Report

Experience-Driven Plasticity in Binocular Vision

P. Christiaan Klink,[1,2,*] Jan W. Brascamp,[3]
Randolph Blake,[3,4,*] and Richard J.A. van Wezel[1,2,5]
[1]Functional Neurobiology, Helmholtz Institute,
Utrecht University, 3584 CH Utrecht, The Netherlands
[2]Division of Pharmacology, Utrecht Institute for
Pharmaceutical Sciences, Utrecht University, 3508 TB Utrecht,
The Netherlands
[3]Vanderbilt Vision Research Center, Vanderbilt University,
Nashville, TN 37240, USA
[4]Brain and Cognitive Sciences, Seoul National University,
Seoul 151-742, South Korea
[5]Biomedical Signals and Systems, MIRA Institute for
Biomedical Technology and Technical Medicine,
Twente University, 7500 AE Enschede, The Netherlands

Summary

Experience-driven neuronal plasticity allows the brain to adapt its functional connectivity to recent sensory input. Here we use binocular rivalry [1], an experimental paradigm in which conflicting images are presented to the individual eyes, to demonstrate plasticity in the neuronal mechanisms that convert visual information from two separated retinas into single perceptual experiences. Perception during binocular rivalry tended to initially consist of alternations between exclusive representations of monocularly defined images, but upon prolonged exposure, mixture percepts became more prevalent. The completeness of suppression, reflected in the incidence of mixture percepts, plausibly reflects the strength of inhibition that likely plays a role in binocular rivalry [2]. Recovery of exclusivity was possible but required highly specific binocular stimulation. Documenting the prerequisites for these observed changes in perceptual exclusivity, our experiments suggest experience-driven plasticity at interocular inhibitory synapses, driven by the correlated activity (and also the lack thereof) of neurons representing the conflicting stimuli. This form of plasticity is consistent with a previously proposed but largely untested anti-Hebbian learning mechanism for inhibitory synapses in vision [3, 4]. Our results implicate experience-driven plasticity as one governing principle in the neuronal organization of binocular vision.

Results

Perceptual advantages of binocular vision, including stereopsis and enhanced contrast sensitivity through binocular summation, require integration of initially separated monocular streams of information. Mechanisms responsible for binocular integration are shaped by activity-dependent neural development, both prenatally, when ocular dominance columns are first established, and for several years postnatally, when binocular mechanisms are refined based on visual experience

*Correspondence: p.c.klink@uu.nl (P.C.K.), randolph.blake@vanderbilt.edu
(R.B.)

[5]. Whereas the neuronal components subserving binocular integration may not change much after this critical period, the computational mechanisms, likely reflected in synaptic connectivity and efficacy, may be continuously recalibrated in response to modified sensory experience. This ongoing neuronal fine tuning might in fact be the reason why some strabismus patients that have not adequately developed stereopsis during childhood can still acquire stereoscopic depth vision later in life through extensive visual therapy (for anecdotal evidence, see [6]).

Exposure to binocular rivalry stimuli [1] creates a well-controlled modified sensory context deviating from the system's standard in the sense that the brain receives incompatible, nonmatching inputs instead of matching ones. Under such conditions, binocular integration fails and, instead, observers tend to alternately perceive the monocular images. This perceptual cycling is commonly believed to arise from neural processes that include mutual inhibition between neuronal representations of the two images [1, 7, 8]. During smaller fractions of the time viewing rivalry, observers also transiently perceive various mixtures of both monocular images [2, 9, 10], the most common being transparent superimpositions of both images and patchwork-like zones of local monocular dominance termed "piecemeal" (Figure 1A). Mixtures suggest that even during rivalry, periods of partial binocular integration occur. The absolute predominance of different mixture percepts depends on stimulus features including size [11], spatial frequency [2, 9, 12], and global context [13], and the incidence of these lapses in perceptual exclusivity plausibly depends on the strength of mutual inhibition [2], a notion supported by simulations with existing binocular rivalry models [14, 15] (see Supplemental Results and Discussion and Figure S1 available online).

To test whether binocular integration is indeed a plastic mechanism that adapts to sensory experience, we presented the eyes with incompatible images for prolonged periods of time, sometimes interspersed with nonrival stimuli, while observers continuously reported whether they perceived either one of the exclusive monocular images or a mixture.

Experiment 1: Perceptual Exclusivity and Binocular Rivalry

Observers viewed rival stimuli for prolonged durations while tracking periods of exclusive dominance and mixed percepts (Figure 1A). The same rival images were presented to each eye throughout the experiment. If initial perceptual exclusivity in binocular rivalry were due to the "unnatural" sensory context of dissimilar images in the two eyes causing strong mutual inhibition and preventing binocular integration, we would expect exclusivity to progressively decrease while experience with the modified sensory context accumulates. As expected from earlier results [16], our observations confirmed this prediction (Figure 1B), demonstrating a substantial decrease in exclusivity over 35 min of rivalry (Figure 1B; Spearman rank correlation, $R = -0.46$, $p < 0.001$). Data points represent averaged data from 100 s rivalry trials, separated by 10 s rests.

The idea that the altered exclusivity in our experiment reflects experience-driven plasticity yields a second, more counterintuitive prediction: Exclusivity should not passively

A

Exclusive percepts   Mixed percepts

Left eye's   Right eye's   Piecemeal   Super-
image   image   imposition
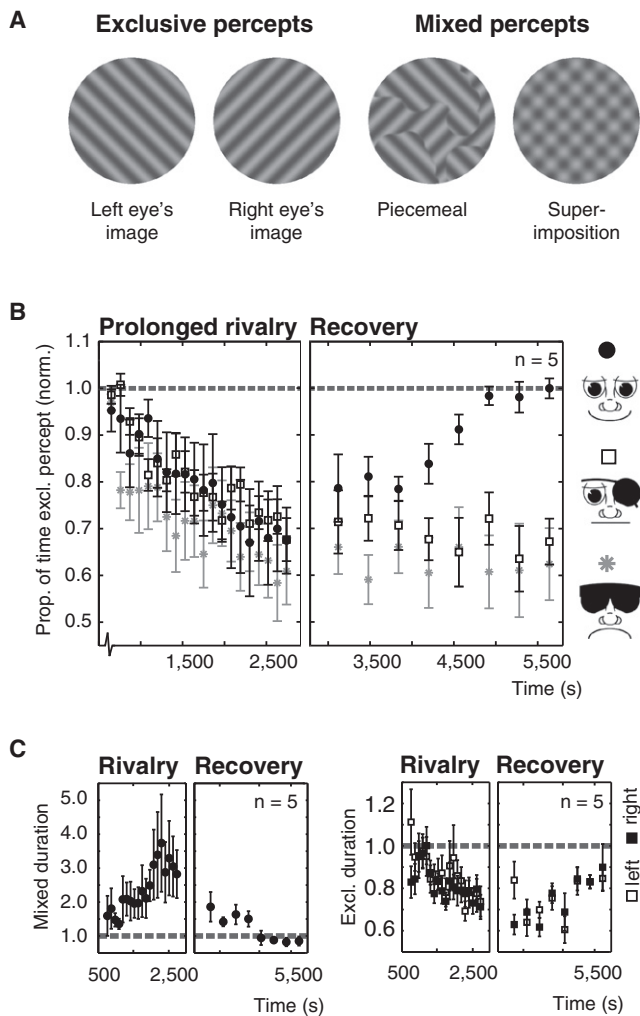
B

C

Figure 1. Dynamics of Perceptual Exclusivity

(A) Perceptual experiences during binocular rivalry. Exclusive percepts correspond entirely to one eye's stimulus. Mixed percepts resemble patch-like (piecemeal) or transparent superimpositions of the stimuli.

(B) The average proportion of exclusivity for five observers, plotted against time and normalized by individual baselines, determined in four rivalry trials directly preceding the experiment. In the recovery stage, observers experienced normal binocular vision (black circles), monocular vision only (white squares), or no visual stimulation at all (gray asterisks).

(C) The average epoch durations for mixed (left panel, black circles) and exclusive "left" and "right" percepts (right panel, white and black squares, respectively) of the both-eyes-stimulated condition.

Dashed lines represent baseline levels. Error bars represent standard error of the mean (SEM).

recover to baseline after having dropped during rivalry but should instead require correspondence of visual signals from both eyes. In the second part of our experiment, immediately following the first, recovery of exclusivity was investigated with periods of exposure to various conditions of monocular or binocular stimulation. In one condition, observers walked around the laboratory with both eyes open. The matching, natural visual input to both eyes should cause a recalibration of the binocular mechanisms and restrengthen the inhibition putatively weakened during rivalry. Because restrengthening should be evidenced by increased perceptual exclusivity, the periods of free viewing were interspersed with brief rivalry

trials. In a second condition, free viewing was replaced by episodes without visual stimulation that should leave exclusivity unaltered. A third condition contained periods of monocular stimulation where one eye was patched during free viewing.

Significant increases in the proportion of exclusive dominance indeed occurred when two eyes received matched stimulation during free viewing (Figure 1B, black circles; Spearman rank correlation, R = 0.75, p < 0.001), both because mixed-percept epochs became briefer and because exclusive percepts became longer (Figure 1C; Spearman rank correlation, R_{mix} = −0.68, p_{mix} < 0.001; R_{excl} = 0.45, p_{excl} < 0.01). Consistent with our prediction, no such recovery was observed throughout 48 min without visual stimulation (Figure 1B, gray asterisks; Spearman rank correlation, $R_{no\ stim}$ = −0.01, $p_{no\ stim}$ = 0.97). Recovery was also entirely absent in the third, monocular stimulation condition (Figure 1B, white squares; Spearman rank correlation, $R_{patched}$ = −0.08, $p_{patched}$ = 0.61), implying that binocular correspondence is essential for recalibration.

To further examine the failure of recovery with monocular stimulation, the first two authors subjected themselves to an extended period of continuous eye-patch wearing for 24 hr. Remarkably, decreased exclusivity levels barely recovered during this day of patching, yet recovery began immediately after both eyes received matched stimulation during free viewing (Supplemental Results and Discussion; Figure S2). The longevity of decreased exclusivity in the absence of binocular input is reminiscent of the enduring time course of contingent adaptation effects (e.g., [17]) and perhaps storage of noncontingent aftereffects [18–20]. The slow decay of adaptation in all of these cases could have a common cause: neurons encoding a specific adapting stimulus may retain their adapted state so as long as they are shielded from novel sensory experience, thereby precluding recalibration [17, 18, 20].

The results of these first experiments support experience-driven plasticity in the connectivity between neuronal representations involved in binocular rivalry by implying both the weakening and restrengthening of inhibition in the anticipated conditions. Although the necessity of binocular stimulation is clear, several remaining questions regarding the exact prerequisites for the observed changes in exclusivity prompted the following experiments.

Experiment 2: Decrease of Perceptual Exclusivity

To establish the prerequisites of decreasing exclusivity, we performed two variations of our first experiment in which we temporarily inverted the stimulus-eye configuration on every fifth trial ("opposite-configuration trials") so that the same monocular stimuli were presented to the opposite eyes. Although this manipulation leaves the global competition between binocular stimulus representations unaffected, it does activate different monocular neurons on those specific opposite-configuration trials. Figure 2A demonstrates the results using the same stimuli as in experiment 1. The opposite-configuration trials (white squares) had significantly higher levels of exclusivity than their temporal neighbors (Figure 2A, gray bands; paired t test, p < 0.05). Additionally, exclusivity decreased only for the eye-stimulus configuration used in the majority of trials (Spearman rank correlation, $R_{majority}$ = −0.48, $p_{majority}$ < 0.001; $R_{opp\ config}$ = −0.22, $p_{opp\ config}$ = 0.36).

Whereas superimposition mixture percepts may be readily understood in terms of weak inhibitory gain, the occurrence
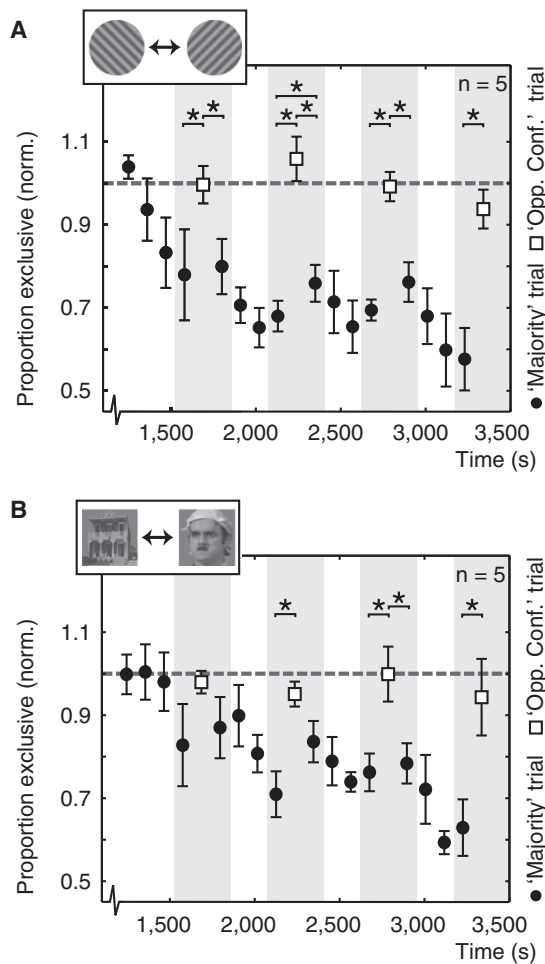
Figure 2. Prerequisites for Decreasing Exclusivity

(A) The average proportion of exclusive grating percepts over time for five observers. The eye-stimulus configuration was the same for most trials ("majority trials," black circles) but was switched in some interleaved trials ("opposite configuration trials," white squares).
(B) Similar to (A), but here the monocular images were complex pictures of a house and a face, not orthogonal sinusoidal gratings.
Dashed lines represent baseline exclusivity; *p < 0.05; error bars represent SEM.

representations of rivaling images comprising eye-of-origin information. If eye-of-origin information were not involved, the stimuli in the majority of trials and the opposite-configuration trials should be equivalent and yield equivalent results. The eye specificity is consistent with current thinking about binocular rivalry as a hierarchical process involving multiple stages of visual processing [22, 23].

Experiment 3: Recovery of Perceptual Exclusivity
We next investigated the requirements for restrengthening of inhibition more closely. When binocular free viewing in experiment 1 caused recovery, both eyes received matching naturalistic input containing a broad range of orientations and spatial frequencies, presumably including those of our rivalry targets. To investigate whether recovery merely requires binocular correspondence or requires specific binocular correspondence of the rivaling stimulus features, we performed experiments in which we replaced our rivalry gratings with a high-contrast plaid stimulus on every fifth trial. "Matching" plaids with the same spatial frequency and orientations as the rivaling gratings (Figure 3A) were presented to both eyes simultaneously (Figure 3B, black circles) or one eye at a time, alternating between eyes every few seconds (Figure 3B, gray asterisks). Plaids with different spatial frequency and orientations (Figure 3A) were also presented to both eyes simultaneously (Figure 3B, white squares). Figure 3C compares the exclusivity levels between trials directly preceding and following plaid presentations. Only binocularly presented matching plaids evoked a significant recovery of exclusivity (paired t tests, $p_{binocular\ match} < 0.001$; $p_{monocular\ match} = 0.10$; $p_{binocular\ no\ match} = 0.35$), supporting the hypothesis that restrengthening of inhibition only occurs during coinciding activity of eye-specific orientation- and spatial-frequency-tuned neurons. This also argues against an alternative hypothesis of reduced exclusivity through contrast adaptation. In principle, such adaptation might reduce exclusivity by lowering the activity of suppressing neurons. However, during presentation of matching plaid stimuli, when the same stimulus features are present as during rivalry, contrast adaptation should continue, causing exclusivity to further reduce, not recover like we observed.

Experiment 4: Replay Rivalry
Our results suggest that prolonged binocular rivalry weakens interocular inhibition through recalibration of binocular integration mechanisms in response to cumulative experience with nonfusible input. If such experience-driven binocular plasticity is a generic property of visual perception, the choice for rivalry stimuli should not be essential. Monocular, nonrivaling stimulation might also weaken inhibition if it activates neurons corresponding to one eye without simultaneously activating their counterparts belonging to the other eye. We tested this prediction using the reported percept durations of baseline rivalry trials to create "replay trials" in which individual eyes were alternately presented with their corresponding monocular images. This manipulation provides the required activity patterns without evoking rivalry (Figure 4A). Observers viewed three sets of two monocular replay trials followed by a single rivalry trial to measure exclusivity. The decreasing exclusivity following replay trials depicted in Figure 4B (t tests, p < 0.05) favors an interpretation in which experience-driven plasticity is not restricted to rivalry but serves as a generic principle of binocular vision.
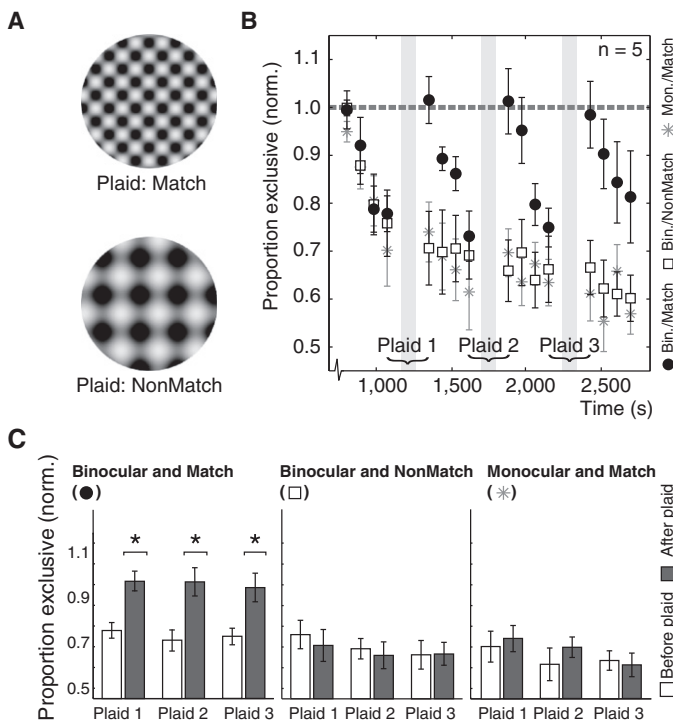
of piecemeal mixtures more likely reflects weak inhibitory spatial coherence or weak excitatory lateral connectivity [13, 21]. We repeated the experiment using images of a house and a face as rival targets to establish whether changes of exclusivity also occur with more complex images for which spatial coherence is particularly strong. Again, exclusivity decreased for the major eye-stimulus configuration, but not for the opposite-configuration trials (Figure 2B; Spearman rank correlation, $R_{majority} = -0.65$, $p_{majority} < 0.001$; $R_{opp\ config} = -0.15$, $p_{opp\ config} = 0.54$). An additional control experiment designed to disentangle the relative contributions of superimposition and piecemeal percepts further suggested that decreases in exclusivity were predominantly caused by increases in the incidence of superimposition (Supplemental Results and Discussion; Figure S3).

The opposite-configuration results support the idea that inhibitory connections involved in experience-driven plasticity are at least partially interocular, promoting inhibition between

A

Plaid: Match

Plaid: NonMatch

B

C

Binocular and Match (●)

Binocular and NonMatch (□)

Monocular and Match (✳)

Figure 3. Prerequisites for Recovery of Decreased Exclusivity

(A) The plaid stimuli that were interleaved with rivalry trials. Matching plaids had the same components as the rivaling gratings, whereas nonmatching plaids' components had different spatial frequencies and orientations.

(B) The average proportion of normalized exclusivity over time for five observers. Rivalry trials were interleaved with plaid presentations (gray bands). Matching plaids were presented simultaneously to both eyes (black circles) or one eye (gray asterisks). Nonmatching plaids were always presented to two eyes (white squares). The dashed line represents baseline exclusivity.

(C) Exclusivity, compared between rivalry trials that directly preceded (white bars) and followed (gray bars) plaid presentation.

*p < 0.05; error bars represent SEM.

Discussion

Experience literally changes our view of the world. Neuronal processes converting retinal images to conscious perception constantly adapt to changing sensory contexts. Our results here demonstrate that upon prolonged exposure to binocular rivalry stimuli, the nature of the accompanying perceptual experience progressively changes. Where observers initially perceive mostly alternations between exclusive representations of monocular images, mixtures of the two images become more prevalent over time [16]. Building upon the idea that binocular rivalry involves inhibition between neuronal populations representing competing images [1, 7, 8], we suggest that the rise in predominance of mixed percepts is caused by weakening of inhibitory efficacy [2].

Anti-Hebbian Plasticity

A theoretical framework for inhibitory plasticity in vision has been constructed around so-called "anti-Hebbian" inhibitory synapses [3, 4]. Hebbian synapses are well known as a neuronal principle for experience-driven plasticity. The basic idea is that when a presynaptic excitatory neuron participates in successfully activating a postsynaptic neuron, their synaptic bond is strengthened and the correlation between their response patterns increases. Whereas there is abundant biological evidence for Hebbian learning in synapses mediating excitatory interactions [24, 25], the related principle for inhibitory connections has received far less attention. Extending Hebb's postulate, Barlow and Földiák have proposed that inhibitory interactions are similarly strengthened and weakened by coinciding pre- and postsynaptic activity or a lack thereof [3]. Because such a plasticity scheme decorrelates pre- and postsynaptic activity, it is sometimes dubbed "anti-Hebbian" [26] (a term also used for several other decorrelating synaptic mechanisms [27]). Anti-Hebbian plasticity is inherent

in several models of unsupervised neuronal learning (e.g., [26, 28]), and an indirect route via inhibitory interneurons has been physiologically demonstrated in several species and brain structures [29–32]. However, plasticity rules for direct inhibitory synapses appear to be more variable [25], and although such anti-Hebbian learning has been suggested in the context of contingent visual aftereffects [3, 4], pattern adaptation [33], and center-surround suppression [34], direct behavioral evidence is sparse.

Our binocular rivalry results are consistent with anti-Hebbian learning mechanisms for interocular inhibition in binocular vision. Assuming that perceptual dominance of one rival image indicates successful suppression of the competing neuronal representation, dominance may entail activity in presynaptic neurons representing the dominant image without equivalent activity in the postsynaptic neurons encoding the (suppressed) opposite image. These are exactly the conditions for which anti-Hebbian weakening of inhibitory efficacy was postulated, explaining why initially high perceptual exclusivity should progressively decrease with viewing time. Furthermore, the anti-Hebbian principle predicts that (re)strengthening of inhibition would require simultaneous activation of the same neurons involved in rivalry. This can arguably be achieved by presenting binocularly corresponding stimuli with features to which those specific neurons are tuned. Our experiments demonstrate both the predicted drop in perceptual exclusivity and the expected dependence of recovery on stimulus features.

Plasticity and Rivalry

Previously demonstrated changes in perceptual experience with prolonged or repeated rivalry include short-term slowing of perceptual switch rates during single binocular rivalry trials [35, 36] and long-term speeding of switch rates when sessions are repeated over many days [36]. Whereas short-term effects were explained by contrast-adaptation buildup [35, 36], long-term effects were attributed to plasticity in neuronal responses and/or connectivity within multiple brain areas [36]. Because none of the abovementioned studies included the dynamics of mixture percepts in their binocular rivalry evaluation, it is difficult to unify the changes in switch rate with our changes of binocular integration. However, one emerging notion is that the adult visual system may be more plastic than previously realized, and future studies of binocular rivalry need to appreciate that exposure to rival stimuli may cause plastic changes in the very neuronal mechanisms targeted for study.

The many similarities and differences in the dynamics of binocular rivalry and other forms of perceptual rivalry [7, 22, 35, 37–39] have promoted the idea that different types of
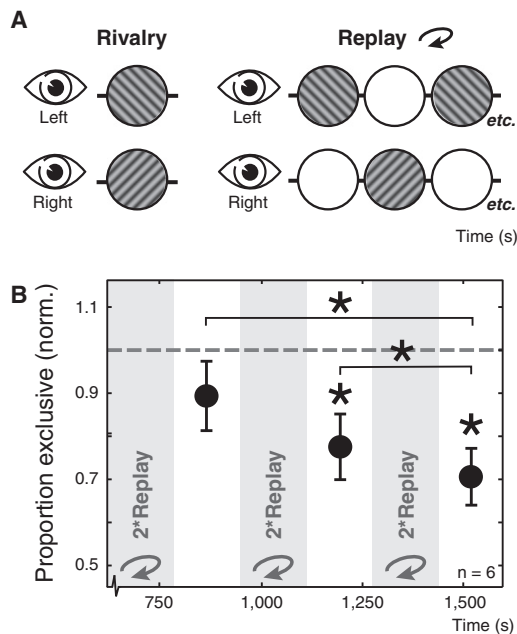
Figure 4. The Effect of Monocular Replay Rivalry

(A) Whereas during rivalry, both eyes are simultaneously stimulated with conflicting images, replay rivalry consists of alternating monocular stimulations with a temporal structure based on individual perceptual reports during real rivalry.

(B) The average proportion of normalized exclusivity in three rivalry trials that were each preceded by two replay trials (gray bands). The dashed line represents baseline exclusivity; *p < 0.05; error bars represent SEM.

rivalry, although perhaps resolved at different processing stages, may share common computational components in their rivalry-resolving mechanisms [7]. Because mutual inhibition is conceivably one of those components [7], it would be interesting to know whether plasticity of inhibitory efficacy also influences other forms of rivalry. The reduced exclusivity observed in our study proved to be specific to eye-stimulus configuration, locating the proposed plasticity mechanism at a stage of binocular rivalry processing that includes eye-of-origin information [22, 23]. Still, this does not entirely preclude the possibility of inhibitory plasticity in other forms of rivalry or at other processing levels. Furthermore, it implies that plastic interocular inhibition may be a general mechanism of binocular vision, raising the intriguing question of what might happen if exposure to rival stimulation were prolonged for hours or days, impractical though it might be to find out.

Conclusions

Our findings suggest experience-driven (anti-Hebbian) plasticity as one governing principle in the neuronal organization of binocular vision. It is tempting to envision this mechanism as a means for interocular gain control during binocular combination. It could balance monocular signals so that the perceived contrast and surface lightness are not noticeably different between binocular and monocular viewing [40]. On this view, our binocular rivalry experiments reveal the operation of such an inhibitory mechanism and its dynamic modification. The experience-driven plasticity we have demonstrated may provide important clues toward answering the longstanding question of how rivalry and stereopsis can emerge from a single neuronal organization of binocular vision [40–44].

Experimental Procedures

Observers viewed stimuli through a mirror stereoscope in a quiet darkened room. Rival stimuli were surrounded by an alignment ring to facilitate binocular fusion. Observers continuously reported perceptual experience by pressing buttons on a keyboard. One of two buttons was held while observers exclusively perceived the corresponding monocular stimulus. Both buttons were released when mixtures were perceived. The basic experimental paradigm consisted of a baseline determination followed by two stages differing in the timing of stimulus presentation. During baseline determination, individual observers' levels of exclusivity were established with stimulus presentations lasting 100 s, separated by 100 s rests during which observers viewed the alignment frame only. During the first part of the actual experiment, stimulus presentations also lasted 100 s, but rests were reduced to 10 s. In experiment 1, a second experimental phase comprised stimulus presentations of 60 s and rests of 300 s. These long rests consisted of 240 s of predefined visual input (depending on the condition) and 60 s of uniform field adaptation during which observers viewed a gray screen. For all rivalry trials, we calculated proportions of exclusivity as the sum of all exclusive percept durations divided by the total trial duration. These proportions were normalized by the average baseline proportion of exclusivity for each observer. For more details, see Supplemental Experimental Procedures.

Supplemental Information

Supplemental Information includes Supplemental Results and Discussion, Supplemental Experimental Procedures, and three figures and can be found with this article online at doi:10.1016/j.cub.2010.06.057.

References

1. Alais, D. and Blake, R., eds. (2005). Binocular Rivalry (Cambridge, MA: MIT Press).
2. Hollins, M. (1980). The effect of contrast on the completeness of binocular rivalry suppression. Percept. Psychophys. 27, 550–556.
3. Barlow, H.B., and Földiák, P. (1989). Adaptation and decorrelation in the cortex. In The Computing Neuron, C. Miall, R.M. Durbin, and G.J. Mitchison, eds. (Wokingham, UK: Addison-Wesley), pp. 54–72.
4. Barlow, H.B. (1990). A theory about the functional role and synaptic mechanism of visual after-effects. In Vision: Coding and Efficiency, C.B. Blakemore, ed. (Cambridge: Cambridge University Press), pp. 363–375.
5. Katz, L.C., and Crowley, J.C. (2002). Development of cortical circuits: Lessons from ocular dominance columns. Nat. Rev. Neurosci. 3, 34–42.
6. Barry, S.R. (2009). Fixing My Gaze: A Scientist's Journey into Seeing in Three Dimensions (New York: Basic Books).
7. Klink, P.C., van Ee, R., and van Wezel, R.J.A. (2008). General validity of Levelt's propositions reveals common computational mechanisms for visual rivalry. PLoS ONE 3, e3473.
8. Wilson, H.R. (2007). Minimal physiological conditions for binocular rivalry and rivalry memory. Vision Res. 47, 2741–2750.
9. Yang, Y., Rose, D., and Blake, R. (1992). On the variety of percepts associated with dichoptic viewing of dissimilar monocular stimuli. Perception 21, 47–62.

10. Brascamp, J.W., van Ee, R., Noest, A.J., Jacobs, R.H., and van den Berg, A.V. (2006). The time course of binocular rivalry reveals a fundamental role of noise. J. Vis. *6*, 1244–1256.

11. Blake, R., O'Shea, R.P., and Mueller, T.J. (1992). Spatial zones of binocular rivalry in central and peripheral vision. Vis. Neurosci. *8*, 469–478.

12. O'Shea, R.P., Sims, A.J., and Govan, D.G. (1997). The effect of spatial frequency and field size on the spread of exclusive visibility in binocular rivalry. Vision Res. *37*, 175–183.

13. Kovács, I., Papathomas, T.V., Yang, M., and Fehér, A. (1996). When the brain changes its mind: Interocular grouping during binocular rivalry. Proc. Natl. Acad. Sci. USA *93*, 15508–15511.

14. Wilson, H.R., Blake, R., and Lee, S.-H. (2001). Dynamics of travelling waves in visual perception. Nature *412*, 907–910.

15. Noest, A.J., van Ee, R., Nijs, M.M., and van Wezel, R.J.A. (2007). Percept-choice sequences driven by interrupted ambiguous stimuli: A low-level neural model. J. Vis. *7*, 10, 1–14.

16. Hollins, M., and Hudnell, K. (1980). Adaptation of the binocular rivalry mechanism. Invest. Ophthalmol. Vis. Sci. *19*, 1117–1120.

17. Vul, E., Krizay, E., and MacLeod, D.I.A. (2008). The McCollough effect reflects permanent and transient adaptation in early visual cortex. J. Vis. *8*, 4, 1–12.

18. Thompson, P.G., and Movshon, J.A. (1978). Storage of spatially specific threshold elevation. Perception *7*, 65–73.

19. Verstraten, F.A., Fredericksen, R.E., Grüsser, O.J., and van de Grind, W.A. (1994). Recovery from motion adaptation is delayed by successively presented orthogonal motion. Vision Res. *34*, 1149–1155.

20. van de Grind, W.A., van der Smagt, M.J., and Verstraten, F.A.J. (2004). Storage for free: A surprising property of a simple gain-control model of motion aftereffects. Vision Res. *44*, 2269–2284.

21. Alais, D., and Melcher, D. (2007). Strength and coherence of binocular rivalry depends on shared stimulus complexity. Vision Res. *47*, 269–279.

22. Blake, R., and Logothetis, N.K. (2002). Visual competition. Nat. Rev. Neurosci. *3*, 13–21.

23. Wilson, H.R. (2003). Computational evidence for a rivalry hierarchy in vision. Proc. Natl. Acad. Sci. USA *100*, 14499–14503.

24. Sejnowski, T.J. (2003). The once and future Hebb synapse. Can. Psychol. *44*, 17–20.

25. Caporale, N., and Dan, Y. (2008). Spike timing-dependent plasticity: A Hebbian learning rule. Annu. Rev. Neurosci. *31*, 25–46.

26. Földiák, P. (1990). Forming sparse representations by local anti-Hebbian learning. Biol. Cybern. *64*, 165–170.

27. Nelson, S.B. (2004). Hebb and anti-Hebb meet in the brainstem. Nat. Neurosci. *7*, 687–688.

28. Deco, G., and Obradovic, D. (1995). Decorrelated Hebbian learning for clustering and function approximation. Neural Comput. *7*, 338–348.

29. Bell, C.C., Han, V.Z., Sugawara, Y., and Grant, K. (1997). Synaptic plasticity in a cerebellum-like structure depends on temporal order. Nature *387*, 278–281.

30. Lamsa, K.P., Heeroma, J.H., Somogyi, P., Rusakov, D.A., and Kullmann, D.M. (2007). Anti-Hebbian long-term potentiation in the hippocampal feedback inhibitory circuit. Science *315*, 1262–1266.

31. Tzounopoulos, T., Kim, Y., Oertel, D., and Trussell, L.O. (2004). Cell-specific, spike timing-dependent plasticities in the dorsal cochlear nucleus. Nat. Neurosci. *7*, 719–725.

32. Yazaki-Sugiyama, Y., Kang, S., Câteau, H., Fukai, T., and Hensch, T.K. (2009). Bidirectional plasticity in fast-spiking GABA circuits by visual experience. Nature *462*, 218–221.

33. Carandini, M., Barlow, H.B., O'Keefe, L.P., Poirson, A.B., and Movshon, J.A. (1997). Adaptation to contingencies in macaque primary visual cortex. Philos. Trans. R. Soc. Lond. B Biol. Sci. *352*, 1149–1154.

34. Falconbridge, M., and Badcock, D.R. (2006). Implicit exploitation of regularities: Novel correlations in images quickly alter visual perception. Vision Res. *46*, 1331–1335.

35. van Ee, R. (2005). Dynamics of perceptual bi-stability for stereoscopic slant rivalry and a comparison with grating, house-face, and Necker cube rivalry. Vision Res. *45*, 29–40.

36. Suzuki, S., and Grabowecky, M. (2007). Long-term speeding in perceptual switches mediated by attention-dependent plasticity in cortical visual processing. Neuron *56*, 741–753.

37. Brascamp, J.W., van Ee, R., Pestman, W.R., and van den Berg, A.V. (2005). Distributions of alternation rates in various forms of bistable perception. J. Vis. *5*, 287–298.

38. Pearson, J., and Clifford, C.W.G. (2005). When your brain decides what you see: Grouping across monocular, binocular, and stimulus rivalry. Psychol. Sci. *16*, 516–519.

39. Klink, P.C., van Ee, R., Nijs, M.M., Brouwer, G.J., Noest, A.J., and van Wezel, R.J.A. (2008). Early interactions between neuronal adaptation and voluntary control determine perceptual choices in bistable vision. J. Vis. *8*, 16, 1–18.

40. Ding, J., and Sperling, G. (2006). A gain-control theory of binocular combination. Proc. Natl. Acad. Sci. USA *103*, 1141–1146.

41. Andrews, T.J., and Purves, D. (1997). Similarities in normal and binocularly rivalrous viewing. Proc. Natl. Acad. Sci. USA *94*, 9905–9908.

42. Blake, R., Yang, Y.D., and Wilson, H.R. (1991). On the coexistence of stereopsis and binocular rivalry. Vision Res. *31*, 1191–1203.

43. Livingstone, M.S. (1996). Differences between stereopsis, interocular correlation and binocularity. Vision Res. *36*, 1127–1140.

44. Grossberg, S., Yazdanbakhsh, A., Cao, Y., and Swaminathan, G. (2008). How does binocular rivalry emerge from cortical mechanisms of 3-D vision? Vision Res. *48*, 2232–2250.