Natural viewing reshapes the spatial logic of ocular dominance plasticity

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Abstract

The adult visual system retains considerable plasticity: short-term monocular deprivation boosts the deprived eye and the earliest component (C1) of the visual evoked potential, suggesting homeostatic plasticity in V1. This effect is strictly retinotopic when gaze is fixed. But during natural vision, we constantly shift gaze, and spatial attention moves with gaze, anchoring perception to objects in the world via a world-centered reference frame rather than to retinal coordinates. Does retinotopic plasticity still govern short-term monocular deprivation under these conditions? Using virtual reality, we immersed participants in a naturalistic environment with gaze-contingent monocular deprivation during movie viewing. Strikingly, the deprivation effect was not retinotopic. However, when we eliminated world-centered reference information by anchoring the movie to the head, the retinotopic effect reappeared. These results show that ecological context dictates the spatial mapping of ocular dominance plasticity, implicating a role for higher-order processes in adapting to changes in visual input.

Full Text

Preamble

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Abstract

adult visual system retains considerable plasticity: short-term monocular deprivation boost deprived earliest component visual evoked potential, suggesting homeostatic plasticity effect strictly retinotopic fixed. during natural vision constantly shift gaze, spatial attention moves anchoring perception objects world world-centered reference frame rather retinal coordinates. retinotopic plasticity still govern short-term monocular deprivation under these conditions?

Using virtual reality, immersed participants naturalistic environment gaze-contingent monocular deprivation during movie viewing Strikingly, deprivation effect retinotopic.

However, eliminated world-centered reference information anchoring movie head, retinotopic effect reappeared These

results

ecological context dictates spatial mapping ocular dominance plasticity, implicating higher-order processes adapting changes visual input.

Keywords

ocular dominance plasticity, non-retinotopic, natural vision, binocular rivalry, virtual reality.

Introduction

often stronger other, phenomenon called ocular dominance. neural level, ocular dominance fixed birth develops postnatally.

Accordingly, ocular dominance plasticity served model studying neuroplasticity While foundational neurophysiological emphasized plasticity restricted critical period during early development Wiesel Hubel, later research beginning around revealed human visual system retains considerable ocular dominance plasticity adulthood. instance, monocular deprivation patching hours induces perceptual boost deprived Dong, Lunghi, Burr, Morrone, Zhou, Reynaud, Hess, behavioral effect accompanied enhancement earliest component visual evoked potential deprived which further indicat residual homeostatic plasticity primary visual cortex Lunghi, Berchicci, Morrone, Russo, Recent using controlled laboratory stimuli found effect short-term monocular deprivation strictly retinotopic, further supporting early locus Alais, MacDougall, Verstraten, However, while compelling, evidence comes controlled laboratory settings involving several minutes deprivation constrained fixation. contrast, traditional short-term monocular deprivation experiments Lunghi participants freely natural environments while performing everyday tasks real-world, active vision thought prioritize allocentric reference frame Chang Golomb, Chen, DeAngelis, Angelaki, Wexler, involves spatial attention tightly linked location current upcoming fixations Bushwell, Cohen, Botch, Robertson, Deubel Schneider, Henderson,

Moore Fallah, Motter Belky, 1998a 1998b Shinoda, Hayhoe, Shrivastava, Yarbus, concise historical overview well-established between visual attention, please refer ppendix Thus, remains untested whether strictly retinotopic plasticity triggered monocular deprivation natural vision this, present study combined virtual reality eye-tracking induce measure deprivation-induced plasticity under natural viewing conditions. developed gaze-contingent monocular deprivation paradigm deprive time, specific region visual field central, peripheral, entire field while participants watched movies manipulat reference frame, movie stimuli presented either world-fixed (i.e. world-centred) -locked (i.e. head-centered) manner. world-fixed movie stimuli displayed virtual office simulate naturalistic environment conducted experiments examine spatial mapping ocular dominance plasticity under reference frames

Method

Participants Twenty-nine participants males, females; years, range: recruited

Experiment

(immersive experiment). Twenty males, females) completed formal experiment.

Thirty-five participants males, females; years, range: recruited

Experiment

(head-anchored experiment), twenty-three completing

experiment

males, females). participants normal corrected-to-normal visual acuity history ocular surgery

visual dysfunction. study protocol approved (H24019, 03/13/2024) Institutional Review Board. participants their informed consent

after the

experiment

finished. 3

Apparatus

experiment

programmed conducted using Unity 2022.3.17f1 GL732W laptop.

Participants viewed stimuli virtual reality headset while having their tracked 60-Hz sampling rate. field resolution pixels refresh panoramic picture generate virtual scene Stimuli section below) taken Ricoh Theta camera.

Stimuli Binocular rivalry Ocular dominance assessed using binocular rivalry. orthogonal grayscale sinusoidal gratings orientation, Michelson contrast) presented midgray background. gratings displayed either central (cVF; eccentricity) peripheral visual field (pVF; eccentricity along horizontal meridian) assess ocular dominance separately location (Figure grating consisted cycles scaled account cortical magnification subtending central visual field periphery. central fixation point diameter) included; turned deviation exceeded promote stable binocular fusion, stimuli surrounded checkerboard frame Michelson contrast.

Monocular deprivation

There conditions deprivation (Figure condition depriving central visual field, condition depriving peripheral visual field, condition depriving whole visual field typical monocular deprivation paradigm.

During deprivation, participants watched video clips comedy series. video subtended conduct deprivation, black manipulable transparency additionally presented monocularly deprived Under condition, gaze-contingent, whose transparency uniform eccentricity (completely opaque transparent) linearly gradient opposite transparency beyond within gaze-contingent could cover location either grating binocular rivalry never (Figure retinal locations deprived condition.

Under condition whole fully opaque deprived could nothing black.

Illustration stimulus experimental procedure. Stimuli

experimental phases superimposed comparison. elements denote grating stimuli binocular rivalry task. elements indicate parameters related monocular deprivation (MD). central (CENT; shown example) peripheral (PERI) deprivation conditions, opacity uniform within linearly ramped between reversed beyond Schematic formal experimental session. shown dominant example.

Stimulus sizes drawn scale. non-dominant Schematic deprivation under immersive viewing.

Schematic deprivation movie head-anchored environmental removed.

Experiment

movie presented virtual office within immersive environment rendered spherical panorama (Figure rotation translation) tracked time, allowing participants naturally explore scene while sitting swivel chair; thus, because natural movements, movie always centered participant visual field.

Experiment

movie (size matched) fixed front against black

background

(Figure tracking disabled, turning headset head-mounted display stationary viewpoint.

Across experiments, gaze-contingent masks accurately deprived specified retinal regions time.

Procedure Practice phase participant completed practice sessions binocular rivalry task, separate Dong, Engel, Jiang, session included warm-up

block trials followed three practice blocks trials each).

Before block, 5-point eye-tracking calibration (error performed. trial began preparation screen indicating grating location (center, left, right).

Participants initiated trial keypress; trials lasted Throughout trial, participants continuously reported their perceived orientation holding left, right, mixed) while maintaining fixation.

Breaks provided between blocks. grating location eye-orientation assignments counterbalanced within block. dominance ratio computed block

$$\text{LvsR} = \quad \text{LE} + \quad \text{mixed} /2$$

mixed where mixed represent total dominance durations right mixed percept, respectively. third session onward, participants proceeded

experiment

maximum across three blocks within minimum. dominant determined based practice session. value greater indicated left-eye dominance, whereas value indicated right-eye dominance. those participants criteria seventh session, required experiment.

Formal phase formal

experiment

comprised sessions separate days, monocular deprivation condition. order conditions counterbalanced across participants. session began 6-trial warm-up block inocular rivalry test.

After 5-minute break, participants completed pre-deprivation inocular rivalry block, 2-hour monocular deprivation period, post-deprivation binocular rivalry block without

interruption. binocular rivalry blocks identical those practice phase. nasal visual field within binocular overlap known sensitive interocular imbalance temporal field Bowering, Maurer, Lewis, Brent, Tieman, Tumosa, Tieman, gratings presented temporal hemifield dominant (e.g., visual field dominant; Figure every participant, preventing

introduction

inter-subject variability could arise randomly stimulating nasal temporal hemifields varying sensitivity. during practice, grating location eye-orientation pairing counterbalanced across trials. 5-point eye-tracking calibration performed before binocular rivalry tests monocular deprivation sessions.

Throughout monocular deprivation, video paused automatically either remained closed seconds, resumed reopened.

analysis

participant completed formal experiment, angle during binocular rivalry tests examined (Figure median angle (MGA) first determined trial.

Then, among trials pooled binocular rivalry blocks (pre- post-tests conditions), calculated trials trials, respectively. participants whose either exceeded average standard deviation rejected. total, participants

Experiment

participants

Experiment

excluded, leaving participants subsequent analyses

Experiment

respectively. measure ocular dominance, ocular dominance index (ODI) calculated

below binocular rivalry block participant,

ODI = DE DE + NDE

where summed phase duration participant reporting perceiving grating orientation dominant non-dominant respectively. shift ocular dominance after monocular deprivation measured ODI = first examined against one-sample -tests submitted (Testing Location: (Deprivation Condition:

CENT, PERI, FULL) repeated measures ANOVA Greenhouse-Geisser correction performed where necessary.

Effect sizes reported Cohen -tests partial squared ANOVAs. stability during binocular rivalry tests.

Across panels, median angle (MGA) lines normalized result. pairs labeled average indicates

Bayes factors provided. performed standard inferential approach Bayes factor Doorn quantify relative evidence provide alternative hypothesis Bayesian analyses conducted using JASP. one-sample -tests, computed which suggests probability generated under compared repeated-measures ANOVA, report inclusion Bayes factors which represent evidence including particular effect across matched models. preferred model selected based minimum Akaike information criterion (AIC), which model without random slopes. quantifying evidence effect, greater supports alternative hypothesis.

Following conventional interpretation, values between considered evidence, values between moderate evidence, values greater strong evidence; similarly, below provides evidence favor hypothesis Doorn

Results

immersive environment rendered spherical panorama. rotation (though translation) tracked time, allowing participants naturally explore scene while sitting chair Monocular deprivation applied gaze-contingently under three conditions (Figure opaque gradient transparent (transparent gradient opaque (full-field opaque mimicking traditional monocular deprivation Throughout viewing, masks dynamically deprived specified retinal regions (Video S1-S3) condition selectively deprived currently fixated/ attended region,

while condition deprived unattended peripheral vision.

These designs allowed whether retinotopically specific plasticity emerge under natural vision whether depriving attended versus unattended regions differentially modulate ocular dominance compared deprivation. inocular rivalry measured orthogonal gratings central (cVF) peripheral (pVF) visual fields before after hours deprivation. immersive setting (Experiment two-way repeated-measures ANOVA change ocular dominance index showed significant effects Deprivation Condition 6.73, 0.007, 0.30, 9.34) Testing Location 4.99, 0.040, 0.24, 0.97), while interaction significant 2.68, 0.096, 0.14, 1.59). shown Figure deprivation significantly shifted ocular dominance towards deprived (one-sample t-tests comparing values against 0.068, [0.016,0.086], 3.11, 0.007, 0.75, 7.47, moderate evidence Surprisingly found similar ocular dominance shift 0.032, [0.001, 0.034], 2.23, 0.041, 0.54, 1.73, evidence where visual input across actually balanced during deprivation. finding strongly challenges notion strictly retinotopic monocular deprivation effect under natural viewing conditions

Ocular dominance changes after gaze-contingent monocular deprivation.

Under immersive iewing, deprivation boosted deprived dominance deprivation showed significant effect either testing location. movie head- anchored environmental removed, deprivation produced effects Conversely, deprivation produced effects Across panels, Circles indicate individual data. 0.05, 0.01,

*** $p < 0.001$; n.s. , not significant. 7

contrast deprivation yielded significant effects either 0.082, [0.044, 0.040], -0.08, 0.934, 0.02, 0.25, moderate evidence 0.079, [-0.033, 0.049], 0.42, 0.680, 0.10, 0.27, moderate evidence despite visual input deprived blocked during deprivation again contradicts notion retinotopic specificity monocular deprivation effect Notably, negative finding cannot simply ascribed insufficient statistical power, because deprivation, ocular dominance increased significantly deprived 0.064, 0.040, 0.106], 4.73,

0.001, 1.15, 137.45, strong evidence 0.040, [0.013, 0.054], 3.45, 0.003, 0.84, 13.71, strong evidence non-retinotopic effects contrast sharply recent study where participants maintained central fixation while viewing artificial laboratory stimuli whether viewing naturalistic movies caused discrepancy, conducted

Experiment

separate group participants. presented movie centered head-mounted display, thereby anchoring head-centered reference frame.

Additionally, surroundings replaced black

background

eliminate environmental cues. shown Figure two-way repeated-measures ANOVA revealed significant effect Deprivation Condition 5.72, 0.012, 0.25, 3.85) significant interaction between Deprivation Condition Testing Location

4.92, 0.017, 0.22, 10.04). effect Testing Location significant 0.01, 0.941, 0.01, 0.29).

Unlike

Experiment

lthough deprivation significantly shifted ocular dominance towards deprived 0.024, [0.007, 0.032], 3.40, 0.003, 0.80, 12.94, strong evidence effect significant 0.020, [-0.004, 0.016], 1.22, 0.241, 0.29, 0.46, evidence Moreover, deprivation produced significant change ocular dominance 0.020, [0.003, 0.023], 2.79, 0.013, 0.66, 4.37, moderate evidence 0.024, [-0.015, 0.010], -0.44, 0.668, 0.10, 0.27, moderate

evidence Again, deprivation induced significant effects 0.033, [0.007, 0.041], 3.04, 0.007, 0.72, 6.85, moderate evidence 0.032, [0.007, 0.039], 3.04, 0.007, 0.72, 6.80, moderate evidence brief, unlike immersive setting, ocular dominance shifted significantly toward deprived those visual field locations where monocular input deprived, significant shift observed locations where inputs remained intact eyes.

Discussion

Contrary monocular deprivation effects intrinsically retinotopic, found retinotopic organization dissolve allocentric spatial present.

Thus, distinct plasticity pattern observed immersive

experiment

compared attributed engagement allocentric reference frame processing, process gated availability spatial cues. propose engagement mediated attentional allocation which under natural viewing conditions automatically directed toward foveated region Bushwell, Cohen Deubel Schneider, Henderson, Moore Fallah, Motter Belky, 1998a 1998b Shinoda Yarbus, Consistent account, deprivation attended central region shifted occular dominance non-deprived peripheral locations, whereas deprivation unattended peripheral regions produced significant changes. ttention therefore, emerges modulator monocular deprivation effects, likely operating through neural mechanisms receptive

fields extend beyond classical retinotopic boundaries. andidate neural substrate non-retinotopic attentional modulation include posterior parietal cortex (PPC) strongly connected regions frontal cortex (e.g. supplementary field) where neurons characterized large, often bilateral receptive fields Andersen, Snyder, Bradley, Xing, Colby, Rawley Constantinidis, These regions well-positioned support allocentric processing through egocentric-to-allocentric coordinate transformations, readout allocentric representations, attentional modulations related these representations. immersive experiment, allocentric attentional modulations provide parsimonious account non-retinotopic effects observed Specifically, condition entire visual scene including masked fovea deprived other visible regions represented allocentric coordinates.

Furthermore, stable environmental could reinforce allocentric anchoring Golomb, Chun, Mazer, McConkie Currie, Sasaki, Anzai, Angelaki, DeAngelis, Since top-down spatial attention during natural viewing mainly deployed fovea Bushwell, Cohen Deubel Schneider, Henderson, Moore Fallah, Motter Belky, 1998a 1998b Shinoda Yarbus, foveal inputs deprived created attentional imbalance between eyes.

According homeostatic theory Castaldi, Lunghi, Morrone, Turrigiano, would trigger compensatory feedbacks fronto-parietal regions early visual cortex.

However, these feedback signals appear retinotopic specificity, potentially their allocentric origin large receptive fields. condition,

foveal inputs remained intact eyes, resulting balanced attentional distribution across consequently visual system registered engage homeostatic compensation attentional control level Surprisingly, higher-level processing virtually overrode local monocular deprivation effects ultimately yielding effects central peripheral visual fields.

Converesly movie fixed head-centered position environmental removed, coordinates became egocentric rendering allocentric reference frame redundant Accordingly, top-down spatial attention operated native retinotopic reference frame Golomb Golomb, Pulido, Albrecht, Chun, Mazer, Moreover, participants movie central vision current upcoming fixations defined retinotopically, which supported retinotopic attention processing Therefore, ensuing homeostatic compensation ultimately exhibited strict retinotopic specificity Mounting evidence recent studies shown adult ocular dominance plasticity induced attentional imbalance between despite balanced visual input Song, Dong, Song, Song, Zhao, Song, Wang, Wang, McGraw, Ledgeway, remained unknown whether attention modulates plasticity induced traditional monocular deprivation. recent study demonstrated feature-based attention modulate short-term monocular deprivation effects Wang, However, relied artificial stimuli tasks, leaving unclear whether attention operates during natural vision. present study, using virtual reality mimic natural viewing, attention critical driver short-term monocular deprivation, operates

through previously unrecognized mechanism involving flexible reference frames.

Contribution eptualized research; X.H., W.N., engineered gaze-contingent monocular deprivation software; designed experiments; X.H., L.C., performed experiments; analyzed data; curated maintained data, X.H., W.N., wrote article.

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A ppendix: Gaze and Visual Attention 15

During natural vision, actively direct towards important interesting scene regions biological constraint acuity fovea Henderson, Therefore, natural vision essentially goal-directed active process, indicat close between visual attention. early investigation gaze-attention relationship traced Buswell Bushwell, Yarbus (1967), final chapter book, profoundly contributed later research equating fixation visual attention, using fixation duration quantify attentional deployment Yarbus, Yarbus documented findings bearing amazing resemblance later known characteristics visual attention. instance, observers fixated longer elements conveyed essential information despite having fewer details hunters bears Fig.s 113), pattern align function attentional selection.

Furthermore, fixations horizon suggested observer hoping something

important there, reflecting top-down attentional control. viewing Repin Unexpected Visitor fixation patterns varied dramatically depending observer task, demonstrating goal-directed attention. seminal pioneered

methodology

studying attention through movements profoundly influenced diverse fields visual search Motter Belky, 1998a 1998b real-world tasks driving Shinoda Since fixation represents focal attention, making saccade object towards another would shift attention object.

Psychophysical demonstrated visual attention saccade programming obligatorily coupled, suggesting single attentional mechanism controlling selection objects perceptual processing provision information motor action Deubel Schneider, Causal evidence comes monkey studies where stimulating frontal field, known saccade programming, improved attentional performance visual locations Moore

Fallah, Thus, converging evidence behavior neural mechanisms firmly establishes tight coupling between visual attention.

Note: Figure translations are in progress. See original paper for figures.

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