkins , D. (1974). Grating visibility as a function of orientation and retinal eccentricity. *Vision*, 239-244.

Boltz, R., Harweth, R., & Smith, E. (1979). Orientation anisotropy of visual stimuli in rhesus monkey: a behavioural study. *Science*.

Campbell, F., Kulikowski, J., & Levinson, J. (1966). The effect of orientation on the visual resolution of gratings. *Journal of Physiology*.

de Graaf, J., Sittig, A., & van der Gorn, J. (1991). Misdirections in slow goal-directed arm movements and pointer-setting tasks. *Exp Brain Res*.

de Graaf, J., Sitting, A., & van der Gon, J. (1994). Misdirections in slow goal-directed arm movements are not primarily visually based. *Exp Brain Res*.

Essock, E. (1980). The oblique effect of stimulus identification considered with respect to two classes of oblique effects. *Perception*.

Furmanski , C., & Engel, S. (2000). An oblique effect in human primary visual cortex. *Nature*, 535-536.

Gentaz, E., Baud-Bovy, G., & Luyat, M. (2008). The haptic perception of spatial orientations. *Experimental Brain Research*.

Gourtzelidis, P., Smyrnis , N., Evdokimidis, I., & Balogh, A. (2001). Systematic errors of planar arm movements provide evidence for space categorization effects and interaction of multiple frames of reference. *Exp Brain Res*, 139:59–69.

Huttenlocher, J., Hedges, L., Corrigan, B., & Crawford, L. (2004). Spatial categories and the estimation of location. *Cognition*.

Huttenlocher, J., Hedges, L., & Duncan, S. (1991). Categories and particulars: prototype effects in estimating spatial location. *Psychol Rev*.

IBM Corp. (Released 2017). IBM SPSS Statistics for Windows, Version 25.0. Armonk, NY: IBM Corp.

Jastrow, J. (1893). On the judgment of angles and positions of lines. *American Journal of Psychology*,

Kaspiris-Rousellis, C., Siettos, C., Evdokimids, I., & Smyrnis, N. (2017). Reaching to virtual targets: The oblique effect reloaded in 3-D. *Neuroscience*.

Koehn, J., Roy, E., & Barton, J. (2008). The “Diagonal Effect”: a Systematic Error in Oblique Antisaccades. *Journal of Neurophysiology* .

Krukowski, A., & Stone, L. (2005). Expansion of direction space around the cardinal axes revealed by smooth pursuit eye movements. *Neuron*.

Lashley, K. (1938). The mechanisms of vision: XV.Preliminary studies of the rat's capacity for detail vision. *Journal of General Psychology*.

Li, B., Peterson, M., & Freeman, R. (2003). Oblique Effect: A Neural Basis in the Visual Cortex. *Journal Of Neurophysiology*.

Liang, L., Zhang, M., & Pan, Y. (2017). Revealing the Radial Effect on Orientation Discrimination by Manual Reaction Time. *Front Neurosci*.

Luyat, M., & Gentaz, E. (2002). Body tilt effect on the reproduction of orientations: Studies on the visual oblique effect and subjective orientations. *Journal of Experimental Psychology: Human Perception and Performance*.

Mach, E. (1861). Über das Sehen von Lagen und Winkeln durch die Bewegung des Auges. *Sitzungsberichte Der Kaiserlichen Akademie Der Wissenschaften*,. Volume 43, Issue 2, Pages 215-224.

Mannion, D., McDonald, S., & Clifford, C. (2010). Orientation Anisotropies in Human Visual Cortex. *Journal of Neurophysiology*.

Mantas, A., Evdokimidis, I., & Smyrnis, N. (2008). Perception action interaction: the oblique effect in the evolving trajectory of arm pointing movements. *Exp Brain Res*, 605-616.

Mikhailova, E., Gerasimenko, N., Krylova, M., Izyurov, I., & Slavutskaya, A. (2015). Mechanisms of orientation sensitivity of human visual system: Part II. Neural patterns of early processing of information about line orientation. *Human Physiology*.

Nasr, S., & Tootell, R. (2012, October). A Cardinal Orientation Bias in Scene-Selective Visual Cortex. *The Journal of Neuroscience*.

Rovamo, J., Virsu, V., Laurinen, P., & Hyvdrinen, L. (1982). Resolution of gratings oriented along and across meridians in peripheral vision. *Ophthalmol.Vis.Sci.*, 666-670.

Shen, G., Tao, X., Zhang, B., Smith, E., & Chino, Y. (2014). Oblique effect in visual area 2 of macaque monkeys. *Journal Of Vision*.

Smyrnis , N., Mantas, A., & Evdokimidis, I. (2014). Two independent sources of anisotropy in the visual representation of direction in 2-D space. *Exp Brain Res.*, 2317-24.

Smyrnis, N., Gourtzelidis, P., & Evdokimidis, I. (2000). A systematic directional error in 2-D arm movements increases with increasing delay between visual target presentation and movement execution. *Exp Brain Re*.

Smyrnis, N., Mantas , A., & Evdokimidis, I. (2007). “Motor Oblique Effect”: Perceptual Direction Discrimination and Pointing to Memorized Visual Targets Share the Same Preference for Cardinal Orientations. *J Neurophysiol*, 1068–1077.

Sutheland, N. (1958). Visual discrimination of the orientation of rec-tangles by octopus vulgaris lamark. *J Comp Physiol Psychol*.

Sutherland, N. (1963). Cat's ability to discriminate oblique rectangles. *Science*.

Westheimer, G. (20003). The distribution of preferred orientations in the peripheral visual field. *Vision Research*.

Xiagmin, X., Collins, C., Khaytin, I., Kaas, J., & Casagrande, V. (2006). Unequal representation of cardinal vs. oblique orientations in the middle temporal visual area. *PNAS*, 17490-17495.