

Distortions in spatial perception accompany whole-field saccadic adaptation

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Saccadic eye movements are used to rapidly orient our gaze to objects and areas of interest, and occur in humans an estimated 150,000 to 250,000 times per day¹. Recently, some researchers have investigated the role of the saccadic system's plastic nature²⁻⁶ in the conscious perception of visual stimuli⁷⁻¹¹. These studies found perceptual misjudgments of stimulus location after the amplitude of a saccadic eye movement had been adapted to compensate for an artificially induced visual error. However, the capacity of motor adaptation to effect perceptual distortion remains unclear, as in these studies only one saccade vector was adapted, the perceptually judged stimuli were flashed only briefly, and misjudgments were usually found only in the presence of a saccadic eye movement⁸⁻¹¹ –a situation where perceptual illusions have also been demonstrated in the absence of saccadic adaptation¹²⁻¹⁵. Here we demonstrate clear evidence of distortions of perceived space following whole-field adaptation of either the horizontal or vertical component of observers' saccadic eye movements. Anisotropic amplitude reduction of observers' eye movements was induced by trans-saccadically shifting the search-display while

participants performed a visual search task⁶. Periodically during observers' adaptation, perceptual state was measured by having observers perform a two-alternative forced-discrimination of the relative lengths of the bars in a cross-figure. Results from the perceptual judgment trials demonstrate that observers' spatial perception of the cross-figure is progressively biased towards perceiving the cross-bar congruent with the adapted component as reduced in length relative to the other bar. These results along with results from previous studies suggest an overlap in the neural mechanisms that maintain the accuracy of saccades and spatial perception.

Each experimental session consisted of three saccadic adaptation blocks interleaved with four perceptual judgment blocks. Adaptation blocks encompassed 75 trials in which participants were instructed to indicate whether a display containing a set of items included a designated target item. During their search, participants were allowed to execute eye movements in any manner they deemed appropriate. To induce saccadic adaptation, we employed a new saccadic adaptation paradigm that we have recently demonstrated to generate uniform reduction of saccadic amplitude across all saccade vectors⁶, which can be thought of as a compression of saccadic motor space. In the present study, we compressed participants' saccadic motor space in the horizontal or vertical dimension during separate experimental sessions. To achieve this, items were uniformly shifted against the adapted component of the saccade by half its amplitude (e.g., a 5° rightward saccade during the horizontal adaptation condition would shift the display 2.5° to the left). Amplitude augmentation was not studied as other studies have found strong inconsistencies between amplitude reduction, augmentation, and the subsequent effects¹⁶⁻¹⁸. Figure 1 illustrates a sample saccade performed during a

horizontal adaptation session. Initially, this resulted in the adapted component of a saccade being perceived as too large since, prior to adaptation, participants' saccadic gain (ratio of saccade amplitude to target eccentricity) is approximately 1 for both components. In order for participants' saccades to land precisely at the intended location, a gain of 0.67 and 1 would be needed for the adapted and unadapted component, respectively. Participants' compensatory saccadic adaptation modifies their saccadic gain towards this pattern.

Adaptation to the display shift began to asymptote after approximately 150 trials to a mean gain of 0.84 and 0.75 (see Methods for measurement technique), which indicates that participants adapted to approximately 48% and 75% of the display shift during the horizontal and vertical adaptation sessions respectively. While the source of these horizontal-vertical adaptation differences is presently unknown, similar asymmetries have been previously reported in saccadic adaptation studies^{3,19,20}. Figure 2a illustrates the spatial specificity of participants' adaptation for both conditions. To facilitate analysis of participants' perceptual changes, we will consider horizontal gain changes as positive and vertical gain changes as negative (see Figure 2b).

Perceptual judgment blocks were designed to estimate participants' current spatial perception of the relative lengths of the horizontal and vertical bars of a 'cross-figure'. This was accomplished through the use of a staircase procedure that attempts to narrow in on the figure that participants perceived to be closest to having bars of equal length. Each perceptual judgment block encompassed 60 trials in which the participant had to make a two-alternative forced-choice perceptual discrimination by declaring either the horizontal or vertical bar of a cross-figure as the longer of the two. The discrimination

was to be made without the use of eye movements by fixating on a small dot located in the center of the cross-figure. Sixteen cross-figures, labeled as zero through fifteen, with relative lengths ordered from most vertically extended to most horizontally extended (see Methods for exact lengths) were available for presentation during the perceptual judgment blocks (see Figure 3c for example cross-figures); cross-figures 7 and 8 were closest to having equal length bars. For each perceptual block of trials, a sigmoid function was fitted to the percentage of trials in which the subject reported a longer horizontal bar (see Figure 3a for example curves). The perceptual index for that block was then operationally defined as the value at which the function crossed 50%; a perceptual index of 7.5 would represent veridical perception.

Despite a relatively large range of initial perceptual indexes, the mean perceptual index was nearly veridical in all conditions for the first (pre-adaptation) block of perceptual judgment trials, 6.5 ± 2.0 (s.d.) and 8.0 ± 2.6 during the horizontal and vertical adaptation sessions respectively. Relative changes in participants' perceptual index (Figure 3b) reveal a systematic shift in their perception of the relative bar-lengths in the cross-figures. During horizontal adaptation sessions, participants exhibit a general shift towards perceiving the horizontal bars of cross-figures to be shorter relative to the vertical bars than they had perceived them prior to adaptation, as evidenced by an increase in their mean perceptual index between the first and last perceptual judgment blocks by an average of 0.83. Reduction of participants' vertical saccadic component had the opposite effect on their spatial perception, as perceptual indexes decreased by an average of 2.14. While the perceptual changes relative to the pre-adaptation assessment were significant for both the horizontal condition, $t(23) = 2.44$, $p < 0.05$, and the vertical

condition, $t(23) = 4.97$, $p < 0.001$, the effect was stronger during the vertical condition than during the horizontal condition, $t(46) = 2.23$, $p < 0.05$, corresponding to the respective saccadic gain changes. Absolute changes in the perception of the relative bar lengths (horizontal: 0.45° ; vertical: 1.18°) were smaller than the absolute saccadic gain changes (average horizontal: 1.62° ; average vertical: 2.65°); that is, perceptual changes were 27% and 45% of motor changes during the horizontal and vertical adaptation sessions, respectively.

Figure 4 shows the relationship between changes in saccadic gain and spatial perception for both conditions of the task. The correlation between relative saccadic gain changes and the subsequent relative perceptual index changes is $r = 0.61$, $p < 0.0001$. Deviations in the relationship between whole-field adaptation and spatial perception are likely the result of noise in the data, as both measures are expected to contain substantial noise due to their complex nature³. A large portion of the variance in the perceptual indexes is due to one participant from each condition deviating from the general trend of perceptual changes. These divergences are presumably due to their use of different – possibly shifting– strategies to perform the perceptual judgment task.

We conducted a control experiment to verify that changes in perception were not simply due to the anisotropic motion of the search display. Again, separate sessions of horizontal and vertical display shifts were performed, but this time, the shifts occurred randomly (per trial) either with or against the relevant component of saccades. As expected, no significant change in saccadic gain was observed (horizontal condition: 0.02 ± 0.08 ; vertical condition: 0.03 ± 0.06). Supporting our hypothesis, there also was no

significant perceptual change (horizontal condition: -0.02 ± 2.23 ; $t(23) = 0.05$, $p > 0.9$; vertical condition: -0.02 ± 1.17 ; $t(23) = 0.09$, $p > 0.93$).

These data indicate that the demonstrated compression of saccadic motor space is accompanied by a compression of perceptual space. In the present study, post-saccadic visual error was imposed on all saccade vectors produced during a visual search task with randomly placed search items. Besides saccadic adaptation, this visual error induced a systematic distortion in the global perception of the large (approximately 15° in diameter) cross markers that were presented at different positions and height-to-width ratios. Since the perceptual judgment procedures lasted for more than two minutes and did not show a reduction in the perceptual effect over their duration, aftereffects cannot explain the current results. Thus, the present data suggest that the same signals that drive saccadic adaptation also contribute to a continuous remapping of visual-perceptual space that keeps our perceptual judgments accurate.

Previous studies on post-adaptation perceptual mislocalization of stimuli during fixation have only tested local effects by adapting individual saccade vectors, and yielded conflicting results. One important difference between the studies that find perceptual distortions (Moidell and Bedell's⁷ and the present study) and those that do not^{9,11} is the presentation duration of the perceptually judged stimulus. In our task, as well as Moidell and Bedell's, the duration of the perceptually judged stimulus was long enough (≥ 250 ms) for participants to spatially shift their attention; this was not the case in the other studies^{9,11}, where the stimulus was presented for 4 or 10 ms. This distinction seems to suggest that visual selection, such as the one that occurs immediately prior to a saccade²¹

or, alternatively, the one that occurs during covert shifts of attention^{22,23}, may be necessary for the remapping of saccadic motor space to affect perception.

Methods

Thirteen naïve students and one author (T. G.) from the University of Massachusetts Boston participated in the experiment; all had normal or corrected-to-normal vision. Participants sat in a dark room in front of a computer screen at a distance of 33 cm. Eye movements were recorded using the SR Research Ltd. Eye-Link II eye-tracker system. Stimuli were presented on a Dell P1130 monitor using a resolution of 1024 x 768 pixels and a refresh rate of 100 Hz. The maximum delay between participants' eye movements and the subsequent display shift was approximately 11 ms. A chin-rest was used to restrict head movements. Participants' responses were recorded using a keyboard and a handset.

Saccadic adaptation displays were prefabricated and consisted of either six or twelve items; half of the displays contained a target item. The minimum distance between neighboring items in the displays were 12.6° and 7.0° in the six- and twelve-item displays, respectively. Targets and distractors were small crosses (2° in diameter) with colored 'legs' such that distractors consisted of four distinct colors whereas targets only used three colors (one color was repeated). Participants completed each trial by pressing one button on the handset to indicate they believed a target item was present and another button otherwise.

Saccadic gain during the visual search task was measured for the first saccade of a series of one or more saccades that started within 2° from the center of an item and eventually landed within 2° of another item, which usually included one or more corrective saccades. Additionally, for a saccade to be included in the measure, its direction had to be within 20° of either the saccade target's initial or shifted position. These criteria were necessary to focus analysis on saccades for which we could confidently designate the target item.

Perceptual judgment displays consisted of a single cross-figure approximately 15° in diameter that was presented in a central position on the screen which included a slight, random offset between trials; a 1500 ms blank period separated consecutive trials. Participants were instructed to press one of two buttons on the keyboard to indicate which bar of the cross-figure they perceived as longer while maintaining fixation on a small dot in the center of the cross-figure; participants were given a maximum of five seconds to make their choice. A trial was discarded from analysis if the participant's fixation was further than five degrees from the center of the cross-figure. Participants that had 25% or more perceptual judgment trials discarded were excluded from analysis

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Acknowledgements

This research was funded, in part, by the U.S. Department of Education through a GAANN (Graduate Assistance in Areas of National Need) Ph.D. scholarship to Tyler W. Garaas.

Author Information

Experimental procedures were approved by the University of Massachusetts Boston IRB. Prior to data collection, all participants signed an informed consent form. Correspondence and requests for material should be addressed to tgaraas@gmail.com.

Figure Legends

Figure 1 Illustration of an unadapted saccade during adaptation of the horizontal component. **a**, Prior to the saccade, the participant is fixating on the item at position **F** and intends to shift his or her gaze to the item at position **T**. **b**, During the saccade (thin blue arrow), the entire stimulus panel (gray area) is shifted horizontally by half of the saccade's horizontal amplitude (indicated by the thick blue arrows). Once the participant's saccade has landed at the intended absolute position **T**, the intended item will be located at **T'**, resulting in a horizontal visual error. A corrective saccade, indicated by the dashed arrow, is then necessary to fixate the intended item, which would cause another display shift (not illustrated).

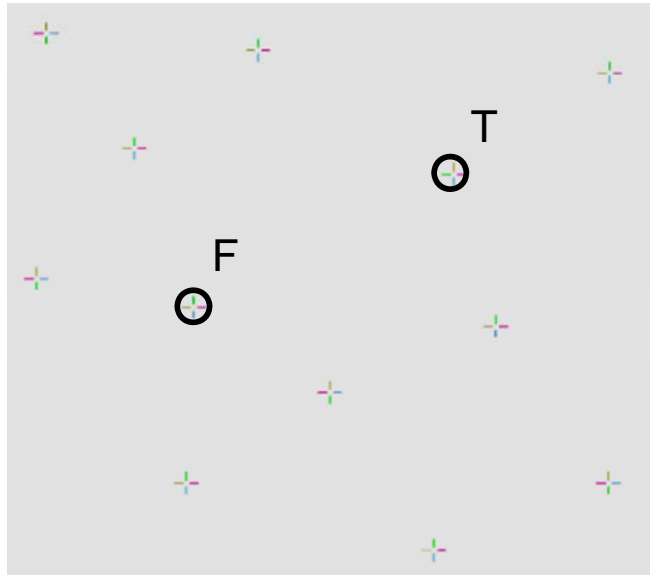
Figure 2 a, Saccadic gain measures grouped by 16 different oculocentric directions. Data points were obtained by individually multiplying each veridical location (black circles) by the horizontal and vertical gain values obtained from saccades $\pm 11.25^\circ$ from the direction of the veridical point. Error bars represent the standard error (s.e.m.). **b**, Individual and mean changes in saccadic gain for each adaptation block. Gain decreases in the horizontal saccadic component are represented by positive changes, and gain decreases in the vertical saccadic component are represented by negative changes.

Figure 3 a, Sample psychometric curves from the first and fourth perceptual judgment blocks, which represent perceptual indices 8.5 and 6.5, respectively.

b, Individual and mean perceptual index changes for each perceptual judgment block relative to the initial block. **C**, Cross-figures 0 and 15.

Figure 4 Relative saccadic gain changes in the adapted component for each adaptation block of the horizontal (positive values) and vertical (negative values) adaptation conditions plotted against the perceptual index changes for the subsequent perceptual judgment block; gain changes are averaged across the adaptation block. Positive perceptual changes indicate a bias towards perceiving cross-figures with longer horizontal bars to have equal-length bars. The data points are taken from eight participants' data for each condition, which includes three measurements per condition.

a



b

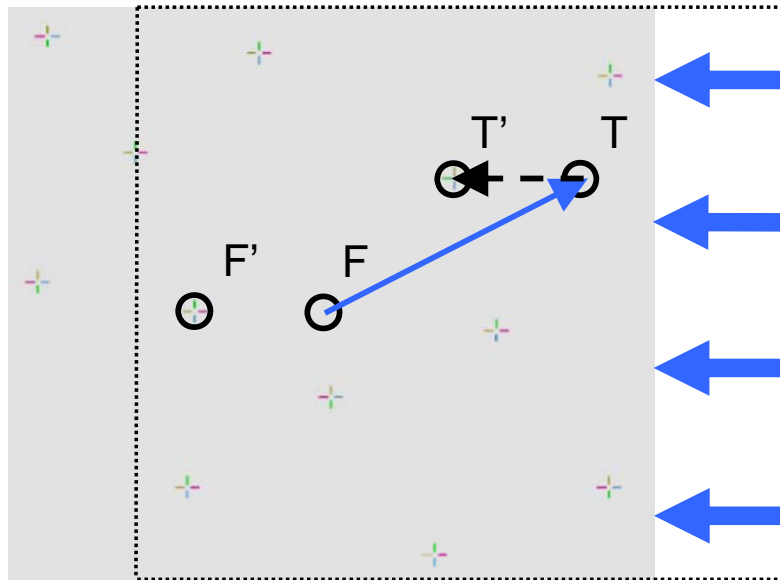


Figure 1

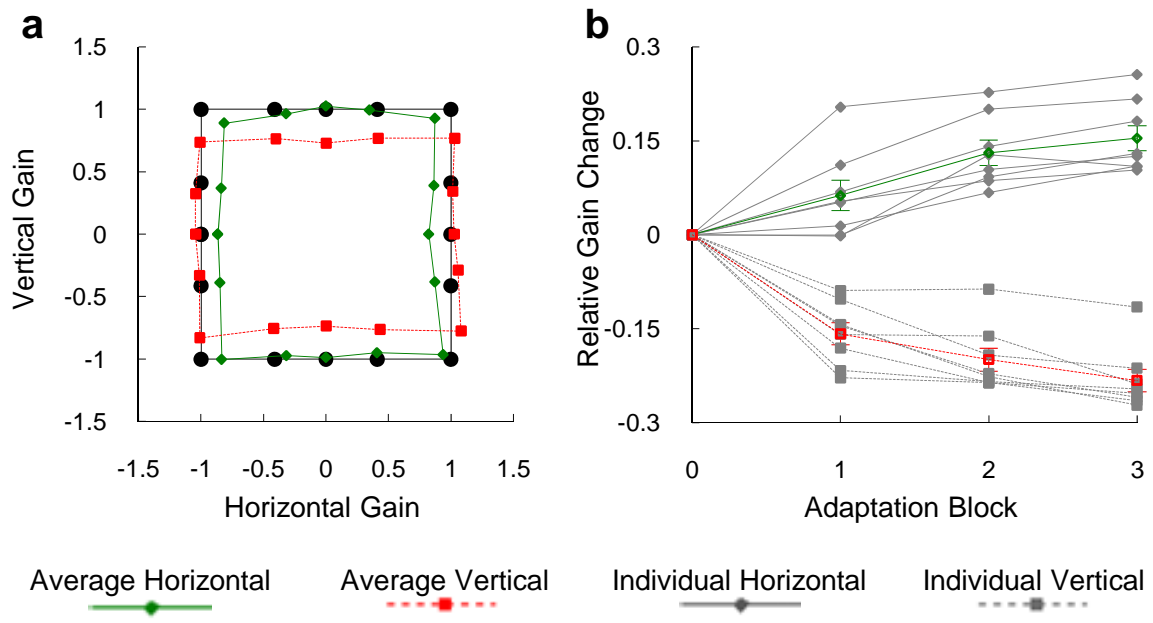


Figure 2

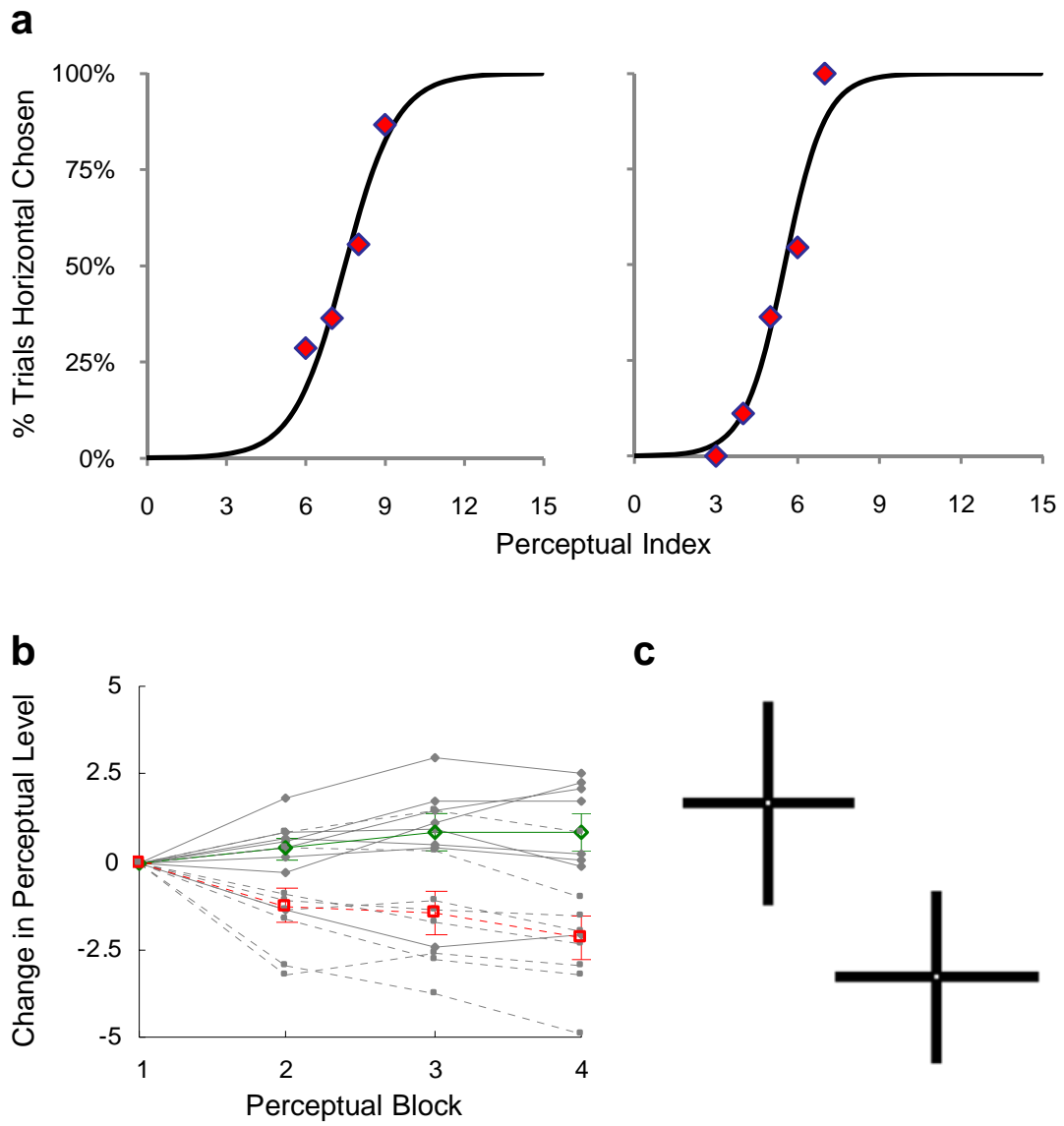


Figure 3

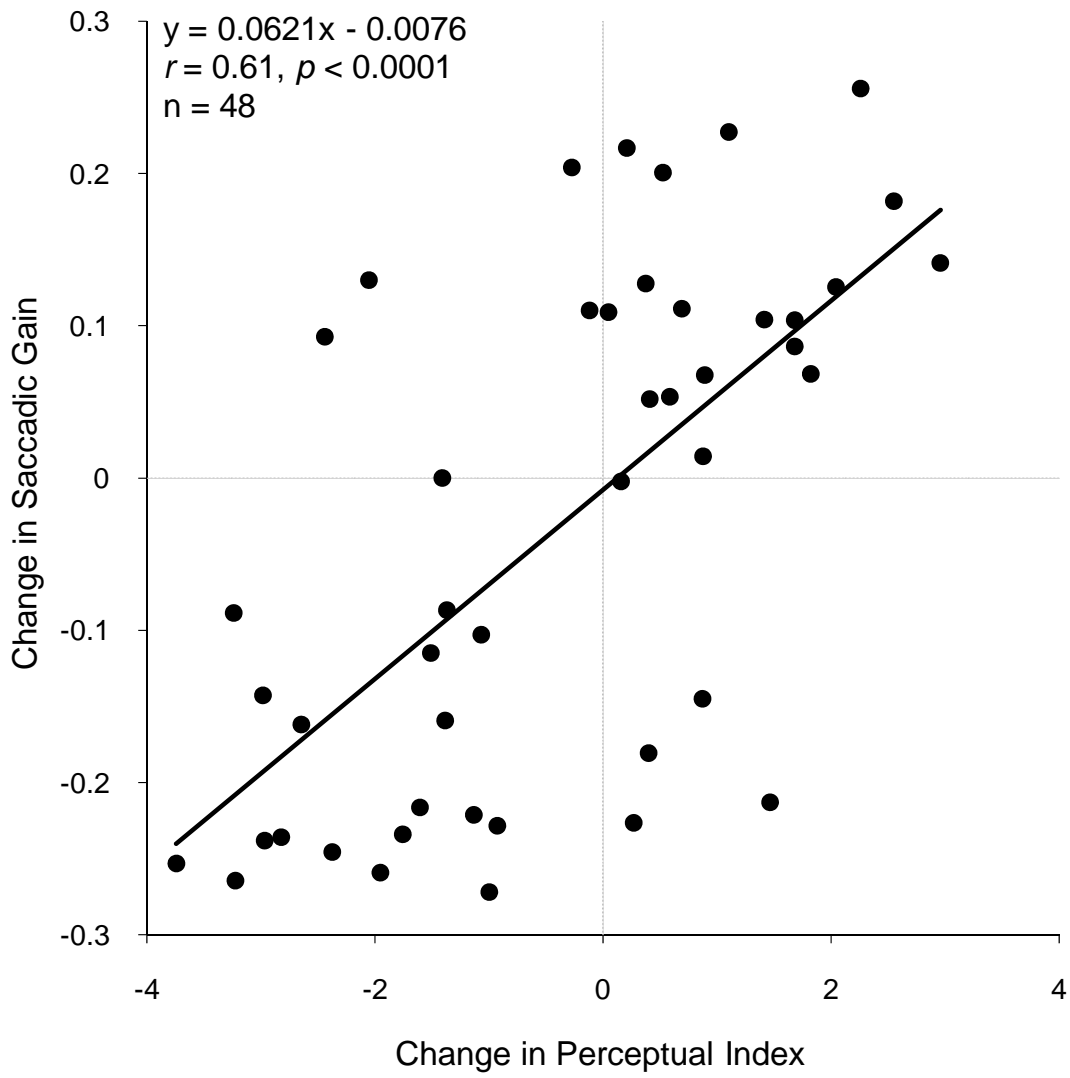


Figure 4