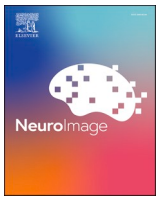
NeuroImage 339 (2026) 122184

Contents lists available at ScienceDirect

NeuroImage

journal homepage: www.elsevier.com/locate/ynimg



GABAergic fluctuations predict mixed perception during binocular rivalry

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ARTICLE INFO

Keywords:
Binocular rivalry
Excitatory/inhibitory balance
Mixed perception
Individual differences

ABSTRACT

Binocular rivalry occurs when two eyes compete for perceptual dominance, leading to alternating awareness of incompatible images over time. Previous studies have linked GABA+ concentrations in the visual cortex to rivalry dynamics and perceptual suppression, but it remains unclear whether perceptual changes are better explained by shifts in excitatory/inhibitory (E/I) balance or by neurochemical responses within specific pathways. Here, we use magnetic resonance spectroscopy to measure concentrations of Glx (glutamine + glutamate) and GABA+ in the visual cortex and a binocular rivalry paradigm to evaluate the effect of 60-min dark exposure on mixed perception and corresponding shifts in neurochemical concentrations in 14 normally sighted observers. Dark exposure increased the proportion of mixed perception and elevated Glx concentrations but did not produce significant changes in GABA+ concentrations or net E/I balance, as indexed by the Glx/GABA ratio. Dark exposure also did not significantly alter ocular dominance, phase durations, rivalry dynamics or perceptual alternation rates. Despite the absence of a group-level GABA+ effect, individual differences in mixed-perception changes were strongly associated with the magnitude of GABA+ fluctuations, whereas no comparable relationship was observed for Glx. These findings suggest that perceptual changes following dark exposure are more closely related to individual differences in GABA+ responses than to mean shifts in E/I balance. More broadly, the results suggest that binocular rivalry may be influenced by specific neurochemical responses that are not captured by directional measures of E/I balance alone, revealing a more nuanced relationship between neurochemistry and binocular perception.

Introduction

Binocular rivalry occurs when two eyes compete for perceptual dominance, leading to alternating awareness of incompatible images over time (Leopold and Logothetis, 1996; Tong and Engel, 2001; Tong et al., 2006). During rivalry, one image typically dominates awareness while the other is suppressed, such that even salient stimuli can temporarily disappear from conscious perception (Blake, 1989; Fang and He, 2005; Alais, 2012). Reciprocal inhibition model of binocular rivalry proposes that these perceptual alternations arise from reciprocal inhibitory interactions between neural populations representing the two eyes, often coupled with adaptation that destabilizes the dominant population over time (Blake, 1989; Alais, 2012; Said and Heeger, 2013; Brascamp, Becker and Hambrick, 2018). Within this framework, stronger interocular suppression promotes exclusive perceptual dominance, whereas weaker suppression allows information from both eyes to reach awareness concurrently in a single image, increasing mixed perception in the form of superimposed or piecemeal percepts (Laing and Chow, 2002; Klink et al., 2010; Seely and Chow, 2011; Said and Heeger, 2013).

Empirical studies examining neurochemical markers in primary visual cortex (V1) through magnetic resonance spectroscopy (MRS) have linked higher GABA concentrations to stronger interocular suppression during rivalry (Robertson, Ratai and Kanwisher, 2016) and slower perceptual dynamics during bistable perception characterized by longer percept durations and fewer perceptual switches (van Loon et al., 2013). Furthermore, pharmacological studies confirm a causal link, reporting that targeting GABA receptors (e.g., $GABA_A$ and $GABA_B$), which can potentially increase inhibitory signaling, can enhance suppression (Mentch et al., 2019) and delay rivalry dynamics (van Loon et al., 2013). Although MRS-derived GABA concentrations do not directly measure inhibitory neurotransmission in the human brain, these findings suggest that neurochemical concentrations related to excitation and inhibition

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https://doi.org/10.1016/j.neuroimage.2026.122184
Received 7 April 2026; Received in revised form 8 August 2026; Accepted 25 August 2026
Available online 26 August 2026

in the visual cortex contribute to binocular perception during rivalry, with higher GABA concentrations associated with stronger perceptual suppression and slower dynamics.

However, recent studies challenge this deterministic relationship between neural E/I balance and visual suppression (Lagas et al., 2016; Abuleil, McCulloch and Thompson, 2021; Min et al., 2023). For example, continuous theta-burst stimulation has been reported to increase GABA concentrations in visual cortex (Stagg et al., 2009) and reduce cortical excitability (Allen et al., 2014), yet paradoxically increases mixed perception (Abuleil, McCulloch and Thompson, 2021), contrary to predictions of binocular rivalry models (Mentch et al., 2019). Similarly, another study using functional MRS indicates that individual concentrations of GABA are not linked to rivalry dynamics (Choi et al., 2020). Moreover, recent work reported weaker associations between GABA levels in the occipital cortex and bistable perception than previously reported, suggesting that GABA concentrations alone may not reliably predict perceptual dynamics (Sandberg et al., 2016). Additionally, while perceptual gains from increased neural excitation have been reported (Dinse, Höffken and Tegenthoff, 2023), enhanced inhibition has also been shown to improve perception (Edden et al., 2009). These findings demonstrate that a specific direction of MRS-derived neurochemical changes does not lead to consistent perceptual outcome in binocular visual processing, indicating that the relationship between neurochemical states of E/I balance and binocular perceptual outcome is more complex than previously assumed.

Most studies have interpreted neurochemical changes primarily in terms of the direction of E/I balance shifts, but whether the magnitude of pathway-specific neurochemical responses predicts corresponding perceptual changes remains unexplored. Given that glutamatergic and GABAergic metabolites are metabolically coupled and often co-vary within visual cortex (Steel et al., 2020; Rideaux et al., 2022), a single estimate of E/I balance may obscure biologically meaningful differences (Dehghani et al., 2016). The same apparent shift in MRS-derived E/I balance can arise from different neurochemical changes; for example, an increase in Glx and a decrease in GABA+ may both be interpreted as shifts toward greater excitation within an E/I framework, yet they may have different functional consequences (Rae, 2014). MRS measures metabolite concentrations across neuronal populations, so individual differences in the magnitude of neurochemical change may provide information that are not apparent from the net direction of E/I balance changes alone. Absolute change therefore provides an operational measure of response magnitude, without implying that increases and decreases have equivalent biological effects. Consistent with this possibility, Min et al. (2023) showed that 60 min of dark exposure increased Glx concentrations without reliably changing GABA in the visual cortex, and that the magnitude of Glx change predicted the magnitude of deprivation-induced plasticity measured with a binocular phase combination task (Min et al., 2023). In that study, the absolute Glx change was explicitly used as a deviation index to capture the magnitude of concentration change in the visual cortex, suggesting that individual differences in neurochemical fluctuations may provide information beyond mean shifts in E/I balance. Here, we extend this work by investigating whether dark exposure affects mixed perception and dynamics during binocular rivalry. We hypothesize that dark exposure alters the proportion of mixed perception and that variation in this perceptual change is related to individual differences in the magnitude of GABA+ or Glx concentration changes measured with MRS in the visual cortex.

Materials and methods

Participants

Fourteen observers (11 female, mean ± SD age = 25.4 ± 1.3 years) with normal or corrected-to-normal vision, including two authors, participated in the MRS and behavioural experiments. This sample was recruited independently of our prior work (Min et al., 2023). All participants except the two authors (NJ and LZ) were naïve to the purpose of the study. They provided written informed consent prior to their enrollment. Experiments conducted during this study adhered to the latest guideline of the Declaration of Helsinki and were approved by the Ethics Committee of Wenzhou Medical University (approval number: 2022KY220) and the University of Science and Technology of China (approval number: 2022KY204). They were not pre-registered in a database prior to the study.

Experimental design

The study consisted of separate magnetic resonance spectroscopy (MRS) and behavioural experiments on different days. Both experiments used the same dark-exposure protocol and were conducted on the same participants.

For the MRS experiment, participants completed three scan sessions. The first session served as a practice scan and was excluded from formal analyses. Following the practice scan, participants spent 60 min in a normally illuminated laboratory environment before completing the baseline MRS scan. Participants then underwent 60 min of dark exposure and immediately completed a second MRS scan. Comparisons between the baseline and post-dark-exposure scans were used to quantify neurochemical changes associated with dark exposure. They were asked to keep their eyes open during the scanning sessions.

For the behavioural experiment, participants completed two baseline binocular rivalry measurements followed by 60 min of dark exposure. Immediately after dark exposure, participants completed two additional rivalry measurements. Results from the two baseline trials and two post-exposure trials were averaged separately to improve measurement reliability. A schematic overview of both experiments is illustrated in Fig. 1C.

While these two experiments were conducted on separate days, we ensured that each subject performed the two experiments in similar time periods of the day.

Dark exposure

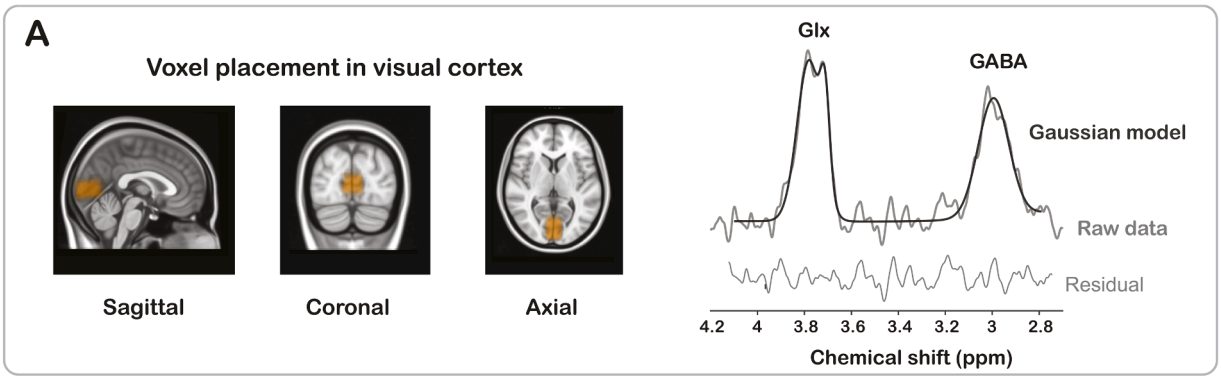
In both experiments, participants underwent 60 min of dark exposure to eliminate visual input. Opaque black eye patches were placed over both eyes to achieve complete binocular deprivation. Participants remained in a fully darkened room and were instructed to keep their eyes open and stay awake throughout the exposure period. The opaque patches blocked all light transmission, preventing any residual or stray light from entering the eyes. To promote compliance, the experimenter remained present throughout the session and periodically confirmed verbally that participants were awake while maintaining the dark environment.

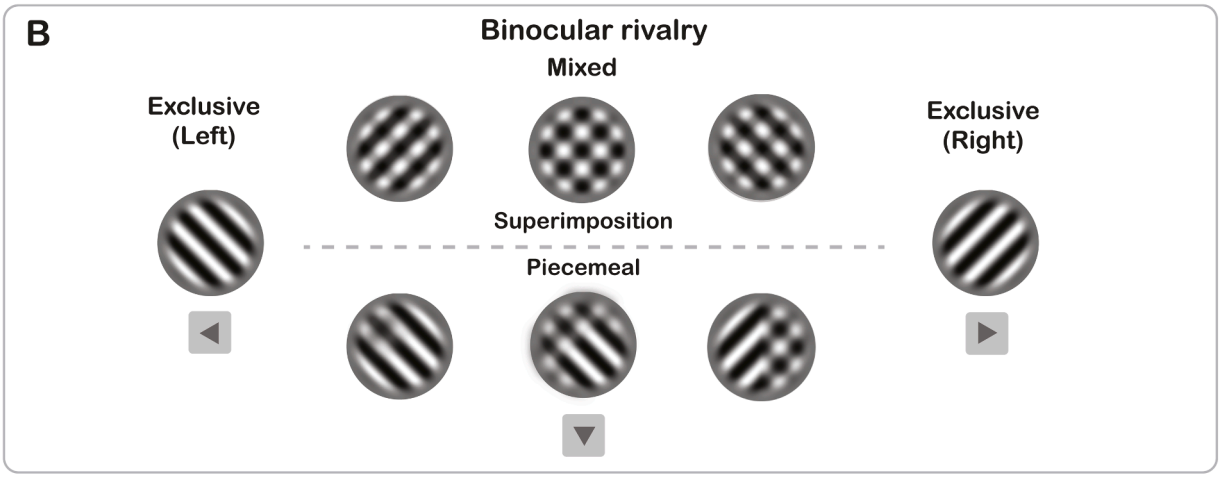
Magnetic resonance spectroscopy

Data acquisition

All magnetic resonance (MR) imaging was performed using a 3T MRI GE Discovery MR750 scanner equipped with an 8-channel head coil at the University of Science and Technology of China. During each scan session, participants were positioned supine and instructed to remain awake with their eyes open. High-resolution anatomical images were obtained using a T1-weighted 3D BRAVO sequence with the following acquisition parameters: repetition time (TR) = 8.16 ms, echo time (TE) = 3.18 ms, a voxel = 1 × 1 × 1 mm, flip angle = 12°, matrix size = 256 × 256, field of view = 256 × 256 mm, and 252 contiguous axial slices with 1 mm thickness.

For neurochemical quantification, we employed proton magnetic resonance spectroscopy (^{1}H-MRS) using a Meshcher-Garwood-Point Resolved Spectroscopy (MEGA-PRESS) sequence (Mescher et al., 1998) to measure glutamate and glutamine (Glx), as well as GABA+





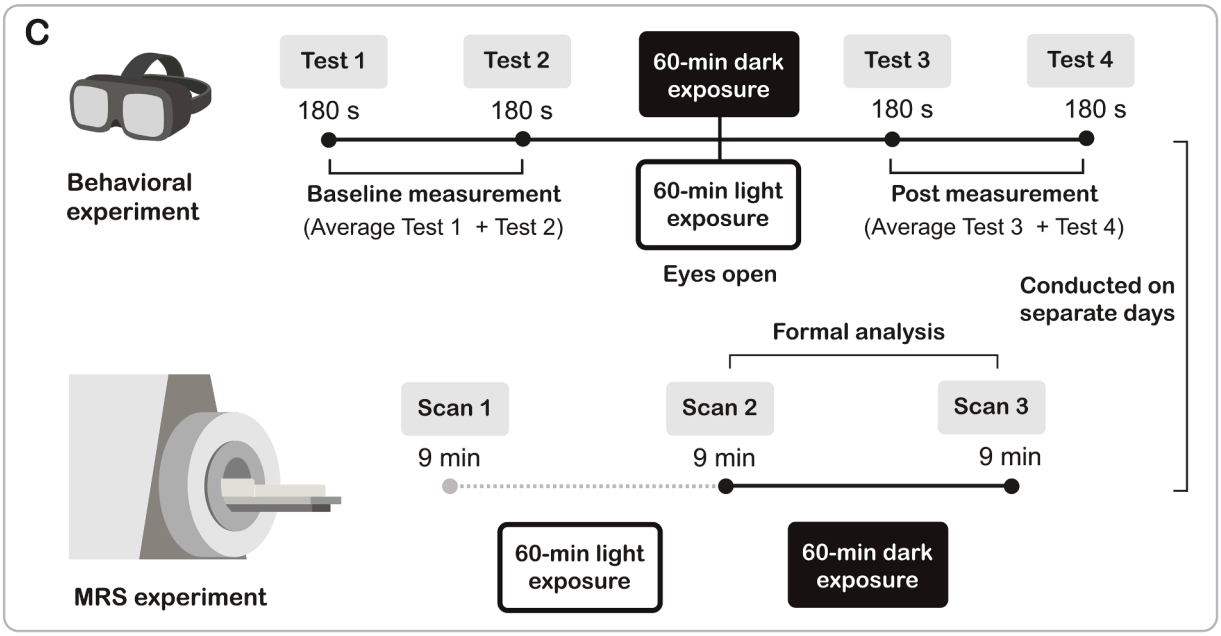


Fig. 1. General procedure of MRS and behavioural experiments. (A) Averaged placement of the magnetic resonance spectroscopy (MRS) voxel in the median occipital cortex near the calcarine sulcus, shown in sagittal, coronal, and axial views. Edited spectra of a representative subject illustrating the Glx and GABA+ peaks are shown alongside the fitted model and residual. (B) Binocular rivalry task. Participants continuously reported exclusive left-eye percepts, exclusive right-eye percepts, mixed percepts using a keyboard. Mixed perception was defined as the combined duration of superimposed and piecemeal percepts. (C) Timeline of the behavioral and MRS experiments. In the behavioral experiment, participants completed two 180 s rivalry trials before exposure (Tests 1–2) and two 180 s rivalry trials after exposure (Tests 3–4); baseline and post-exposure measures were calculated by averaging the two trials within each period. Participants completed both a 60-min dark-exposure condition and a 60-min light-exposure control condition on separate days. In the MRS experiment, the same participants underwent three 9-min MRS scans: a baseline scan (Scan 1), a second scan following 60 min of light exposure with eyes open (Scan 2), and a third scan following 60 min of dark exposure (Scan 3). Formal analyses focused on changes in GABA+ and Glx concentrations using Scans 2 and 3. The behavioral and MRS experiments were conducted in separate sessions/days using the same participants.

levels (Fig. 1A). Spectral data were acquired with TE = 68 ms, TR = 2000 ms, 8 averages, and 256 transients of 4096 data points sampled at 5 kHz, resulting in a total acquisition time of 9 min and 20 s. As in the previous study (Min et al., 2023), 20 × 30 × 20 mm voxel was positioned in the medial occipital cortex near the calcarine sulcus to sample neurochemical concentrations within the early visual cortex. This voxel size was chosen to maximize anatomical specificity within the early visual cortex by minimizing inclusion of neighboring non-visual cortical regions and reducing partial-volume effects from surrounding tissue (Kurcyus et al., 2018; DeMayo et al., 2023). The protocol incorporated a 7 ms Gaussian editing pulse applied at 1.9 ppm (ON) and 7.46 ppm (OFF), with water suppression achieved through chemical shift selective saturation (CHESS) (Haase et al., 1985) and outer volume suppression (Felmlee and Ehman, 1987) techniques at 4.68 ppm. Additional signal suppression was implemented using very selective suppression (VSS) within the outer volume suppression framework (Edden et al., 2014).

The MEGA-PRESS acquisition included both edited (ON) and unedited (OFF) spectra. To establish steady-state conditions, the sequence began with 8 dummy TR scans. Prior to spectral acquisition, we obtained a water reference scan for calibration purposes. During phase correction reference signal collection, the CHESS water suppression was disabled for 16 TR periods to ensure optimal signal quality.

Data processing

All neuroimaging data were processed using FSL (Jenkinson et al., 2012). For each scan, a binary mask representing the MRS voxel of interest (VOI) was reconstructed in native T1 space using voxel centre coordinates and fixed voxel dimensions (20 × 30 × 20 mm) extracted from the spectroscopy acquisition. T1-weighted structural images were skull-stripped using BET (Smith, 2002), and tissue segmentation was performed in native space using FSL FAST with bias-field correction enabled (Zhang, Brady and Smith, 2001). FAST generated voxel-wise tissue classifications of gray matter, white matter, and cerebrospinal fluid (CSF). Voxels within the MRS voxel were classified according to their assigned tissue type. Tissue proportions were calculated as the fraction of total VOI voxels occupied by each tissue class. All preprocessing, segmentation, masking, and tissue quantification scripts were implemented using FSL command-line tools and custom Python scripts, and are available at https://osf.io/u3k8r.

Spectra acquired through the MEGA-PRESS sequence were processed using the Gannet Analysis toolkit (Edden et al., 2014). MRS data underwent several preprocessing steps: water reference and edited spectra signals were extracted, with the former used to calibrate the latter. After applying zero-padding and Fourier transformation, we performed frequency-domain phase correction. The edited spectra signals were aligned so that creatine (Cr) signals were positioned at 3.02 ppm (standard). Subtraction of ON/OFF spectra yielded difference spectra containing GABA+ and Glx signals. Quantification involved Gaussian modeling of GABA+ (~3 ppm) and Glx (~3.8 ppm) peaks in these difference spectra. Peak areas were calculated to estimate concentrations, which were quantified relative to both creatine (Cr) and unsuppressed water. This is because water referencing offers advantages for tissue composition correction while Cr referencing provides comparable or superior reproducibility to referencing to water (Bogner et al., 2010). Following the MRSinMRS reporting recommendations (Lin et al., 2021), spectral quality was assessed using linewidth (full width at half maximum; FWHM) and signal-to-noise ratio (SNR) metrics generated by Gannet. Spectral quality metrics and tissue-composition measures are reported in the Supplementary Materials (Tables S1 and S2). No spectra were excluded on the basis of spectral quality criteria.

Tissue-Composition correction of metabolite concentrations

To account for differences in tissue composition within the MRS voxel, metabolite concentrations were corrected using the α-correction procedure described by Harris et al. (2015) and adopted by Ip et al. (2021). This approach accounts for differences in metabolite concentrations between gray matter (GM) and white matter (WM). Based on previous literature, α values of 0.5 and 0.7 were used for GABA and Glx, respectively, reflecting the assumption that GABA is approximately twice as concentrated in GM as in WM, whereas Glx exhibits a smaller tissue-dependent difference (Porges et al., 2017; Maier et al., 2022).

First, water-referenced metabolites were corrected for cerebrospinal fluid (CSF) partial volume effects:

$$c_{CSF_{corr}} = \frac{c_{meas}}{1 - f_{CSF}} \tag{1}$$

where c_{meas} is the uncorrected metabolite concentration and f_{CSF} is the participant's CSF fraction. For Cr-referenced metabolites, no CSF correction was applied, as the creatine signal originates from the same tissue compartments as the metabolite of interest.

Subsequently, α-correction was applied to all metabolites (water- and Cr-referenced) using the same formula:

$$c_{\alpha corr} = c_m \times \frac{1}{\left(f_{gm} + \alpha f_{wm}\right)} \times \frac{\mu_{GM} + \alpha\mu_{WM}}{\mu_{GM} + \mu_{WM}} \tag{2}$$

where c_{in} is either the CSF-corrected value (for water-referenced metabolites) or the uncorrected value (for Cr-referenced metabolites), f_{GM} and f_{WM} are the participant's GM and WM fractions, α represents the ratio of metabolite concentration in white matter relative to gray matter, and μ_{GM} and μ_{WM} are the mean gray- and white-matter fractions calculated across all participants and scan sessions. The normalization term $(\mu_{\mathrm{GM}} + \alpha\mu_{\mathrm{WM}})/(\mu_{\mathrm{GM}} + \mu_{\mathrm{WM}})$ scales metabolite estimates to the group-average tissue composition.

Behavioural measurement

Apparatus. All experiments were programmed using MATLAB with Psychtoolbox (Brainard, 1997) and run on a MacBook Pro laptop. Visual stimuli were presented dichoptically using Goovis Pro head-mounted goggles (NED Optics, Shenzhen, China) with a resolution of 1920 × 1080 pixels per eye, 60 Hz refresh rate, and 41.6 pixels per degree. The OLED displays had a mean luminance of 75 cd/m^2 and maximum luminance of 150 cd/m^2, which was suitable for displaying high-contrast (50%) grating stimuli. The behavioural experiments were conducted at Wenzhou Medical University.

Psychophysical method. Participants viewed dichoptic rivalry stimuli consisting of orthogonal sinusoidal gratings oriented at +45° and −45° The gratings had a spatial frequency of 1 cycle/degree and were presented within a 4.2° x 4.2° area. To minimize edge artifacts, each grating was multiplied by a raised-cosine blur envelope with a 2.8° diameter, defining the effective stimulus region and producing a smooth transition at the stimulus boundary (Fig. 1B). The orientation presented to each eye was randomized across trials as in previous studies (Finn et al., 2019; Sheynin et al., 2020; Min et al., 2021).

A noise-pixelated fusion frame surrounded each stimulus and remained visible throughout the trial to promote stable binocular alignment. Participants continuously reported their perceptual experience using the keyboard. The left and right arrow keys indicated exclusive dominance of one grating or the other, whereas the down arrow key indicated mixed perception, including both superimposed percepts (both gratings visible simultaneously across the stimulus) and piecemeal percepts (different regions dominated by different gratings). Participants were instructed to maintain a single response corresponding to their current percept and update their response whenever their percept changed. Each rivalry trial lasted 180 s.

Percept proportions. Perceptual reports were recorded continuously

throughout each trial. Consecutive reports of the same perceptual state were merged into a single perceptual epoch. For each trial, the cumulative duration of dominant-eye percepts, non-dominant-eye percepts, and mixed percepts were calculated.

Our primary outcome measure was the proportion of mixed perception, defined as $P_{mixed} = T_{mixed} / (T_{DE} + T_{Mixed} + T_{NDE})$, where T_{Mixed} denotes the total duration of mixed percept reports, T_{DE} denotes the total duration of dominant-eye percepts, and T_{NDE} denotes the total duration of non-dominant-eye percepts. Thus, mixed perception proportion was expressed as the fraction of total reported perceptual time occupied by mixed percepts. Periods during which no response was recorded were excluded from the calculation. The two baseline trials were averaged to obtain a baseline estimate, and the two post-dark-exposure trials were averaged to obtain a post-exposure estimate. Proportions of dominant-eye and non-dominant-eye percepts were computed analogously by replacing T_{Mixed} in the numerator with T_{DE} and T_{NDE}, respectively to compute sensory eye balance (see below).

Sensory eye balance. To quantify the relative dominance of the two eyes during binocular rivalry, we computed an ocular dominance index (ODI) for each trial. The ODI was defined as (DE - NDE) / (DE + NDE + Mixed), where DE denotes the proportion of total reported time occupied by dominant-eye percepts, NDE denotes the proportion occupied by non-dominant-eye percepts, and Mixed denotes the proportion occupied by mixed percepts. Positive values indicate dominance of the initially dominant eye, while negative values indicate a shift toward the non-dominant eye, and values near zero reflect balanced ocular dominance. Baseline ODI was computed by averaging across the two pre-exposure trials, and post-exposure ODI was computed by averaging across the two trials following exposure.

Phase duration and perceptual stability. To examine rivalry dynamics, we analyzed phase durations separately for dominant-eye (DE), non-dominant-eye (NDE), and mixed percepts. Consecutive reports of the same percept were merged into a single perceptual epoch. Phase durations shorter than 100 ms were excluded from all analyses to minimize the influence of spurious responses or button press artifacts. Since rivalry phase durations are not normally distributed (Finn et al., 2019), our primary measure of perceptual stability was median phase duration, computed for each percept type, trial, condition, and participant. Median durations were then averaged across the two test repetitions per condition for each participant.

Next, we fitted gamma distributions to the phase duration data for each participant, condition, session, and percept type using maximum likelihood estimation (see details of modeling in Supplementary Materials), pooling phase duration epochs from the two test repetitions within each session, as described in previous studies (Wang, McGraw and Ledgeway, 2021; Sarı and Lunghi, 2023; Zhou et al., 2024). The gamma distribution captures the right-skewed distribution of phase durations during rivalry (Steinwurzel et al., 2020), with shape parameter (κ) governing distribution skewness and scale parameter (θ) governing temporal persistence. Goodness-of-fit was assessed using a quantile-quantile (Q-Q) based coefficient of determination (R^2): for each fit, empirical phase durations were sorted and compared against theoretical quantiles drawn from the fitted gamma distribution, and R^2 was computed as the squared Pearson correlation between empirical and theoretical quantiles.

Alternation rate. Furthermore, we computed alternation rate (switches per second) for each trial. Alternation rate was defined as the number of perceptual switches divided by the total reported duration, where the number of switches equaled the total number of perceptual epochs minus one. Values were averaged across the two test repetitions per participant and condition.

Statistical analysis

For the rivalry data, linear mixed-effects models were fitted using the *lme4* package (Bates et al., 2015). For each outcome measure (mixed percept proportion, ocular dominance index (ODI), median phase duration, alternation rate, and gamma shape and scale parameters), Session (before, after) and Condition (Dark, Light) were entered as fixed effects together with their interaction, and Subject was included as a random intercept. Follow-up comparisons were conducted using estimated marginal means with Tukey correction for multiple comparisons. Where specific within-condition contrasts were of a priori interest, paired *t*-tests were additionally reported, with effect sizes quantified using Cohen's *d* for paired samples.

For the MRS data, GABA+ and Glx concentrations were corrected for tissue composition using the α-correction procedure (Harris, Puts and Edden, 2015). Water-referenced metabolites were first corrected for CSF partial volume effects and then α-corrected, whereas Cr-referenced metabolites were α-corrected only. Group-level changes in metabolite concentrations following dark exposure were assessed using paired *t*-tests and confirmed using permutation tests (10,000 iterations; described below).

To examine whether individual differences in neurochemical responses were associated with perceptual changes following dark exposure, standardized change indices were calculated as (Post − Pre)/(Post + Pre) for mixed percept proportion, ODI, phase-duration measures, alternation rate, and metabolite concentrations (Lunghi et al., 2015; Min et al., 2023). This standardization accounts for baseline differences between participants while preserving the direction of change. Additional deviation indices were computed by taking the absolute value of metabolite change indices. These indices quantify the magnitude of neurochemical fluctuations irrespective of direction and were used to test whether deviations from baseline neurochemical concentrations are associated with perceptual changes regardless of whether metabolite concentrations increase or decrease.

Associations between perceptual and neurochemical change indices were evaluated using Pearson correlations. P-values were corrected for multiple comparisons using both the false discovery rate (FDR; Benjamini and Hochberg, 1995) and Holm procedures. To assess robustness, all correlation analyses were repeated after excluding two participants who exhibited unusually high mixed-percept proportions (>70%). P-values after multiple corrections are labelled as FDR-p or Holm-p throughout the paper.

To further evaluate robustness, permutation tests and bootstrap procedures (10,000 iterations) were conducted for both mean differences and neurochemical–behavioral associations. For before–after exposure comparisons, participant labels were randomly permuted between sessions and the mean difference recomputed at each iteration. Also, a non-parametric bootstrap procedure was applied in which participants were resampled with replacement at each iteration while preserving within-subject pairing of before and after values, and the mean post–pre difference in neurochemical concentrations was recomputed from the resampled data to generate a bootstrap distribution of mean differences. For correlation analyses, behavioral change indices were randomly shuffled across participants while metabolite change values were retained, and regression slopes were recalculated for each permutation. Two-tailed permutation p-values were computed as the proportion of permuted statistics whose absolute values were greater than or equal to the corresponding observed statistic. Bootstrap confidence intervals for mean differences were derived using the percentile method (2.5^{th} and 97.5^{th} percentiles of the bootstrap distribution). All permutation and bootstrap analyses were conducted with a fixed random seed. Data analyses and visualizations were conducted in R (Min, 2024).

Results

Dark exposure increases mixed perception during binocular rivalry

To determine whether changes in mixed percept proportion differed between dark- and light-exposure conditions, we fitted a linear mixed-effects model with mixed percept proportion as the dependent variable. Session (before vs. after exposure) and Condition (dark vs. light exposure) were treated as fixed effects together with their interaction. Subject was included as a random intercept.

The analysis revealed a significant main effect of Session ($\beta = 0.095$, $p = 0.016$), indicating an overall increase in mixed percept proportion from before to after exposure. The main effect of Condition was not significant ($\beta = 0.071$, $p = 0.066$), nor was the Session × Condition interaction ($\beta = -0.070$, $p = 0.197$). Post-hoc estimated marginal means analyses with Kenward–Roger degrees-of-freedom correction showed that mixed percept proportion increased significantly following dark exposure (estimated change = 0.095, $p = 0.016$, Cohen's $d = 0.73$; left bars of Fig. 2A), whereas no significant change was observed following light exposure (estimated change = 0.025, $p = 0.51$, Cohen's $d = 0.44$; right bars of Fig. 2A). The increase in mixed perception following dark exposure was also observed after excluding two participants who reported unusually high rates of mixed perception (> 70%), though the effect of dark exposure on mixed perception proportion became marginal after their exclusion ($\beta = 0.088$, $p = 0.052$, Cohen's $d = 0.63$; see Supplementary Materials).

To further assess the robustness of the observed increase in mixed perception following dark exposure, we conducted a permutation test with 10,000 iterations. For each iteration, the sign of each participant's after–before difference in mixed percept proportion was randomly flipped (equivalent to randomly exchanging the before and after labels within each participant), and the mean of the resulting permuted differences was recalculated to generate a null distribution of mean differences under the assumption of no effect. The observed mean difference of 0.095 fell outside the null distribution ($p = 0.0096$), supporting the robustness of the observed increase in mixed perception following dark exposure (see Fig. 2B for bootstrapped distributions of mixed percept proportions before and after exposure). Lastly, test–retest reliability was evaluated by comparing baseline sessions across the two experimental conditions. A Pearson correlation analysis indicated strong consistency between sessions ($r = 0.73$, $p = 0.0031$), confirming that the binocular rivalry task provided reliable measurements of mixed-perception proportions.

Ocular dominance does not predict changes in mixed perception

To determine whether the increase in mixed perception following dark exposure could be explained by changes in sensory eye dominance, we calculated ODI (see Methods) for each subject before and after exposure. Baseline ODI values were close to zero (mean = 0.048 ± 0.043 in the dark condition), indicating binocular balance before exposure. A linear mixed-effects model revealed no significant effects of Session ($\beta = -0.003$, $p = 0.87$), Condition ($\beta = 0.001$, $p = 0.98$), or their interaction ($\beta = -0.004$, $p = 0.89$). Likewise, paired *t*-tests showed no change in ODI following either dark exposure ($t(13) = -0.25$, $p = 0.81$, Cohen's $d = -0.07$; Fig. 2C) or light exposure ($t(13) = -0.293$, $p = 0.77$, Cohen's $d = -0.08$; Fig. 2C). If shifts in eye dominance contributed to the observed increase in mixed perception, changes in ODI would be expected to covary with changes in mixed percept proportions. However, according to Pearson's correlation test, ODI change was unrelated to changes in mixed perception following dark exposure ($r = 0.12$, $p = 0.67$; Fig. 2D) or light exposure ($r = 0.27$, $p = 0.34$; Fig. 2D). Together, these findings suggest that dark exposure did not alter sensory eye dominance and that the observed increase in mixed perception cannot be explained by changes in eye dominance.

Dark exposure does not impact phase durations

Next, we examined phase duration. Since binocular rivalry phase durations typically follow a positively skewed gamma distribution rather than a normal distribution, median phase durations were calculated for each participant, session, condition, and percept type and averaged across the two repetitions. A linear mixed-effects model revealed no significant main effects or interactions (all p's > 0.18), including the Session × Condition × Percept interaction, $F(2, 143) = 0.41$, $p = 0.67$. Within the dark-exposure condition, median phase duration for mixed percepts increased slightly from before to after exposure but this effect was not significant, $t(65) = -1.45$, $p = 0.15$, Cohen's $d = 0.33$. Median durations for DE ($p = 0.55$) and NDE percepts ($p = 0.57$) also remained unchanged. Consistent with these findings, additional analyses showed that neither the overall distribution of phase durations, characterized by fitting gamma distributions to rivalry dynamics (Fig. S3), nor perceptual alternation rates changed significantly following dark or light exposure (see Supplementary Materials).

Dark exposure selectively increases Glx concentrations without altering GABA or net E/I balance

To determine whether dark exposure modulates excitatory and inhibitory metabolite concentrations in the visual cortex, we first analyzed changes in GABA and Glx concentrations at the group level. Paired *t*-tests revealed no significant change in GABA following dark exposure for either water- ($t(13) = 1.02$, $p = 0.32$, Cohen's $d = 0.27$) or Cr-referenced ($t(13) = 0.80$, $p = 0.44$, Cohen's $d = 0.21$; Fig. 3A) concentrations. Glx increased significantly for both water- ($t(13) = 2.89$, $p = 0.013$, Cohen's $d = 0.77$) and Cr-referenced ($t(13) = 2.44$, $p = 0.030$, Cohen's $d = 0.65$; Fig. 3B) concentrations with moderate-to-large shifts. We additionally conducted repeated-measures linear mixed model analysis for each metabolite changes following dark exposure. It revealed that Glx increased significantly after dark exposure (water: $\beta = 1.06$, $p = 0.013$; Cr: $\beta = 0.015$, $p = 0.030$) while GABA did not (water: $\beta = 0.16$, $p = 0.24$; Cr: $\beta = 0.0077$, $p = 0.41$). These results collectively reveal that Glx significantly increased following dark exposure.

To validate the observed changes in these neurochemical concentrations, we performed a non-parametric bootstrap procedure (10,000 iterations) for the mean differences between post- and pre-exposure levels for Glx and GABA+, separately for water- and creatine-referenced concentrations. At each iteration, participants were resampled with replacement (preserving within-subject pairing of before and after values), and the mean post-pre difference was recomputed from the resampled data, generating a bootstrap distribution of mean differences. The observed mean differences for GABA were not significant for water-referenced ($p = 0.29$) or Cr-referenced ($p = 0.41$; see Fig. 3C for the overlap between before and after distributions) levels. In contrast, the observed mean difference for Glx was unlikely to occur by chance for both water-referenced ($p = 0.0032$) and creatine-referenced ($p = 0.011$; see Fig. 3D for distance between before and after distributions) concentrations. Also, both tissue composition within the MRS voxel (gray matter, white matter, and CSF fractions) and spectral quality metrics (linewidth/FWHM and SNR for GABA+, Glx, creatine, and water) remained stable across sessions (see Supplementary Materials). These results suggest that dark exposure robustly elevates Glx, while GABA levels remain unchanged.

Additionally, E/I balance was estimated by converting Glx/GABA concentration ratios into logarithmic decibel units ($20 \times \log([Glx]/[GABA])$) to avoid bias against one direction of change. Paired *t*-tests revealed no significant change in net E/I balance following dark exposure for metabolite concentrations with both water and creatine references ($t(13) = -0.92$, $p = 0.38$, Cohen's $d = -0.24$). Thus, dark exposure did not produce consistent group-level shifts in mean inhibitory signaling. We next examined whether individual differences in

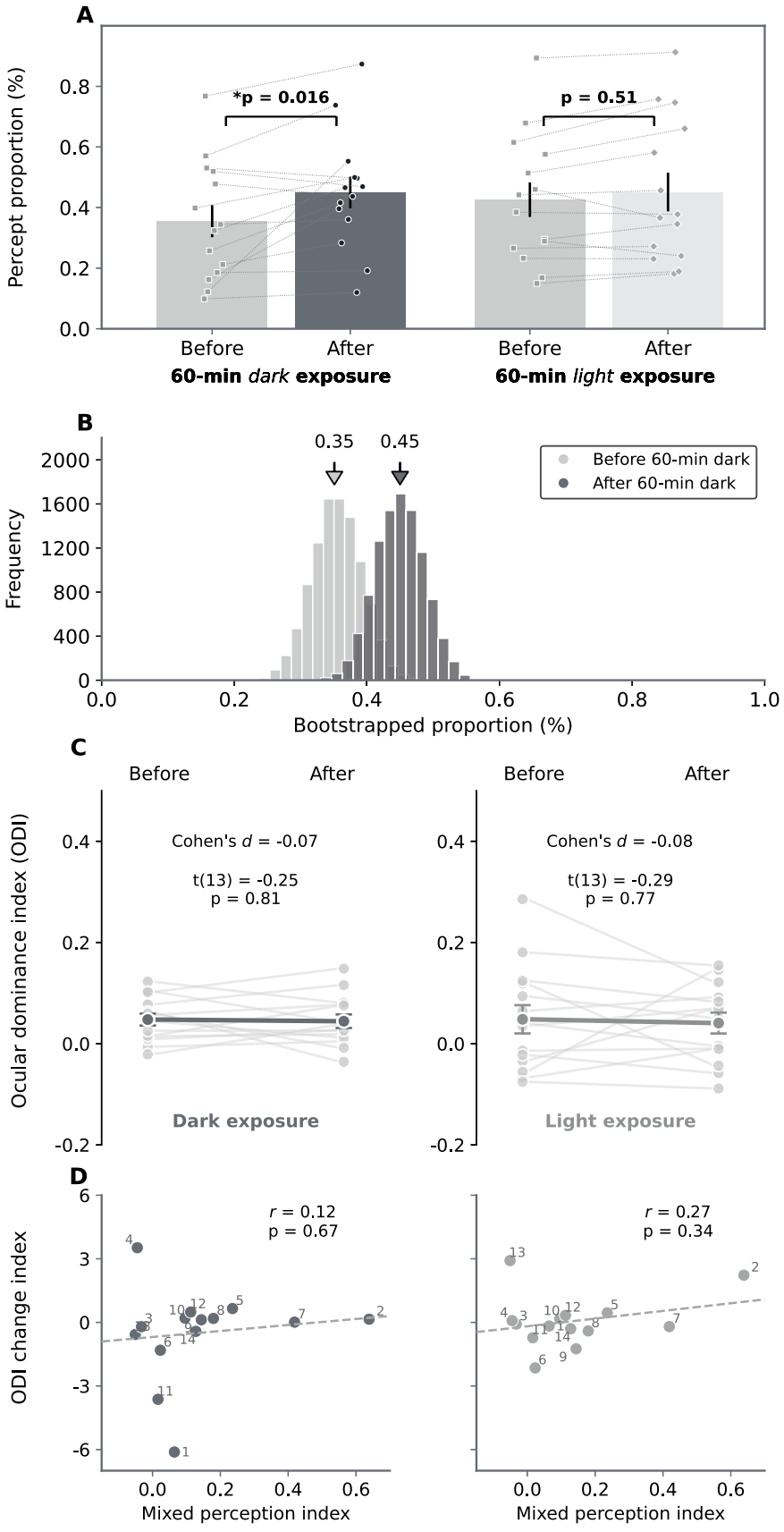


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Fig. 2. Effects of dark exposure on proportion of mixed perception and ocular dominance obtained during binocular rivalry in 14 observers. (A) Mean proportion of mixed perception before and after 60-min dark exposure (left) and 60-min light exposure (right). Points represent individual participants and dashed lines connect repeated measurements. Bars show group means and error bars indicate standard errors of the mean. The asterisk denotes statistical significance from a linear mixed model analysis (*$p < 0.05$). (B) Bootstrap distributions of mixed-perception proportions before and after dark exposure. Arrows indicate the observed group means before (0.35) and after (0.45) dark exposure. (C) Ocular dominance index (ODI) before and after dark exposure (left) and light exposure (right). Points represent individual participants and error bars indicate standard errors of the mean. (D) Relationship between changes in mixed-perception index and changes in ODI following dark exposure (left) and light exposure (right). Each point represents one participant.

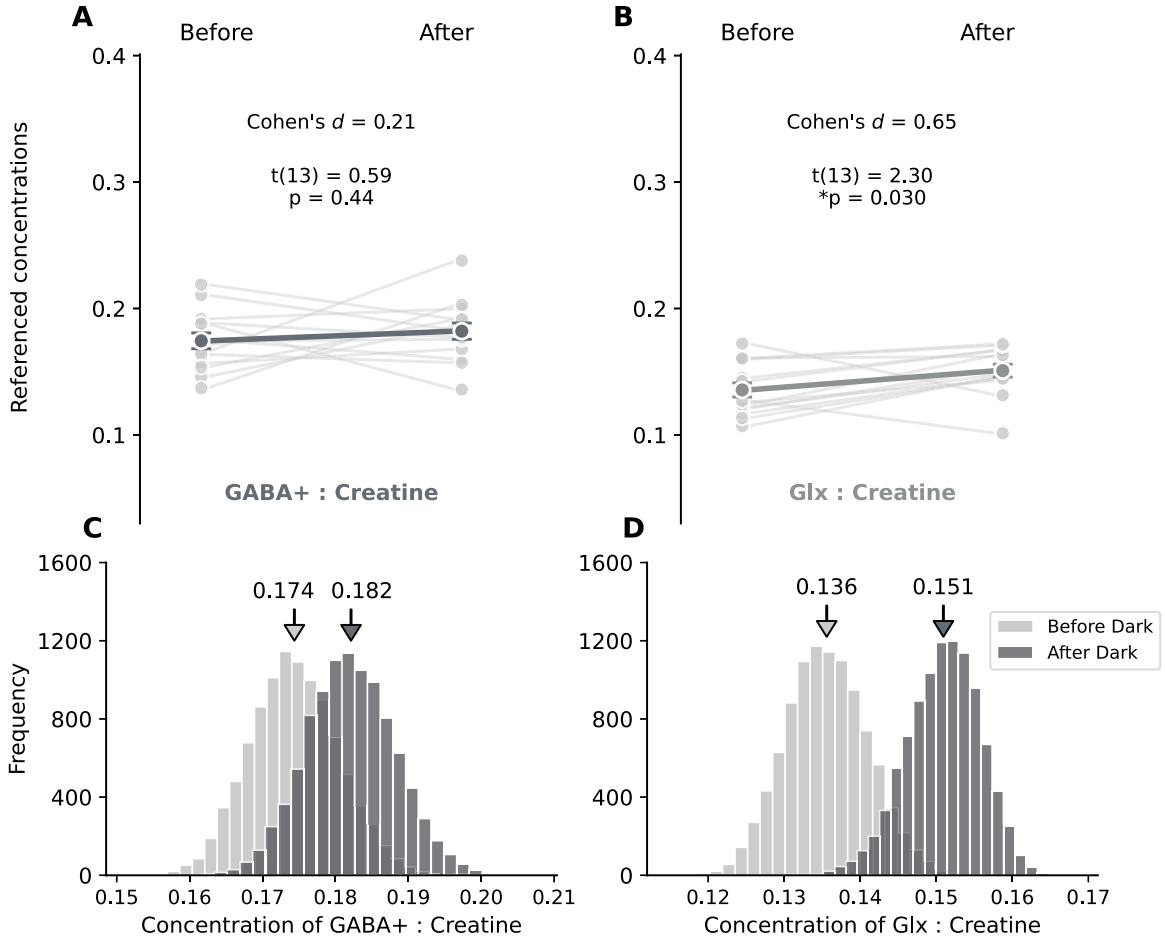

Fig. 3. Effects of 60-min dark exposure on GABA+ and Glx concentrations in the visual cortex. (A) Creatine-referenced GABA+ concentrations before and after dark exposure. Individual participants are shown as light gray points connected by lines. Dark points and error bars represent group means ± standard error. (B) Creatine-referenced Glx concentrations before and after dark exposure. (C) Bootstrap distributions (10,000 iterations) of mean GABA+:Creatine concentrations before and after dark exposure obtained by resampling participants with replacement while preserving within-subject pairing. Arrows indicate the observed group means. (D) Bootstrap distributions (10,000 iterations) of mean Glx:Creatine concentrations before and after dark exposure. Arrows indicate the observed group means. Similar results were obtained using water-referenced metabolite concentrations (see Results).

perceptual changes were associated with individual differences in neurochemical responses to dark exposure.

Individual differences in GABA± fluctuations predict changes in mixed perception during binocular rivalry

Using Pearson correlation analysis between perceptual and neurochemical indices of changes, we found that individuals showed greater increases in mixed perception with larger increases in GABA+, both when GABA+ was quantified relative to water (r = 0.59, 95% CI [0.085, 0.853], FDR-p = 0.054, Holm-p = 0.13) and relative to creatine (r = 0.64, 95% CI [0.173, 0.876], FDR-p = 0.034, Holm-p = 0.077; triangle points in Fig. 4A(i)). In contrast, individuals with larger changes in Glx did not show correspondingly larger changes in mixed perception, either when Glx was quantified relative to water (r = −0.26, 95% CI [−0.697, 0.311], FDR-p = 0.48) or relative to creatine (r = −0.16, 95% CI [−0.634, 0.408], FDR-p = 0.67; Fig. 4A(ii)). When analyzing absolute (deviation) indices, which capture the magnitude of concentration changes irrespective of direction, the relationship between GABA+ and mixed perception strengthened markedly for both water-referenced (r = 0.74, 95% CI [0.346, 0.913], FDR-p = 0.0098, Holm-p = 0.017) and Cr-referenced concentrations (r = 0.83, 95% CI [0.545, 0.946], FDR-p = 0.0017, Holm-p = 0.0017; circle points in Fig. 4B(i)). Absolute Glx remained unrelated to mixed perception changes for both water-referenced (r = −0.35, 95% CI [−0.743, 0.221], FDR-p = 0.35) and Cr-referenced values (r = −0.13, 95% CI [−0.616, 0.433], FDR-p = 0.67; Fig. 4B(ii)). These findings suggest that GABA+, but not Glx, is associated with perceptual alterations following dark exposure. Moreover, associations based on the magnitude of GABA+ fluctuations were stronger and survived both FDR and Holm correction, suggesting that the extent of GABA+ change is a more robust predictor of perceptual outcomes in mixed perception than the direction of GABA+ change

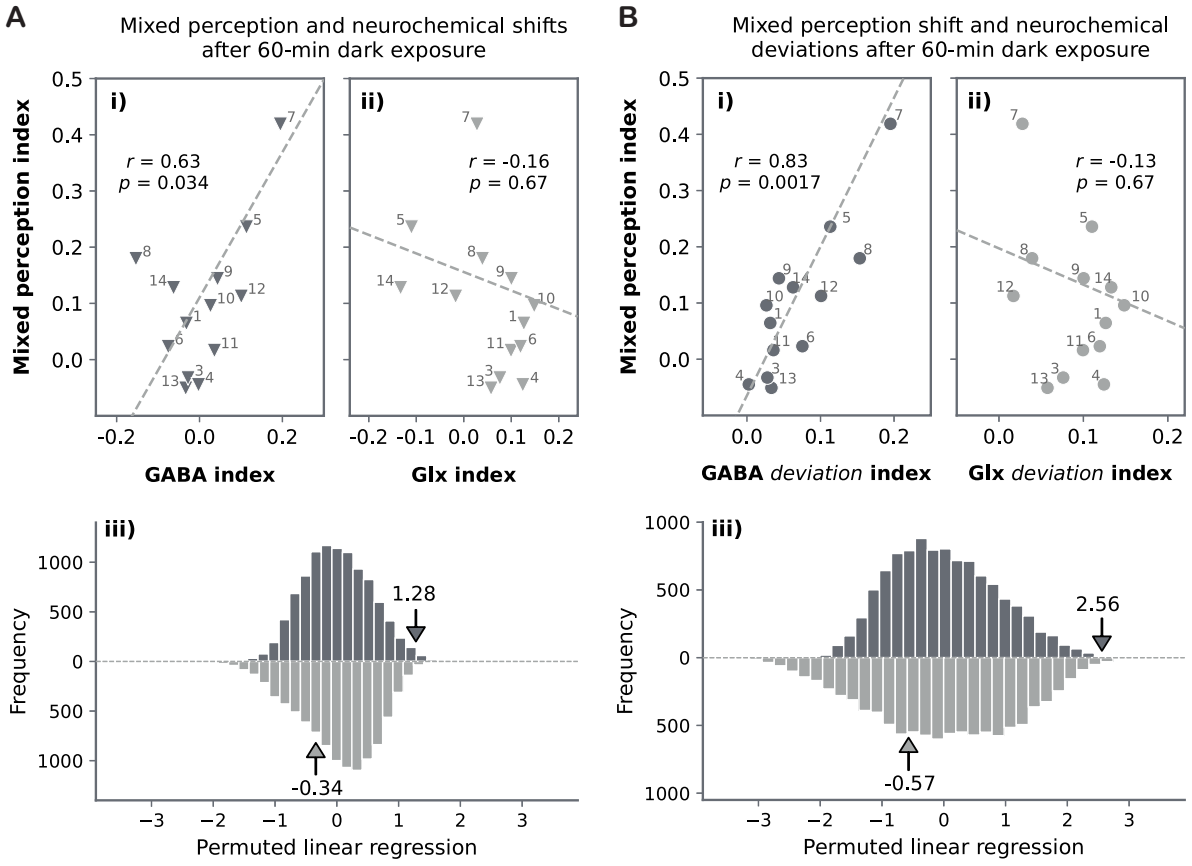

Fig. 4. Individual differences in neurochemical changes predict changes in mixed perception. (A) Scatterplots of mixed perception index versus raw neurochemical changes show that individual differences in mixed perception are associated with GABA+ changes (i), but not Glx (ii). (iii) Permutation test distributions (10,000 iterations) of regression slopes (dashed lines in scatterplots) indicate that the observed GABA+ slope (1.28, p = 0.012) is unlikely to occur by chance, whereas the Glx slope (−0.34, p = 0.61) falls within the null distribution. (B) Scatterplots of mixed perception index versus absolute (deviation) changes show that individual differences in mixed perception are strongly associated with GABA+ fluctuations (i), but not Glx (ii). (iii) Permutation tests confirm that the observed GABA+ slope (2.56, p = 0.0003) is unlikely to occur by chance, whereas the Glx slope (−0.57, p = 0.67) is consistent with chance. P-values for the correlations are FDR-corrected.

alone. Notably, further analyses revealed that individual differences in alterations of ODI, median phase duration, perceptual dynamics and alteration rates were not associated with GABA+ or Glx fluctuations (see Supplementary Materials), suggesting that the observed neurochemical relationships were specific to changes in mixed perception proportion.

After excluding the two participants with unusually high rates of mixed perception (Subjects 1 and 14 in Fig. 4), the correlation between raw changes in GABA and mixed perception was not significant after FDR or Holm correction (GABA Water: r = 0.60, 95% CI [0.042, 0.874], FDR-p = 0.077, Holm-p = 0.192; GABA Cr: r = 0.66, 95% CI [0.138, 0.895], FDR-p = 0.052, Holm-p = 0.117; see Supplementary Materials for more details). In contrast, the relationship between absolute changes in GABA and shifts in mixed perception remained significant after both FDR and Holm corrections (|GABA Water|: r = 0.75, 95% CI [0.312, 0.926], FDR-p = 0.019, Holm-p = 0.034; |GABA Cr|: r = 0.83, 95% CI [0.494, 0.952], FDR-p = 0.006, Holm-p = 0.006). Both relationships were comparable in magnitude to those observed in the full sample. Together, these findings demonstrate that the association between absolute GABA changes and perceptual outcomes is robust.

To verify these associations, we performed permutation testing (10,000 iterations) of linear regression slopes across 14 subjects. The mixed perception change index was randomly shuffled across participants while neurochemical change values were retained, and the regression slope was recomputed at each iteration (Fig. 4A(iii) and 4B (iii) show the resulting null distributions). The observed slope for raw GABA+ changes was unlikely to occur by chance for both water-referenced (β = 1.16, p = 0.026) and Cr-referenced (β = 1.28, p = 0.012) values, whereas slopes for Glx changes were not significant (water: β = −0.62, p = 0.36; Cr: β = −0.34, p = 0.61). Similarly, the observed slope for GABA+ deviation (absolute change) had a very low probability of occurring by chance for both water-referenced (β = 2.29, p = 0.0020) and Cr-referenced (β = 2.56, p = 0.0003) values, while absolute Glx slopes remained nonsignificant (water: β = −1.70, p = 0.23; Cr: β = −0.57, p = 0.67). In sum, these results suggest that the magnitude of GABA+ fluctuations, but not Glx changes, reliably predicts alterations in mixed perception following dark exposure.

Discussion

Our findings suggest a more nuanced relationship between neurochemical changes and perceptual dynamics than predicted by reciprocal inhibitory models of binocular rivalry that propose that inhibitory competition between neural populations representing the two eyes promotes perceptual exclusivity, whereas weakening this competition promotes mixed perception (Alais, 2012; Said and Heeger, 2013). Consistent with these models, several studies have linked higher concentrations of GABA+ in the visual cortex with stronger perceptual suppression (Mentch et al., 2019) and slower rivalry dynamics (van Loon et al., 2013). If GABA concentrations from MRS measurements are associated with neurochemical processes relevant to interocular competition (Sheynin et al., 2020), the increase in mixed perception observed after dark exposure would be expected to accompany a

reduction in neurochemical markers associated with stronger perceptual suppression. However, we observed an increase in mixed perception following dark exposure without producing a significant group-level reduction in GABA+. We also did not observe significant changes in ocular dominance and perceptual dynamics during rivalry following dark exposure. Moreover, changes in the proportion of mixed perception from dark exposure, but not ocular dominance and rivalry dynamics, were more strongly related to the magnitude of GABA+ fluctuations than to the direction of change itself. Thus, the present findings are not readily explained by a simple directional account in which higher MRS-derived GABA+ concentrations are associated with greater perceptual exclusivity and lower concentrations are associated with greater mixed perception. Instead, they suggest that the magnitude of GABA+ change may be more closely associated with changes in binocular perceptual competition than the direction of neurochemical change alone.

Empirical (Okun and Lampl, 2008) and theoretical (Vogels and Abbott, 2009; Marín-Burgin et al., 2012) works support the idea that a stable E/I balance is a fundamental feature of normal brain function (Shadlen and Newsome, 1994). For this reason, along with the fact that concentrations of GABA+ and Glx are region-specific (Puts et al., 2011; Greenhouse et al., 2016), MRS has become a valuable tool in human neuroscience. Metabolite concentrations obtained from MRS have been associated with different visual functions and clinical characteristics. For example, concentrations of GABA in the visual cortex from neurotypical subjects have been associated with binocular rivalry dynamics (Robertson, Ratai and Kanwisher, 2016), orientation discrimination (Edden et al., 2009) and surround-suppression (Cook, Hammett and Larsson, 2016). In contrast, abnormal levels of GABA+ and Glx levels in the visual cortex are associated with clinical conditions, such as autism (Robertson, Ratai and Kanwisher, 2016) and glaucoma (Bang et al., 2023). Also, interventions such as perceptual learning (Shibata et al., 2017) and short-term monocular deprivation (Lunghi et al., 2015) can dynamically alter GABA+ concentrations in visual cortex, highlighting that alterations in GABA+ concentrations can accompany functional changes in visual perception following these interventions. When reporting the neurochemical changes from these interventions, MRS studies often examine the direction of the shift in E/I balance by computing changes in GABA+ and Glx concentrations within an E/I balance framework, for example by examining changes in metabolite concentrations or Glx/GABA ratios.

However, computing changes in Glx and GABA+ levels as a proxy for E/I balance may oversimplify the underlying physiology. Glx and GABA+ concentrations are metabolically linked, as glutamate serves as a precursor for GABA synthesis (Rae, 2014) and their levels often co-vary in the occipital cortex (Steel et al., 2020; Rideaux et al., 2022). In other words, since Glx+ and GABA concentrations are correlated, the net E/I balance derived from metabolite concentrations might not change even if the neurochemical concentration levels shift. For instance, concurrent decreases in both Glx and GABA+ have been observed in normal (Min et al., 2023) and clinical populations (Bang et al., 2023). These findings challenge the traditional E/I dichotomy, suggesting that the direction of neurochemical change (e.g., increased excitation) may not fully describe what is occurring in the brain. For example, while reduced Glx and increased GABA+ levels may both be interpreted within an E/I framework as reflecting greater inhibition in the region of interest, they can arise from different metabolic pathways and therefore may not reflect identical underlying processes. Our results suggest that a simple E/I dichotomy may not fully capture the relationship between neurochemical measures and perceptual outcomes during rivalry.

In the present sample, individual differences in GABA fluctuations were correlated with individual differences in mixed perception alterations following dark exposure despite no change in net GABA+ level or Glx/GABA ratio. These findings suggest that binocular rivalry may be more sensitive to changes within specific neurochemical pathways than to the net direction of E/I balance change alone. For example, increased Glx and decreased GABA+ can both be interpreted as shifts toward greater excitation within a conventional E/I framework, yet evidence linking binocular rivalry to visual-cortical neurochemistry has primarily involved GABA+ rather than Glx (van Loon et al., 2013; Robertson, Ratai and Kanwisher, 2016; Pitchaimuthu et al., 2017; Mentch et al., 2019). This contrasts with ocular dominance plasticity (Lunghi et al., 2015; Min et al., 2023), binocular disparity (Matuszewski et al., 2025) and action selection (Rodríguez-Nieto et al., 2025), where both Glx and GABA+ concentrations have been linked to behavioral performance. If reciprocal inhibitory interactions between the eyes depend in part on GABA concentrations in the visual cortex, then perturbations in GABA-related neurochemistry measured by MRS may be associated with changes in interocular competition regardless of whether GABA+ concentrations increase or decrease. Under this interpretation, larger perturbations may be associated with larger perceptual changes. Although speculative, this interpretation is consistent with our finding that the magnitude of GABA+ change was more strongly associated with changes in mixed perception than either the direction of GABA+ change or changes in the Glx/GABA ratio.

An alternative explanation for the increase in mixed perception is that dark exposure alters binocular processing through adaptation mechanisms that are independent of the neurochemical changes measured with MRS. Previous work shows that suppression weakens during prolonged rivalry viewing, with exclusive percepts gradually giving way to mixed perception (Klink et al., 2010). By this logic, dark exposure – which heightens sensitivity of each eye (Hess and Min, 2023) – should strengthen suppression and reduce mixed perception (Said and Heeger, 2013). However, our findings that dark exposure increased mixed perception are inconsistent with this prediction, suggesting that simple adaptation alone may not fully explain the observed increase in mixed perception. Importantly, we found no evidence that increased mixed perception was accompanied by a reduction in GABA+ concentrations in visual cortex, suggesting that changes in visual suppression cannot always be inferred directly from changes in GABA+ concentrations alone. Together, our findings suggest that individual differences in neurochemical fluctuations may be associated with perceptual changes even in the absence of measurable shifts in group-level E/I balance. These results suggest the importance of considering individual differences in neurochemical responses, in addition to mean E/I balance estimates, when inferring the relationship between metabolite concentrations from MRS and perceptual performance in humans.

Several limitations should be considered when interpreting the present findings. First, the sample size was relatively small ($n = 14$), which limits the precision of the estimated correlations and may have reduced statistical power (Vankelecom et al., 2024;Lengersdorff and Lamm, 2025) to detect weaker associations between neurochemical and perceptual measures. Second, the behavioral and MRS experiments were conducted on separate days. Although the same participants completed both protocols and dark exposure was applied using an identical procedure, this design prevents direct assessment of relationships between neurochemical and perceptual changes within a single session. Third, MRS measurements were acquired during a resting, task-free state with participants' eyes open rather than during the binocular rivalry task. Consequently, the measured metabolite concentrations do not reflect neurochemical processes occurring during perceptual competition. Future studies combining binocular rivalry with functional MRS may help clarify how moment-to-moment neurochemical fluctuations relate to perceptual dynamics before and after dark exposure.

Data and code availability statement

The data and script files are available online in the primary author's repository in Open Science Framework (https://osf.io/u3k8r).

Declaration of generative AI use

During preparation of the manuscript, the authors used ChatGPT to refine the grammar and clarity of the main text. The authors reviewed and edited the content as needed, and assume full responsibility for the text.

CRediT authorship contribution statement

Seung Hyun Min: Writing – review & editing, Writing – original draft, Visualization, Software, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Conceptualization. **Rongjie Hu:** Writing – review & editing, Software, Methodology, Data curation. **Nan Jiang:** Writing – review & editing, Methodology, Data curation, Conceptualization. **Liying Zou:** Writing – review & editing, Methodology, Data curation, Conceptualization. **Xiaoxiao Wang:** Writing – review & editing, Supervision, Software, Methodology, Investigation, Formal analysis, Conceptualization. **Jiawei Zhou:** Writing – review & editing, Validation, Supervision, Resources, Methodology, Investigation, Funding acquisition, Formal analysis, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

This work was support by a grant from the National Natural Science Foundation of China (32350410414) and a start-up fund (25062241-Y) from Zhejiang Sci-Tech University to S.M, as well as by grants to J.Z from the National Natural Science Foundation of China (82471118), National Key Research and Development Program of China grant (2023YFC3604104), Non-Profit Central Research Institute Fund of Chinese Academy of Medical Sciences (2023-PT320-04), and Project of State Key Laboratory of Ophthalmology, Optometry and Vision Science, Wenzhou Medical University (J02-20210203).

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.neuroimage.2026.122184.

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