UNIVERSITÀ DEGLI STUDI FIRENZE

DOTTORATO DI RICERCA IN NEUROSCIENZE

CICLO XXXVI

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Behavioural, pupillometric and imaging evidence of experience-dependent changes in visual perception

Settore Scientifico Disciplinare BIO /09

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Anni 2020/2023

Summary

This thesis presents four experiments involving adult human participants, where we combined a range of techniques (psychophysics, pupillometry and neuroimaging) to explore the many ways in which sensory processing adapts to the context, as set by behavioural goals (attention) or experience (sensory deprivation).

Chapter 1 (General Introduction) presents our main methodological tools: binocular rivalry, the classical paradigm to investigate ocular dominance and binocular vision; pupillometry, a non-invasive technique to index the strength of visual representations; monocular deprivation, a standard paradigm to boost or suppress visual cortical representations; and functional MRI (magnetic resonance imaging), which allowed us to study the functional connectivity of the visual brain at rest.

In chapter 2, we analyzed the reliability of a set of indices that may be extracted from binocular rivalry and have been traditionally associated with a variety of perceptual and cognitive functions. On the one hand, our findings advise caution when interpreting the association between stable psychological characteristics (e.g., personality traits) and the rate of switching or the probability of fused percepts, given the state-dependent variability of these parameters. On the other hand, they provide strong support for the use of binocular rivalry to track ocular dominance, given the excellent stability and reliability of this parameter.

Chapter 3 proceeded to using this binocular rivalry-based index of ocular dominance for investigating the effects of endogenous cueing. We combined this with a pupillometry measurement, to objectively index the dominance of the two stimuli during rivalry. We found that attention biases binocular rivalry dynamics, boosting the dominance of the cued stimulus; however, it does not enhance the associated pupil response. These results are consistent with two interpretations. One possibility is that attention biases rivalry dynamics without affecting the perceptual representation of the stimuli, but merely shifting the decision criterion that participants use for reporting their percepts. Another possibility is that attention does affect the perceptual representation of the cued stimulus, but only when there is competition between the two stimuli (e.g., during mixed percept, when we do see a transient pupil-size modulation); once one of the two stimuli has gained exclusive perceptual dominance, there is no more room for attention to enhance or suppress visual representations. Preliminary evidence against this second possibility was acquired in Chapter 4, which used the same

combined paradigm to investigate the perceptual consequences of short-term sensory deprivation. Two hours of monocular deprivation reliably boosted the dominance of the stimuli in the deprived eye, replicating previous studies and altering rivalry dynamics in a way that was qualitatively similar to the effects of endogenously cueing attention. However, contrary to what was found with attention cueing, here we observed that the perceptual boost was accompanied by a measurable change in the associated pupil responses. Thus, sensory deprivation had an effect on the dynamics of binocular rivalry that, unlike the effect of attention cueing, was faithfully reflected by the pupil-size modulations. This supports the concept that short-term sensory deprivation reliably, although transiently, affects the strength of visual representations, boosting visually evoked responses to stimuli in the deprived eye in a way that is reflected in perception as well as in basic visually evoked responses like pupil-size modulations.

Chapter 5 showed that the effects of sensory deprivation extend beyond perceptual dynamics and visually evoked responses, influencing the functional connectivity of the visual brain at rest. In a series of fMRI tests, we found that 2h of monocular deprivation were sufficient to reduce the functional connectivity of the visual cortex with the ventral pulvinar, while leaving the connectivity with the lateral geniculate nucleus unaltered. We propose that this reflects a reconfiguration of the flow of information within the visual system, which could change the way bottom-up sensory evidence (sensory input) is combined with top-down predictions (what we expect to see, which may be carried through cortico-pulvino-cortical connections). As discussed in Chapter 6 (general discussion), this provides initial evidence for the pathway through which contextual factors could affect sensory evidence – without interfering with the first swipe of signals from the periphery through the sensory cortex but modulating the recurrent exchange of information across brain areas, which combines sensory data with a priori information.

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1 Chapter 1 – General Introduction

If two observers were shown identical images, they would be very unlikely to have identical perceptual experiences. Even when the same observer is repeatedly exposed to the same image, their perceptual experience would exhibit variability.

This is because our perception of the environment is not merely a reflection of the external world but is rather a dynamic and subjective construction of reality. It constitutes an active process influenced by past experiences, expectations, and attentional mechanisms. As such, the study of perception extends far beyond the mere processing of sensory input and delves into the intricate neural mechanisms that give rise to our conscious experiences. Throughout this dissertation, I will focus on how these modulatory signals shape visual perception.

1.1 Binocular rivalry and competition between eyes

A paradigmatic example of how perception goes beyond mirroring the external reality is the phenomenon of binocular rivalry. Binocular rivalry is a form of visual bistability that arises when incompatible images are presented to the two eyes. Despite the absence of any physical change in the stimuli, individuals experience perceptual alternations between the two stimuli at irregular intervals (Brascamp et al., 2015). The most interesting aspect of binocular rivalry is having unchanging physical stimulation and varying awareness, which allows for a comparison of neural events between moments that differ only for the contents of consciousness, not the physical input. This property gained binocular rivalry the title of "window into consciousness" (Leopold & Logothetis, 1999) and it has been useful for studying a variety of brain functions.

Despite the interest it received, the nature of the competitive interactions that mediate binocular rivalry is partially unresolved (Tong, 2001). The core assumption is that rivalry arises from mutual inhibition between monocular neurons. When one monocular input is stronger than the other, it activates an inhibitory neuron that can entirely suppress inputs from the other eye. However, the response to the dominating input progressively adapts and thereby generates progressively weaker inhibition; this eventually leads to the other eye breaking suppression and becoming dominant. The underlying circuit may be identified in inhibitory feedback signals from V1 to monocular layers of the lateral geniculate nucleus (Lehky, 1988),

but it could be applied equally well to competitive lateral interactions among monocular V1 neurons as has been proposed in Blake's model (Blake, 1989). This eye-based competition framework is supported by several bits of behavioral evidence (Blake et al., 1980; Fox & Check, 1972; Wales & Fox, 1970). For example, if a left-eye vertical grating is dominant and a right-eye horizontal grating is suppressed, a sudden exchange of the two monocular patterns leads to the perception of the left-eye horizontal grating (Blake et al., 1980), strongly suggesting that the dominant/suppressed state is attached to the eye, not to the stimulus, consistent with the predictions of interocular competition. This model has undergone evaluation also through neurophysiological and neuroimaging studies, revealing a strong alignment between neural activity and subjective perception (Tong, 2001). In line with pioneering EEG studies (COBB et al., 1967; Lansing, 1964), subsequent MEG investigations demonstrated that binocular rivalry induces extensive neural modulations not only in the occipital cortex but also in temporal and frontal regions (Tononi, 1998). Functional MRI studies aimed to identify the source of these rivalry-related responses and suggested that the competition underlying binocular rivalry is already resolved by the time visual information reaches the extra-striate cortex (Tong et al., 1998), and its resolution may be achieved within the primary (or striate) visual cortex, at a level where representations are still monocular (Tong & Engel, 2001). This model posits a direct connection between perceptual dominance during binocular rivalry and eye-of-origin strength, which implies that binocular rivalry should be an ideal tool to assess eye dominance (see Ooi & He, 2020). In chapter two, we put this assumption to a test, examining the many different parameters that can be used to capture the dynamics of perceptual alternations (dominance proportions, speed of rivalry alternations, occurrence of mixed percepts) and assessing their reliability.

1.2 Binocular rivalry and competition between stimuli

The eye-based competition model is well supported by several bits of experimental evidence, but it has also been challenged by some experimental observations (Lehmkuhle & Fox, 1975; Wade & Wenderoth, 1978). One of these is the phenomenon of interocular grouping rivalry, which occurs when presenting two different but complementary images to the two eyes, which are perceptually bound into a coherent picture (Kovacs et al., 1996). This interocular grouping would not be predicted by any eye competition model, which would predict only the

alternation of monocular percepts. Based on this and other findings, an alternative model was formulated a pattern-competition model (Leopold & Logothetis, 1999; Logothetis et al., 1996) where reciprocal inhibition occurs between different patterns rather than between monocular channels. There was also a proposal for a hybrid model, where inhibitory interactions could take place both between monocular neurons (interocular competition) and between pattern-selective neurons (pattern competition;(Tong et al., 2006)).

Irrespectively of the elements competing for perceptual dominance, eye- or pattern-selective, the competition has been traditionally related to physical strength: the physically stronger stimulus, the one triggering the greater sensory responses, wins. Stimulus strength was first related by Levelt (LEVELT, 1966)to stimulus features as density, luminance contrast, and sharpness of image contours and later joined by color contrast and motion coherence (Brascamp et al., 2015).

However, recent studies have shown that the competition between the rivalling stimuli can be biased beyond physical strength, by cognitive factors like training (Dieter et al., 2016), reward (Marx & Einhauser, 2015; Wilbertz et al., 2017), emotional content (Alpers et al., 2011) and attention.

1.3 Binocular rivalry and attention

Exogenous attention, often referred to as stimulus-driven attention, is the result of salient external stimuli that automatically capture our awareness (K. N. Nguyen et al., 2020). In the context of binocular rivalry, exogenous attention can dramatically influence the duration and dominance of one image over the other (Chong et al., 2005; Ooi & He, 1999) and initiate a perceptual alternation (Paffen & Van der Stigchel, 2010). Moreover, drawing attention away from the rivalry stimuli can slow down the perceptual alternation rate (Alais, van Boxtel, et al., 2010; Brascamp & Blake, 2012; Paffen et al., 2006) or even abolish the alternations altogether (Zhang et al., 2011). Endogenous attention, on the other hand, is driven by internal goals, intentions, or cognitive processes. In the context of binocular rivalry, endogenous attention can be voluntarily directed toward one of the rival images, amplifying its dominance (Chong et al., 2005; Hancock & Andrews, 2007; Meng & Tong, 2004; Ooi & He, 1999).

The observation that not only the physically stronger stimulus wins, but also the one where we direct our (endogenous or exogenous) attention, led to revising the definition of stimulus strength in the context of binocular rivalry.

One possibility is that attention acts by amplifying the sensory responses to the attended stimuli, increasing their perceptual or "effective" strength (for a review see Carrasco & Barbot, 2019) in rivalry like in the standard non-rivalrous situations; supporting evidence mainly comes from behavioural measures, which rely exclusively on introspection. This is problematic because perceptual reports do not reflect only the dynamic construction of perception but also depend on an additional factor, decision. Every time we perceive a stimulus, we categorize it in our minds; this phenomenon is called perceptual decision-making and attention has been convincingly shown to drive this process (Rangelov & Mattingley, 2020; Yang, 2017). Our recent work, described in Chapter 3, aimed at investigating whether endogenous attention affects perception by altering the effective strength of the cued stimulus, or rather by biasing the decision criteria that guide its categorization. We did so by combining binocular rivalry and the relative behavioural reports of perceptual dominance, with the use of a non-invasive, objective measure of the content of perception: pupil size.

1.4 Pupil size as a marker of perceptual strength

Two muscles are responsible for changing the size of the pupil: the iris sphincter muscle, which constricts the pupil, and the iris dilator muscle, which dilates it (Kardon, 2005; McDougal & Gamlin, 2008). When luminance increases, the pupil constricts. This pupillary light response (PLR) is largely supported by a subcortical reflex pathway. Luminance information from the retina is relayed to the midbrain pretectal nucleus, which in turn projects to the Edinger-Westphal nucleus, which finally induces contraction of the pupillary sphincter (McDougal & Gamlin, 2014). A separate circuit supports pupil dilation, as produced by luminance decrements as well as changes in arousal levels. Noradrenaline released from the Locus Coeruleus stimulates α-adrenoceptors with an excitatory influence on the iris dilator muscle and an inhibitory influence on the Edinger–Westphal nucleus. The net result of these effects is a pupil dilation response that, in conditions of constant illumination, accompanies the increase of sympathetic tone (Steinhauer et al., 2004).

Besides these subcortical circuits, pupil responses are likely to be modulated by cortical signals, given that they are not only set by the physical strength of the visual input, but also affected by the way it is selected, processed, and interpreted (for reviews, Binda & Murray, 2015; Mathôt, 2018; Mathôt & Van der Stigchel, 2015). A prominent example of this phenomenon is the attentional modulation of pupillary light responses (Binda et al., 2013a, 2014; Binda & Murray, 2015; Bombeke et al., 2016; Ebitz et al., 2014; Mathôt et al., 2013; Mathôt et al., 2014; Olmos-Solis et al., 2018; Unsworth & Robison, 2016). Several studies have shown that covertly attending to a brighter or darker stimulus is sufficient to trigger a pupil response, just like (although much weaklier than) directly looking at something that is bright or dark (Binda et al., 2013a, 2014; Binda & Murray, 2015b; Bombeke et al., 2016; Ebitz et al., 2014; Mathôt et al., 2013, 2014; Naber et al., 2013; Olmos-Solis et al., 2018; Unsworth & Robison, 2016). This effect is so robust that it can even be used to decode whether people are covertly attending to something bright or dark, with around 90% accuracy on a single-trial level (Mathôt et al., 2016). Neurophysiological studies have shown similar effects (Ebitz & Moore, 2017; C.A. Wang & Munoz, 2016). Ebitz and his group in 2017 stimulated frontal eye field neurons to trigger a covert shift of attention to the receptive field of these neurons; next, they flashed a stimulus either within, or outside of, the stimulated receptive field. Crucially, they observed a stronger pupillary light response to stimuli flashed within the stimulated receptive field, compared to outside of the stimulated receptive field —a result that echoes behavioral studies (Binda & Murray, 2015a; Olmos-Solis et al., 2018). Other results suggest that pupillary constrictions may even be induced in the absence of visual stimulation, by merely asking participants to mentally visualize a bright scene (Laeng & Sulutvedt, 2014) or by stimuli that evoke the idea of bright objects, like pictures of the sun (Binda et al., 2013b) or words conveying brightness (Mathôt et al., 2017).

Pupil size changes have also been observed during binocular rivalry, where stimuli of different luminance or contrast perceptually alternate, and pupil size follows the brightness of the currently dominant stimulus: constricting when seeing bright, dilating when seeing dark. Initial work on binocular rivalry and pupil changes dates back to 1966, when Lowe and colleagues showed that the same monocular light flash elicited a smaller pupil response when delivered to the suppressed eye than the dominant eye (LOWE & OGLE, 1966). This idea was followed up by demonstrating that pupil size depended on the characteristics of the dominant percept: during the intervals where the grating of higher luminance or contrast was dominant,

pupil size was smaller than in intervals when the other grating was dominant (Einhäuser et al., 2008; Fahle et al., 2011; Naber et al., 2011). A second component of pupil modulations systematically accompanied rivalrous perception, irrespectively of the luminance of the stimuli (Einhäuser et al., 2008; Fahle et al., 2011). Both in binocular rivalry and other types of perceptual rivalry (Necker cube, auditory rivalry, visual plaids), pupil traces show a transient dilation around the time of perceptual switch, which may be informative of the duration of the subsequent dominance phase. This pupil response has been related to the activation of the Locus Coeruleus and the consequent noradrenaline release. This release would consolidate the behavioural decision (Einhäuser et al., 2008) either by enhancing cortical responsivity to the dominant stimulus (HURLEY et al., 2004) or by favouring its processing and integration with a priori knowledge (Murphy et al., 2021; Reimer et al., 2014, 2016). These studies suggest that pupil size could keep track of both sensory and cognitive processing (Binda & Murray, 2015a). Even though attention-related pupillary responses happen on a very small scale, in the order of 0.1 mm or less, these pupil modulations might be the marker of the ubiquity of top–down influences on sensory processing (Binda & Murray, 2015a), including complex ones such as attention and contextual modulation of perception.

In Chapter 4, we applied the lessons learned from applying pupillometry to the study of attention during binocular rivalry, to the investigation of another factor: monocular deprivation.

1.5 Ocular dominance plasticity shapes perception

In the wake of the ground-breaking research conducted by Hubel and Wiesel in the 1960s (Hubel & Wiesel, 1965; Wiesel & Hubel, 1963) ocular dominance plasticity has emerged as a fundamental model for neural adaptability. Hubel and Wiesel recorded the visual cortex activity in cats at various developmental stages, including those with normal vision and those subjected to monocular deprivation through eyelid suture (Wiesel & Hubel, 1963). Their investigations revealed that monocular deprivation disrupted the establishment of ocular dominance columns in the primary visual cortex (V1). This disruption was evident both anatomically, with a reduction in the cortical area representing the deprived eye, and functionally, leading to persistent effects throughout the animal's life, resulting in a condition known as amblyopia (Levi & Carkeet, 1993), characterized by decreased visual acuity and

diminished responsiveness to stimuli in the deprived eye. However, the efficacy of this manipulation was contingent on the timing of monocular deprivation. Applying the same or even longer periods of MD to adult animals had negligible effects (HENSCH & QUINLAN, 2018). This introduced the concept of a 'critical period' during which the application of MD is most impactful.

Notably, over the past few decades, various interventions were found to effectively reopen windows of plasticity throughout adulthood. This suggests that a form of plasticity remains viable in the adult visual cortex, featuring effects and mechanisms that are partly distinct from those supporting developmental plasticity (He et al., 2006; Kalogeraki et al., 2014; Sale et al., 2007; Spolidoro et al., 2011; Vetencourt et al., 2008).

In adult humans, functional changes have been observed with a short-term version of a visual deprivation paradigm (Binda & Lunghi, 2017; Kwon et al., 2009; Lunghi, Berchicci, et al., 2015; Lunghi et al., 2011, 2013; Zhang et al., 2009; J. Zhou et al., 2013, 2014). Two hours of monocular contrast deprivation are followed by a counterintuitive transient boost of the deprived eye – opposite to the amblyopia induced by several days of monocular deprivation during the critical period. This effect has been dubbed “homeostatic plasticity” to distinguish it from the “Hebbian plasticity” that is characteristic of the critical period and to foreshadow the possible underlying mechanisms: automatic regulation of cortical excitability aimed at keeping response levels at an approximately constant level in the face of reduced stimulation. This counterintuitive “homeostatic plasticity” effect has been reported several times, mainly (but not exclusively) using binocular rivalry as a behavioural index of eye dominance. Two hours of monocular deprivation (through the application of a translucent patch over the dominant eye) transiently but strongly affect the dynamics of binocular rivalry: after deprivation, the deprived eye dominates rivalrous perception for twice as long as the non-deprived eye and the effect may last for up to 90-180 minutes after eye-patch removal (Binda et al., 2018; Lunghi et al., 2011, 2013). The shift in ocular drive is compatible with a boost in perceptual strength of the stimulus shown to the deprived eye (Lunghi et al., 2011). This hypothesis has been supported by EEG and fMRI studies, that showed an increase of visual evoked responses elicited by the stimulus shown to the deprived eye (Binda et al., 2018; Lunghi, Berchicci, et al., 2015). However, it is interesting to note that these physiological indices of the boost of the deprived eye are not directly related to the behavioural effect,

because they were acquired in conditions that are very different from those used in behavioural testing. Visual evoked responses (EEG or FMRI) were recorded by presenting stimuli passively, in absence of any perceptual report; in addition, stimuli for VEP and FMRI measurements were delivered monocularly, i.e., separately to each eye (Binda et al., 2018; Lunghi, Berchicci, et al., 2015). All this contrasts with the conditions of the behavioural experiments, where participants were continuously engaged in reporting their perception, which tracked the competitive interactions between the stimuli presented to the two eyes. In Chapter 4, we combined binocular rivalry with pupillometry, aiming at providing a sensitive, non-invasive, and direct measure of short-term monocular deprivation on the effective strength of the deprived eye – collected simultaneously with the behavioural test.

The analysis of the physiological effects of short-term monocular deprivation has allowed an extensive description of the characteristics of the deprived eye boost (Binda et al., 2018; Lunghi, Berchicci, et al., 2015). Pattern-onset visual evoked potentials (VEPs) before and after monocular deprivation showed opposite effects for the two eyes (Lunghi, Berchicci, et al., 2015). The amplitude of the C1 component of the VEP responses, typically reflecting the earliest stage of visual processing in V1 (F. Di Russo et al., 2002), and the peak in alpha band after monocular deprivation were enhanced for the deprived eye but reduced for the non-deprived eye. Moreover, the amplitude of later components, such as P1 and P2, were equally altered by monocular deprivation, suggesting that the variations in cortical excitability propagate to extra-striate areas and may vary feed-back projection to V1.

Coherent observations came from the analysis of BOLD responses in the visual cortex. Binda and colleagues (Binda et al., 2018) performed ultra-high field fMRI during the presentation of high contrast dynamic visual stimuli, delivered separately to the two eyes, before and after 2 hours of monocular contrast deprivation. They found a paradoxical increase of the BOLD responses for the eye that was deprived of contrast vision and a decrease for the eye exposed to normal visual experience. This effect has been related to contrast gain-control mechanisms that, to compensate for the reduced incoming signal in the patched eye, would boost the neuronal responses of the deprived eye (Castaldi et al., 2020) or increase of inhibition of the non-deprived eye (Gong et al., 2023; Lyu et al., 2020).

Crucially, these modulations were not only observed in the visual cortex, but also in the ventral Pulvinar, a nucleus of the visual thalamus (Kurzawski et al., 2022). On the other hand, there

was no modulation of responsiveness before/after modulation in an adjacent thalamic nucleus: the Lateral Geniculate Nucleus, which provides the main feedforward input to V1. This indicates that short-term monocular deprivation has a cortical origin and may propagate to the ventral Pulvinar through the dense cortico-pulvino-cortical connections (Arcaro et al., 2018; Benarroch, 2015; Sherman, 2005; Shipp, 2003). These connections have been related to the modulation of bottom-up and top-down cortical pathways integrating visual inputs and predictions (Bridge et al., 2016; Galuske et al., 2019; Jaramillo et al., 2019; Kanai et al., 2015; Z. Liu et al., 2012).

This could suggest a radical reinterpretation of the short-term monocular deprivation phenomenon; rather than reflecting a homeostatic regulation of V1 responses, it could be linked to the predictive processing of sensory information and more specifically to a revision of internally generated predictions triggered by systematically incoherent sensory information (one eye failing to transduce the signals expected based on the other eye input and based on the observer's own actions). In line with this hypothesis, there is mounting evidence that, even in absence of any contrast deprivation, a mismatch between perception and expectations is sufficient to trigger ocular dominance plasticity (Bai et al., 2017; Kim et al., 2017; Ramamurthy & Blaser, 2018; Steinwurzel et al., 2023).

In Chapter 5, we tested the hypothesis that the distorted sensory experience induced by monocular patching has modulatory effects not only on visual evoked responses but also on the thalamo-cortical circuitry supporting the integration of sensory and prediction signals.

2 Chapter 2- Measuring the reliability of binocular rivalry

2.1 Introduction

Binocular rivalry is a form of perceptual bi-stability that occurs when the two eyes are simultaneously presented with incompatible images (Alais, 2005; LEVELT, 1966). Observers track and report their visual perception by indicating periods of complete dominance of the image presented in either eye and periods of mixed percepts, i.e., transient periods of binocular fusion in which either a piecemeal combination or a superimposition/fusion of the two images is perceived. This technique is a widely used tool in visual psychophysics to study various aspects of vision and cognition (Baker, 2010).

One characteristic that is often studied with binocular rivalry is ocular dominance, or the degree to which our visual perception relies on the input from either eye (Dieter et al., 2017b; Ding et al., 2018; Handa et al., 2006; Ooi & He, 2001). The dynamics of binocular rivalry provide an elaborated measure of ocular dominance, more quantitative and precise (Ooi & He, 2020), than other sighting eye dominance tests, such as the Porta test (Lederer, 1961; Porta, 1593) or the hole in card test (DURAND, 1910). For example, binocular rivalry made it possible to unveil a form of plasticity in adult humans, consisting of an ocular dominance shift after a brief period (about 2 hours) of monocular deprivation (Han et al., 2020; Lunghi et al., 2011, 2013; M. Wang et al., 2020).

Besides ocular dominance, the dynamics of binocular rivalry have been linked to multiple aspects of perceptual and cognitive function. The temporal frequency with which alternative percepts take turns during binocular rivalry (measured by the duration of exclusive dominance phases or its inverse, the switch rate) shows large inter-individual variability (Dieter et al., 2017b; Gallagher & Arnold, 2014; Ooi & He, 2001) and it correlates with switch rates in other forms of perceptual rivalry [(Carter & Pettigrew, 2003), but see (Brascamp et al., 2018) for a recent re-evaluation of this result]. These and other observations suggest that rivalry dynamics may be an intrinsic ultradian rhythm – a stable, trait-like characteristic of every individual. There is evidence of genetic factors affecting this rhythm (Miller et al., 2010; Shannon et al., 2011), which tends to be similar across monozygotic twins. There is also evidence for the association between the rhythm of perceptual alternations during binocular rivalry and psychological traits or disorders. For instance, binocular rivalry dynamics are slower

in individuals with autism (Robertson et al., 2013; Spiegel et al., 2019), in neurotypical individuals with stronger self-reported autistic traits (Dunn & Jones, 2020), and in patients with schizophrenia (Xiao et al., 2018; Ye et al., 2019). Other studies found that rivalry dynamics are slower in people with bipolar disorder and depression (Jia et al., 2015; MILLER et al., 2003; Ngo et al., 2011), but faster in those with anxious personality traits (Jia et al., 2020; Nagamine et al., 2007). Thus, differences in binocular rivalry dynamics may emerge as a potential proxy for complex psychological constructs, such as personality traits and disorders.

Given the diverse uses of binocular rivalry, it is important to establish its reliability. Indices such as mean phase duration and proportion of mixed percepts have been shown to be stable within a given experimental session (K. C. Dieter et al., 2017b, 2017a; van Ee, 2005), implying good internal consistency. What is missing is an assessment of their test-retest reliability, i.e., their stability over experimental sessions performed on different days, which is expected to be high for any trait-like characteristic. For ocular dominance, reliability was recently questioned by Min et al., (2021), who compared different techniques for the assessment of ocular dominance (binocular rivalry, binocular phase combination, and dichoptic masking). The authors report that ocular dominance estimates obtained by parallel-oriented dichoptic masking and binocular phase combination tasks show higher test-retest reliability compared to binocular rivalry, which exhibited poor stability across experimental sessions. In particular, ocular dominance estimated on different days using binocular rivalry showed high variability and no significant correlation across participants. These results partially contradict previous studies, which show that binocular rivalry provides precise and reliable estimates of ocular dominance across days (K. C. Dieter et al., 2017a), and even proposed binocular rivalry as the standard technique to quantify sensory eye dominance in adult humans (see Ooi & He, 2020 for review).

To address these issues, here we examined the reliability of binocular rivalry dynamics and derived ocular dominance measures using four relatively large datasets, and a variety of methods and stimuli. Inspired by Min et al.'s approach, we separately assessed two aspects of reliability: internal consistency, based on the variability of estimates within a single experimental session, and test-retest reliability, based on the variability across experimental sessions conducted on separate days.

2.2 Materials & Methods

2.2.1 Participants

A total of 118 volunteers with normal or corrected to normal vision participated in the four experiments presented here. All except the authors were naïve to the purposes of the study. Part of these data were collected in the context of past studies, the results of which have been reported previously.

40 volunteers (Mean age 28.6 ±0.72 years, 25 females including authors I.S. and C.L) took part in experiment 1 (Sarı & Lunghi, 2023).

33 volunteers (Mean age 25.8 ±0.11 years, 18 females including authors M.A. and C.L.) took part in experiment 2 (Acquafredda et al., 2022).

34 volunteers (Mean age 23.9 ±0.79 years, 24 females including authors C.L. and C.S.) took part in experiment 3 (Lunghi & Sale, 2015; Steinwurzel et al., 2020).

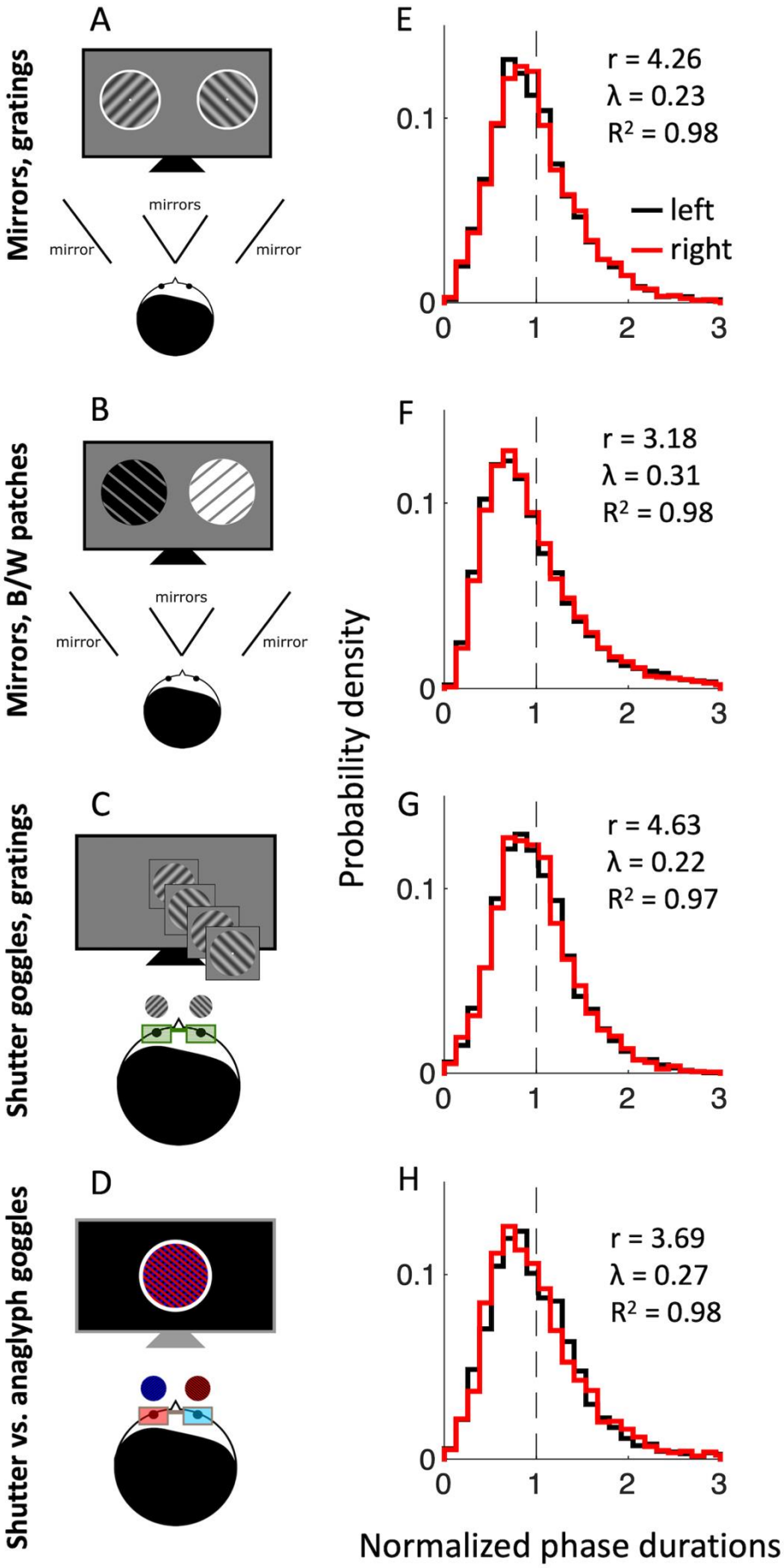
20 volunteers (Mean age 27.5 ±0.4 years, 14 females including author C.S.) took part in experiment 4 (Unpublished); 7 of these had also participated in experiment 3.

2.2.2 Ethics statement

All four experimental protocols were approved by local ethics committees. The “Comité d’éthique de la Recherche de l’université Paris Descartes” approved experiments 1 & 2 (CER-PD:2019-16-LUNGHI) and the “Comitato Etico Pediatrico Regionale—Azienda Ospedaliero-Universitaria Meyer—Firenze” approved experiments 3 & 4 (protocol “Plasticità del Sistema visivo”). All experiments were performed in accordance with the Declaration of Helsinki (DoH-Oct2008). All participants gave written informed consent.

2.2.3 Apparatus, stimuli and procedure

A diagram of the experimental setups for the four experiments included in the study is reported in Figure 1 (A-D). All experiments shared the same logic and design, which we describe first, followed by the specific features of each individual experiment.


A
Mirrors, gratings
mirrors
mirror
mirror
B
Mirrors, B/W patches
mirrors
mirror
mirror
C
Shutter goggles, gratings
D
Shutter vs. anaglyph goggles
E
r = 4.26
λ = 0.23
R² = 0.98
left
right
F
r = 3.18
λ = 0.31
R² = 0.98
G
r = 4.63
λ = 0.22
R² = 0.97
H
r = 3.69
λ = 0.27
R² = 0.98
Probability density
0.1
0
0
1
2
3
Normalized phase durations

386

Figure 2-1. Experimental set-ups and parameters of rivalry dynamics

A-D: Schematics of the stimuli and set-ups. E-H: Probability density function of the normalized phase durations for exclusive dominance of left and right eyes (respectively black and red lines), with best-fitting parameters of the Gamma distribution.

For all experiments, participants took part in two experimental sessions, at least 24 hours apart. Each session was divided into 2 trials of 3 minutes each (6 minutes in total), except for experiment 2 where 4 three-minute long trials (12 minutes in total) were tested. Participants viewed the monitor from a 57 cm distance; a chin/forehead rest stabilized head position. The stimuli consisted of small circular gratings presented dichoptically in central view; they were inscribed in a binocular frame to facilitate fusion. Participants reported rivalrous alternations through the computer keyboard, by continuously pressing one of three keys to report exclusive percepts of orthogonally oriented gratings (right-arrow for clockwise and left-arrow for counter-clockwise) or a mixture of those (piecemeal or fusion: down-arrow key). The orientation of gratings presented in either eye was counter-balanced across participants and switched on every trial to avoid adaptation. For experiment 1, the swapping procedure was done every 90 seconds i.e. halfway through a trial.

Experiments mainly differed in the method used for dichoptic stimulation. Experiments 1 and 2 used a mirror stereoscope placed in front of an LCD monitor (BenQ XL2420Z, 1920 x 1080 pixels, 144 Hz refresh rate, Taipei, Taiwan). Experiment 3 and the first session of experiment 4 used CRS ferromagnetic shutter goggles (Cambridge Research Systems, Kent, United Kingdom) and a CRT monitor (Barco 6551, 800 × 600 pixels, 140 Hz refresh rate, Kortrijk, Belgium). The second session of experiment 4 used anaglyph red-blue goggles and a LED monitor (LG IPS 24EA53, 1920 × 1080, 60 Hz refresh rate, Seoul, South Korea).

There were also differences in the stimuli used to induce rivalry (recall that these experiments were run for independent studies). In experiments 1 and 3 and in the first session of experiment 4, stimuli were monochromatic sinusoidal gratings (orientation: ±45°, spatial frequency: 2 cpd, contrast: 50%, size: 3° or 2° in experiments 1 and 3 and experiment 4 respectively) presented against a uniform grey background (Experiment 1: luminance 110

cd/m^2, C.I.E. x = 0.305, y = 0.332; Experiment 3 and 4: luminance 37.4 cd/m^2, C.I.E. x = 0.442, y = 0.537). In the second session of experiment 4, stimuli were red and blue gratings (orientation: ±45°, size: 3°, spatial frequency: 2 cpd, maximum luminance: 0.5 cd/m^2), presented against a black uniform background. In experiment 2, stimuli were 3° disks, one white (maximum screen luminance 295 cd/m^2) and one black (minimum screen luminance 10 cd/m^2) shown against a uniform grey background (luminance 152 cd/m^2). To discourage binocular fusion, the disks were overlaid with orthogonal grey lines (45° clockwise or counterclockwise, 0.033° or 1 pixel wide, and 0.5° apart).

2.2.4 Descriptive statistics

For each binocular rivalry trial, we used our participants' continuous perceptual reports to extract the following parameters.

Exclusive dominance phases were defined as periods of time during which participants reported seeing exclusively the image presented to their right or left eye. Phase durations were computed separately for each eye; durations shorter than 0.25 sec were considered keypress errors and discarded from the analysis.

We also measured the time spent reporting mixed percepts (fusion or piecemeal combinations of the images presented in the two eyes) and expressed it as a proportion of the total testing time.

Ocular dominance was defined as the proportion of exclusive right-eye dominance, according to the following equation:

$$ODI = \frac{Time_{RE} - Time_{LE}}{Time_{RE} + Time_{LE}}$$

Equation 2-1

where ODI stands for Ocular Dominance Index and $Time_{RE}$ and $Time_{LE}$ are the total amount of time (in seconds) spent seeing through the right eye or left eye respectively. Participants with an ODI > 0.25 or < -0.25 in the first session were excluded from further testing, leaving the sample sizes as reported in the above section. This exclusion criterion was applied because all studies were aimed at investigating the impact of external factors (e.g. short-term monocular deprivation or voluntary attention) on ocular dominance. Participants showing extreme ocular dominance values at baseline were excluded to avoid a possible saturation effect.

We checked that the distribution of exclusive dominance phase durations followed a Gamma distribution. First, we normalized phase durations separately for the right and left eye to their mean phase duration. Next, we pooled phase durations from all participants.

Finally, these normalized phase duration distributions (Figure1E-H) were fit with a two-parameter Gamma distribution, with shape α and scale β parameters:

$$f(x|\alpha,\beta) = \frac{1}{\beta^{\alpha}\Gamma(\alpha)}\, x^{\alpha-1} e^{\frac{-x}{\beta}} \qquad \text{for } x,\alpha,\beta > 0$$

Equation 2-2

Where Γ is the gamma function, x the number of dominance phases. Best fit parameters are reported in the text insets of Figure1E-H.

2.2.5 Measurement reliability: test-retest reliability and internal consistency

Estimates of internal consistency and test-retest reliability were obtained from the intra-session and the inter-session variability, respectively, of the three main parameters of interest: ocular dominance index, mean phase durations (pooled across eyes) and mixed percept proportions.

By internal consistency, we mean the stability of a parameter within a given trial (i.e., a portion of an experimental session that was run without interruptions). Our aim was to compare this with the stability of the same parameter across sessions. The latter was measured as the difference in the parameter estimates from one trial in the first session vs estimates from one trial in the second session. For each trial, we represented perceptual reports as a list of phases, each linked with its duration and type (left eye, right eye, mixed). This list was resampled 10,000 times with reinsertion; for each resampling, we estimated the three parameters of interest and computed their difference between the two trials coming from different sessions. Finally, we took the standard deviation across these 10,000 differences as a measure of standard error and combined standard errors across trials by taking the median. We used this value as indicative of internal consistency. By including this step in our analysis, we estimated intra-session variance in a way that (1) does not need the a priori assumption of equal variance on the two sessions, (2) is independent of the means, and (3) is directly comparable to inter-session variance (from which we derived our measure of test-retest reliability). By test-retest

reliability, we mean the stability of a parameter across experimental sessions conducted on separate days. To estimate this, we computed inter-session correlations and inter-session differences as visualized in Bland-Altman plots.

Inter-session correlations were computed as the Pearson's r of the values obtained for each parameter in the two sessions; vertical and horizontal lines around each data point (leftmost panels of Figures 2-5) showing the bootstrapped standard error of the index obtained for each session.

Bland-Altman plots (Altman & Bland, 1983) were generated by plotting, for each parameter, the difference between the two sessions (inter-session difference) against the mean across sessions. We integrated this representation with our measure of internal consistency by showing the bootstrapped standard error of the intersession difference as vertical lines around each data point. Horizontal dashed lines show summary statistics of both test-retest reliability and internal consistency in the form of 95% confidence intervals, allowing for a direct comparison of the two. Dark Blue/Red/Green horizontal dashed lines show the 95% limits of agreement, computed as the mean ±1.96 × standard deviation of the inter-session differences across participants. Light Blue/Red/Green horizontal lines show the 95% confidence interval of the inter-session difference, computed as the ±1.96 × the median bootstrapped standard error across participants. We show these representations in two versions, before and after z-scoring of the data (central and rightmost panels of Figures 2-5, respectively); the latter allows for comparing test-retest reliability and internal consistency across indices (note that x- and y-scales of the rightmost plots are kept consistent across all figures). To facilitate comparison with Min et al. (Min et al., 2021), the z-scored confidence intervals of the ocular dominance indices are also reported in Table 1.

2.2.6 Hypothesis testing

We checked that all variables were normally distributed (Kolgorov-Smirnov test (Limiting form), $p > 0.05$). Statistical significance was evaluated using both p-values and log-transformed JZS Bayes Factors, computed with the default scale factor of 0.707 (Wagenmakers et al., 2012). The Bayes Factor is the ratio of the likelihood of the two models H1/H0 given the observed data, where H1 is the experimental hypothesis (effect present) and H0 is the null hypothesis (effect absent). A base 10 logarithm of the Bayes Factor (*logBF*) larger than |0.5| corresponds to a likelihood ratio larger than 3 in favour of either H1 (when *logBF* > 0.5) or H0 (when *logBF*

< -0.5) and this value is conventionally used to indicate substantial evidence in favour of either hypothesis. Comparisons across parameters (Figure 6) were performed using two-tailed, paired-samples t-tests. The p-values were corrected for multiple comparisons with Bonferroni correction.

2.3 Results

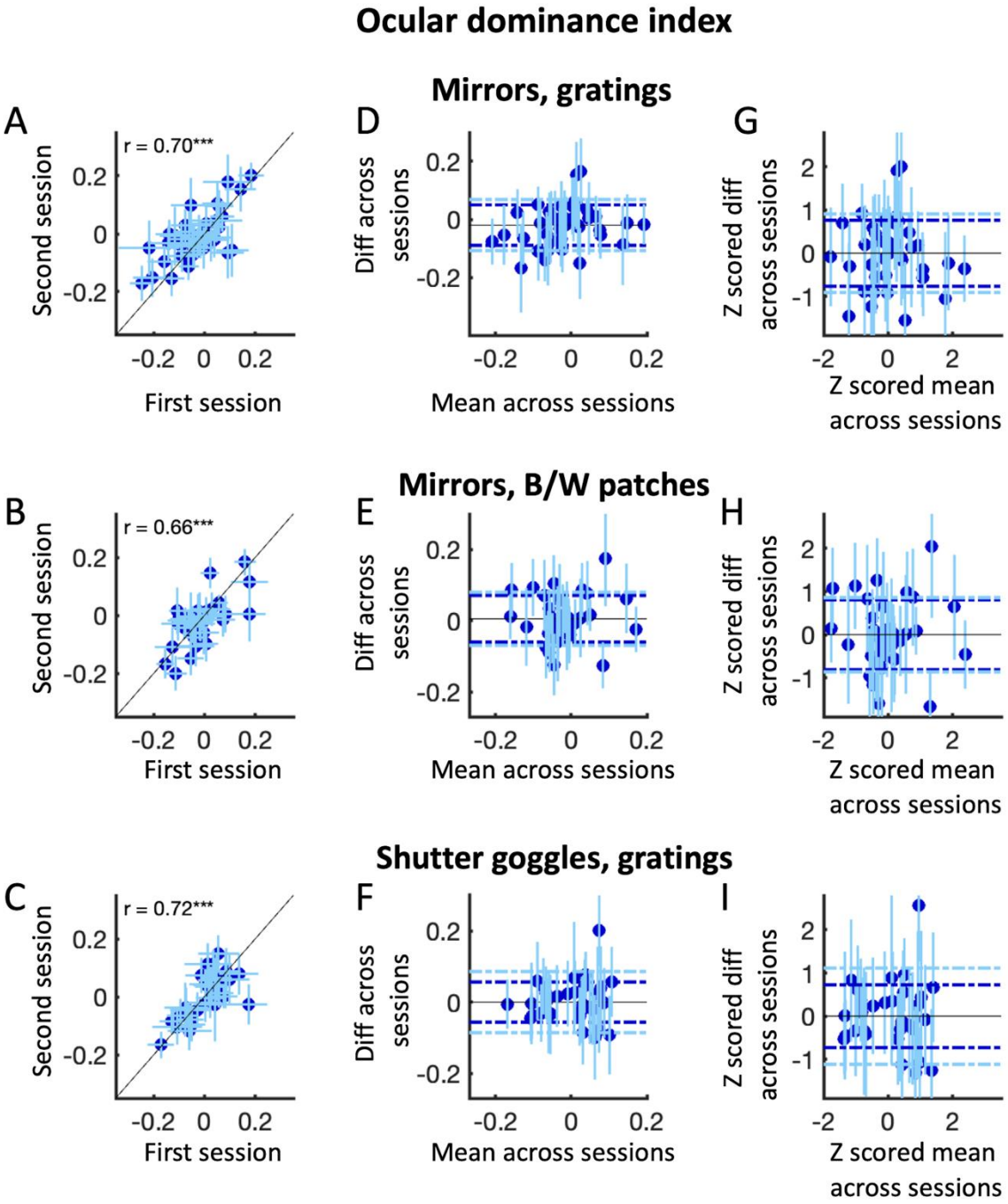
We measured binocular rivalry in a total of 118 participants with three dichoptic stimulation set-ups and four different stimuli. Dichoptic stimulation was achieved through a mirror stereoscope in experiments 1 and 2 (Figure 1A-B), shutter goggles in experiment 3 (Figure 1C), and anaglyph red/blue goggles in experiment 4 (Figure 1D). In experiments 1-3, data collection was repeated twice with identical stimuli and set-up, on different days, allowing us to gauge a measure of stability and reliability of rivalry indices; in experiment 4, data were acquired with two different set-ups testing the stability of those indices across time and stimulation conditions.

Figure 1E-H reports data from experiments 1-4. In all cases, the distribution of the normalized mean durations of exclusive dominance phases was well modelled by the Gamma function (all $R^2 > 0.96$; best-fit parameters are reported as text insets in Figure 1E-H), as expected (LEVELT, 1966, 1967). Based on the Gamma-fits we gauged that all four experiments elicited a typical binocular rivalry phenomenon.

Next, we focused on three main indices of rivalry dynamics from the first three experiments: ocular dominance (Figure 2), mean phase durations (Figure 3), and mixed percept proportions (Figure 4). Results for the three indices from the fourth experiment are shown in Figure 5.

Ocular dominance (computed as in Equation 1) is well correlated across the two sessions of data collection (Experiment 1: $r = 0.70$, $p < 0.001$, $lgBF = 4.42$; Experiment 2: $r = 0.66$, $p < 0.001$, $lgBF = 2.83$; Experiment 3: $r = 0.72$, $p < 0.001$, $lgBF = 4.49$, Figure 2A-C). Inspection of the Bland-Altman plots shows that the confidence intervals of test-retest reliability (horizontal dashed blue lines) are within the confidence intervals of the internal consistency (horizontal dashed cyan lines). In other words, the test-retest reliability (distance of blue symbols from the y=0 line) is expected from the internal consistency of the parameter (vertical blue lines representing ±1 bootstrapped standard error). This means that the variance between sessions

546 is fully explained by the variance within session (internal consistency), indicating that ocular
547 dominance is not significantly affected by state-dependent day-to-day variations.
548



549
550

551 *Figure 2-2. Ocular dominance: variability across sessions and within-session.*

552 *A-C: individual participants' ocular dominance indices for the first (x-axis) and the second*
553 *session (y-axis). The cyan error bars around data points represent the bootstrapped standard*
554 *error of a single participant's ocular dominance index within a single session. Continuous black*

*lines mark the bisector, indicating no difference between the two sessions. In-text values report Pearson's correlation indices and significance (*p < .05; ** p < .01; *** p < .001).*

D-F: Bland–Altman plots where the difference in ocular dominance between the first and second sessions is plotted as a function of the mean across two sessions. The horizontal continuous black line indicates the mean difference across subjects. The outer horizontal dark blue dashed lines indicate the relative 95% limits of agreement, indicative of test-retest reliability. Cyan continuous lines around each point show the bootstrapped standard error of the single-subject measurements, indicative of internal consistency. Cyan horizontal dashed lines indicate the 95% confidence interval of internal consistency across participants. In all panels, the three rows report data from experiments 1,2, and 3 respectively.

G-I: Bland-Altman plots based on z-scored data. All indicators are the same as D-F. The continuous black line reports the y=0 function.

Table 1 reports summary statistics from Figure 2 using similar conventions as in Min et al., 2021 (including z-scoring of the data and reporting 95% limits of agreements and 95% confidence intervals to index test-retest reliability and internal consistency respectively). Our values are not far from the values reported by Min et al (Min et al., 2021) for their binocular rivalry experiments; in particular, measures of internal consistency are comparable across studies or marginally larger. However, our 95% limits of agreements are smaller than those in Min et al. (Min et al., 2021), indicating better test-retest reliability of our ocular dominance indices than any of the measures in Min et al. (Min et al., 2021), both those derived from binocular rivalry and other tasks and paradigms.

	Method	Inter-session	Intra-session
Current study	Binocular rivalry: mirrors, gratings (n=40)	±1.53	±1.82
	Binocular rivalry: mirrors, B/W patches (n=33)	±1.62	±1.73
	Binocular rivalry: shutter goggles, gratings (n=34)	±1.46	±2.23
Min et al., 2021	Binocular rivalry: shutter goggles, luminance modulated gratings (n=45)	±2.49	±1.69
	Binocular combination at many contrasts (n=34)	±2.08	±0.59
	Parallel-oriented masking (n=14)	±1.83	±0.50

578
579
580 *Table 2-1. Comparison of test-retest reliability and internal consistency*
581 *The first three rows (pink) show results from our experiments 1-3: the 95% limits of agreement*
582 *of ODI (a measure of test-retest reliability) and the 95% bootstrapped confidence interval (a*
583 *measure of internal consistency). All values are z-scored, as in* Min et al., 2021 *reported in the*
584 *bottom rows (grey).*
585
586 Figure 3 uses the same format as Figure 2 to report the mean duration of exclusive dominance
587 phases (pooled across eyes). Again, we found excellent correlations across sessions,
588 irrespectively of the type of stimuli or set-up (Experiment 1: $r = 0.85$, $p < 0.001$, *lgBF* = 9.35;
589 Experiment 2: $r = 0.87$, $p < 0.001$, *lgBF* = 8.49; Experiment 3: $r = 0.85$, $p < 0.001$, *lgBF* = 9.45).
590 However, contrary to what was observed for ocular dominance, the Bland-Altman plots
591 (Figure 3D-F) show that the test-retest reliability (distance of red symbols from the y=0 line) is
592 worse than expected from the internal consistency of the parameter (vertical light red lines
593 representing ±1 bootstrapped standard error), suggesting that a significant portion of the
594 between-sessions variance cannot be explained by the internal fluctuations occurring within
595 the session, but is instead related to external or state-dependent factors.
596
597 Z-scored values in the third column can be compared with the same values computed for ODI
598 (Figure 2 G-I). The spread of the data points indicating the differences across sessions is similar

between the two measurements, and their limits of agreement are comparable. However, the light bars are much shorter for mean phase durations compared to ODI, indicating much higher internal consistency for mean phase durations than for the ocular dominance index.

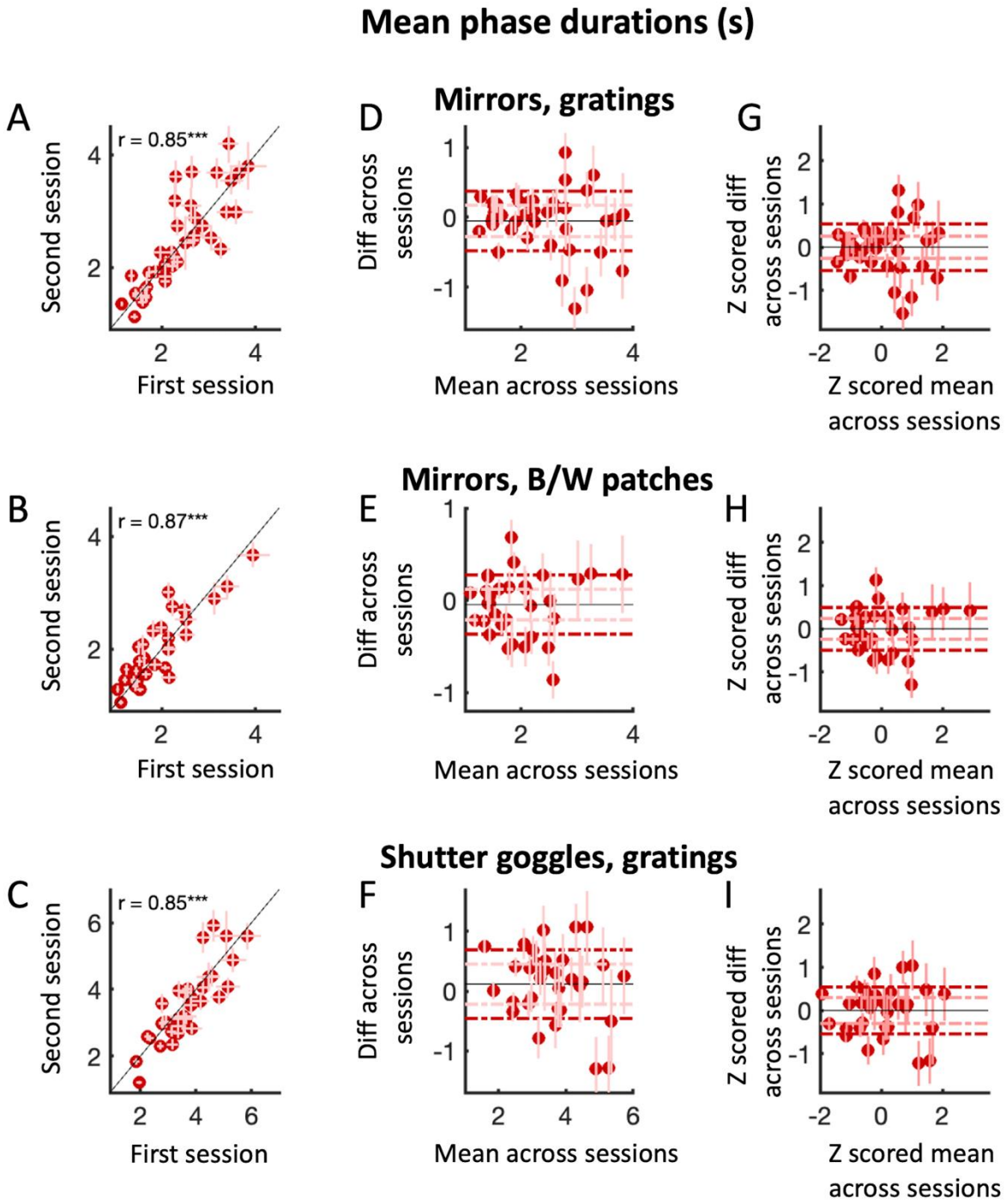


Figure 2-3. Mean durations of exclusive dominance phases: variability across-sessions and within-session.

A-C: individual participants' mean phase durations (s) for the first session (x-axis) and second session (y-axis). All indicators are the same as in Figure 2.

D-F: Bland–Altman plots. All indicators are the same as in Figure 2. Horizontal dark red lines mark the 95% confidence interval of test-retest reliability and light red ones mark that of internal consistency.

G-I: Bland-Altman plots based on z-scored data. All indicators are the same as D-F.

Figure 4 uses the same format as Figures 2 and 3 to report the proportion of mixed percepts. Values are well correlated across sessions (Experiment 1: $r = 0.81$, $p < 0.001$, lgBF = 7.74; Experiment 2: $r = 0.77$, $p < 0.001$, lgBF = 5.06; Experiment 3: $r = 0.76$, $p < 0.001$, lgBF = 4.86). However, as seen for the mean phase durations in Figure 3, the Bland-Altman plots (Figure 4D-F) show that the test-retest reliability (distance of blue symbols from the y=0 line) is worse than expected from the internal consistency of the parameter (vertical green lines representing ±1 bootstrapped standard error). The same conclusions hold for the z-scored values plotted in the panels G-I.

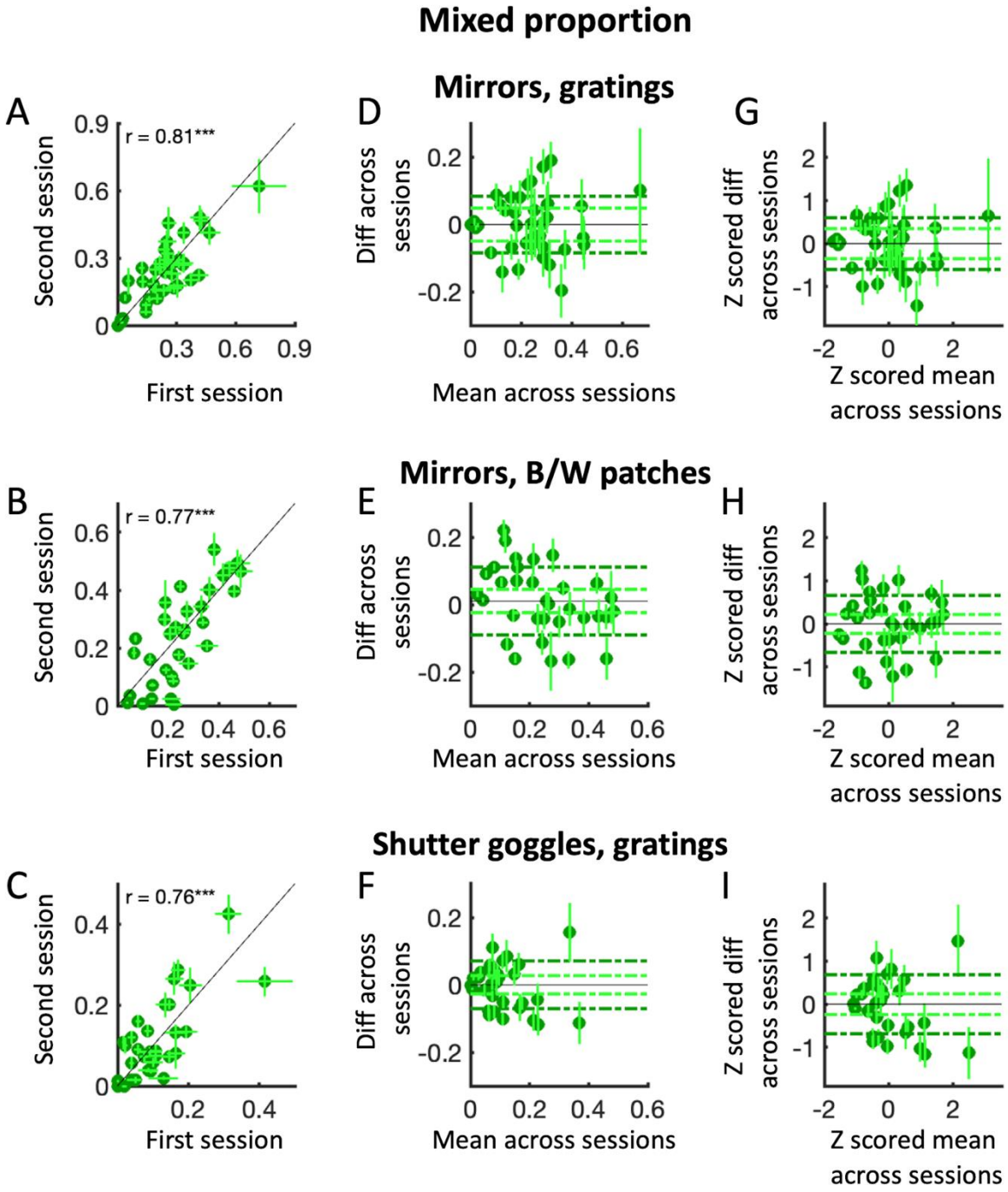


Figure 2-4. Mixed percept proportions: variability across-sessions and within-session.

A-C: individual participants' mixed percept proportions for the first session (x-axis) and second session (y-axis). All indicators are the same as in Figures 2 and 3. Horizontal dark green lines mark the 95% confidence interval of test-retest reliability and light green ones mark that of internal consistency

D-F: Bland–Altman plots. All indicators are the same as in Figures 2 and 3.

G-I: Bland-Altman plots based on z-scored data. All indicators are the same as D-F.

In our fourth experiment, we asked whether similar conclusions would hold when comparing binocular rivalry dynamics and ocular dominance indices across sessions collected on different days and with different stimulation conditions. We measured rivalry using either the stimulus of experiment 3 (first session: monochromatic gratings delivered via shutter goggles) or a new stimulus (second session: colored gratings delivered via anaglyph glasses). Figure 5A-C shows that rivalry dynamics were still correlated across sessions (ODI: $r = 0.52$, $p = 0.02$, $lgBF = 0.41$; mean phase durations: $r = 0.73$, $p < 0.001$, $lgBF = 2.14$; mixed proportions: $r = 0.85$, $p < 0.001$, $lgBF = 4.01$), although mean phase durations were systematically longer in the first session, as expected from the much lower contrast of the stimuli.

Bland-Altman plots show that the main difference across indices is in their internal consistency (better for mixed percept proportions**,** followed by mean phase durations and worse for ODI), in the face of homogeneously high and fairly similar test-retest reliability. This pattern of results is confirmed by the z-scored data (Figure 5G-I). Thus, the results of experiment 4 (comparison across days and experimental set-ups) are in line with the results of experiments 1-3 (comparison across days with identical experimental set-ups).

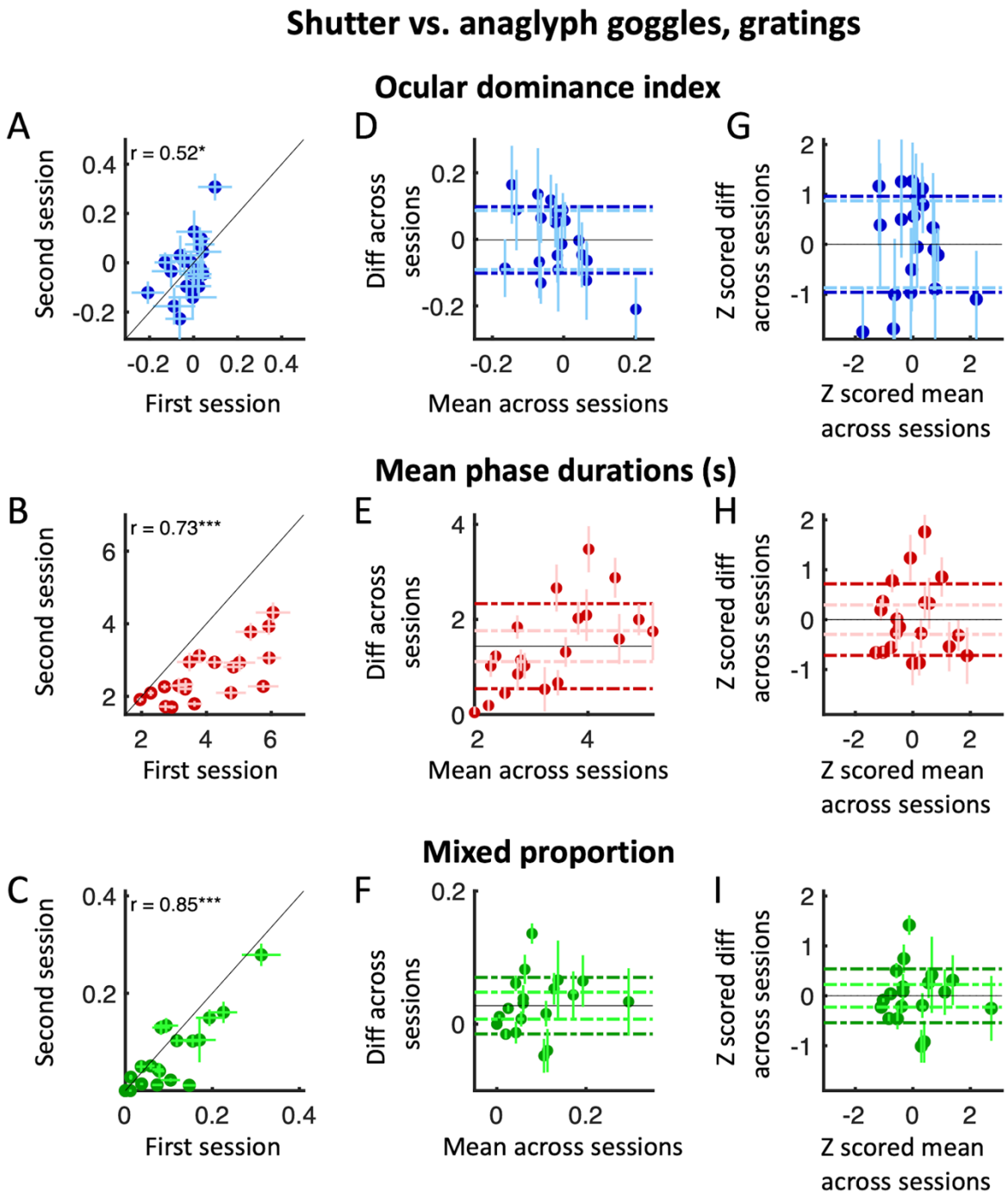


Figure 2-5. Consistency of binocular rivalry parameters across set-ups (Experiment 4).

In all panels, the three rows show data from Experiment 4 for ocular dominance index, mean phase duration and mixed percept proportions respectively.

A -C: Individual participants' measurement of interest for the first session (x-axis: shutter goggles) and the second session (y-axis: anaglyph goggles). All indicators are the same as in Figures 2,3 and 4.

D-F: Bland–Altman plots where the difference in measurement of interest between the first and second sessions is plotted as a function of the mean across two sessions. All indicators are the same as in Figures 2,3 and 4.

G-I: Bland-Altman plots based on z-scored data. All indicators are the same as D-F.

Figure 6 illustrates more directly the relationship between internal consistency and test-retest reliability for the three parameters of interest. For each parameter, we considered each individual participant's test-retest reliability (measured as the difference between sessions) and the same participants' internal consistency (instability of the measure in each session, measured as the bootstrapped standard error); we took the ratio of these measures, log-transformed to distribute normally and finally averaged ratio values across participants. Large ratio values imply that indices vary more across sessions than within sessions, while small values imply that intersession differences are largely accounted for by internal (in-)consistency. A two-way ANOVA with within-subjects factor "binocular rivalry parameter" (three levels: ODI, mean phase durations and mixed percepts) and between-subjects factor "experiment" (four levels, from 1 through 4) revealed significant effects of parameter ($F(2,246) = 57.63$, $p < 0.001$), experiment ($F(3,123) = 10.65$, $p < 0.001$), and parameter by experiment interaction ($F(6,246) = 2.15$, $p = 0.048$). Post-hoc t-tests revealed that, in all experiments, ODI showed the smallest value; smaller than mean phase durations (Experiment 1: $t = 3.27$, $p < 0.001$, Experiment 2: $t = 4.88$, $p < 0.001$, Experiment 3: $t = 5.35$, $p < 0.001$, Experiment 4: $t = 5.11$, $p < 0.001$) and smaller than mixed percept proportions (Experiment 1: $t = 4.01$, $p < 0.01$, Experiment 2: $t = 5.48$, $p < 0.001$, Experiment 3: $t = 7.39$, $p < 0.001$, Experiment 4: $t = 2.77$, $p < 0.05$).

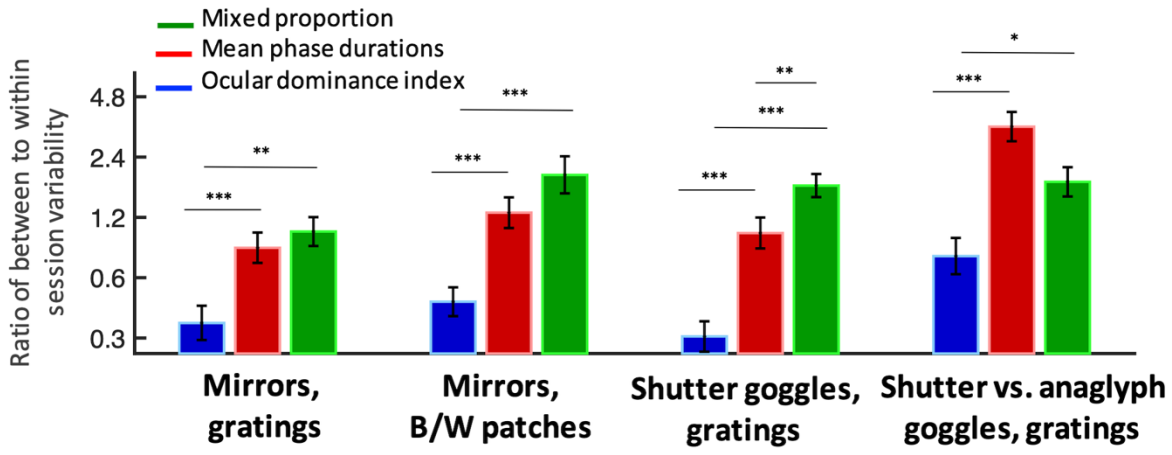


Figure 2-6. Comparison of the ratio of test-retest reliability and internal consistency.

*Bar plot of the ratio of test-retest reliability to internal consistency for ocular dominance index (blue bars), mean phase duration (red bars) and mixed percept proportion (green bars), separately for our four experiments. Ratios were log-transformed before averaging and comparing; their means and SEM (shown by the error bars) were transformed back into their natural values and visualized on a logarithmic scale; consequently, a value of 2 indicates that, on average, the variability between sessions is twice as large as the variability within sessions. Asterisks report significance of the post-hoc t-tests (*p < .05; ** p < .01; *** p < .001).*

2.4 Discussion

We measured the reliability of three main parameters of binocular rivalry (an index of ocular dominance, the mean of dominance phase durations, and mixed percept proportions), related to two physiological constructs: sensory eye dominance and rivalry switch rate. We measured their stability over time (test-retest reliability) and their stability within each experimental trial (internal consistency).

The ocular dominance index showed lower internal consistency than the other two indices: phase durations and mixed percepts. However, this internal noise was sufficient to account for its variability across sessions, implying good stability of this index over time. On the contrary, the high internal consistency of mean phase duration and mixed percept proportions would have predicted higher test-retest reliability than observed. This implies that the test-retest reliability of these measurements is disturbed beyond their internal noise by other external or state-dependent factors.

Binocular rivalry is often used to estimate ocular dominance (K. C. Dieter et al., 2017a; Ooi & He, 2020; Xu et al., 2011). In particular, it has been key to reveal a residual form of ocular dominance plasticity in adult humans (Bai et al., 2017; Binda et al., 2017; Chadnova et al., 2017; Lunghi, Berchicci, et al., 2015b; Lunghi, Emir, et al., 2015; Lunghi et al., 2011, 2013; B. N. Nguyen et al., 2021; M. Wang et al., 2020; Xu et al., 2010), with potential translational impact for the treatment of amblyopia (Lunghi et al., 2019; Ooi et al., 2013; J. Zhou et al., 2019). This approach is predicated upon the reliability of the ocular dominance measurements made with binocular rivalry. Min et al., (2021) recently questioned this assumption, reporting that results from binocular rivalry are not particularly stable over time and far worse than

713 other tasks like binocular combination or masking. In the present study, using four
714 independent binocular rivalry experiments, we found strong evidence in support of the
715 stability of ocular dominance indices, which showed excellent test-retest reliability for a
716 variety of methods and stimuli and demonstrated remarkable concordance even when
717 comparing ocular dominance indices obtained with two very different rivalry-inducing stimuli
718 and methods (shutter vs. anaglyph goggles, displaying monochromatic vs. colored stimuli).
719 Using similar metrics as Min et al., 2021, we obtained similar estimates of internal consistency;
720 however, we observed generally better test-retest reliability, implying better stability of our
721 ocular dominance estimates over time (Table 1). We suggest that few differences between our
722 binocular rivalry experiments and the experiment in Min et al., 2021 could account for this
723 discrepancy. One is the larger amount of data per measurement: one session lasted between
724 6 and 12 minutes in our study (2 or 4 trials), but only 3 minutes in Min et al.'s. Another
725 methodological issue concerns the possible impact of perceptual biases and/or adaptation. In
726 all our experiments, we swapped grating orientations across eyes on every trial, to minimize
727 the effects of adaptation and counterbalance the potential impact of subtle non-corrected
728 anisometric refraction errors. In Min et al., most participants were tested without this
729 orientation-swapping step. A third potential difference between our study and Min et al
730 (2021) concerns the participants' ocular dominance range. In Min et al.'s sample, ocular
731 dominance values range between approximately -0.8 and 0.5, while the largest range in our
732 samples covers values from -0.25 to 0.4. The inclusion of participants with extreme ocular
733 dominance in Min et al.'s sample might be adding to the difference in their reliability
734 estimation and ours, suggesting that binocular rivalry dynamics might be less stable for
735 participants with extreme ocular dominance.
736 We conclude that, provided that some methodological steps are taken, and that participants
737 don't show extreme sensory eye dominance, binocular rivalry provides a robust and stable
738 estimate of ocular dominance, which can be trusted for evaluating its short-term changes like
739 those induced by monocular deprivation.
740 Turning to the other main parameters that may be extracted from binocular rivalry, the mixed
741 percept proportions showed good internal consistency and test-retest reliability. A similar
742 pattern was observed for the mean duration of dominance phases for which we observed high
743 test-retest reliability, comparable to or better than the ocular dominance index, in line with
744 previous reports (Carter & Pettigrew, 2003; K. C. Dieter et al., 2017a, 2017b; van Ee, 2005).

Mean phase durations were also well correlated across binocular rivalry measures obtained with different stimuli and methods, despite an overall difference in the average mean phase duration – lower contrast stimuli inducing slower switch rates (Experiment 4). This indicates that some participants have faster/lower switch rates compared to the average across our sample and maintain this behaviour irrespective of the exact stimuli and methods used to induce bistable perception. There is growing evidence that binocular rivalry switch rate reflects a perceptual trait and an internal ultradian rhythm (Carter & Pettigrew, 2003), i.e. a stable and distinctive feature of each individual participant. While our results confirm that part of the variance in this parameter is trait-like, they also highlight the impact of state-dependent factors. When comparing measurements collected on separate days, we found that differences between sessions were larger than could be expected from the internal inconsistency of this parameter. This suggests that a participant's psychological and/or physiological state contributes to setting their binocular rivalry switch rate while leaving ocular dominance estimates unaffected. This is coherent with evidence showing that, when a binocular rivalry task is repeated over several days, ocular dominance estimates remain stable, while the switch rate is consistently altered by the task repetition (Bao et al., 2018); it is also coherent with our previous observation that switch rates are not predictive of ocular dominance or its plasticity (Steinwurzel et al., 2020). Our data offer no elements to understand the nature of these state-dependent variables. We speculate that they could be related to fluctuations in the participant's motivation and focus on the task, as attention could artificially reduce switch rates (Paffen et al., 2006). In addition, they could be related to fluctuations in other ultradian rhythms that have similar rates as binocular rivalry, such as respiratory rates (0.16-0.33 Hz, (M. A. Russo et al., 2017)) and sympathetic/parasympathetic dynamic balance (e.g. spontaneous fluctuations in pupillary diameter < 1Hz (Reimer et al., 2014) and metabolic factors, given previous indications of a relationship between these factors and cognitive/perceptual function (Animali et al., 2023; Binda & Lunghi, 2017; Pfeffer et al., 2022; Pomè, Burr, et al., 2020).

In conclusion, our findings provide evidence for the reliability of the two main parameters extracted from binocular rivalry: ocular dominance and switch rate. We show that the switch rate is liable to state-related changes, which limits the possibility of reliably associating this parameter to trait-like characteristics like genetic make-up and psychological traits. On the

other hand, we provide evidence that ocular dominance is a trait-like characteristic stable over time, and thereby qualifies binocular rivalry as a valid tool to follow short-term changes of sensory eye-dominance.

3 Chapter 3- Attention Cueing in Rivalry: Insights from Pupillometry

3.1 Introduction

When stimuli in the two eyes are incompatible, binocular fusion fails and perception alternates between the monocular images (Alais & Blake, 2015; Wheatstone, 1838). Rivalry has been shown to depend on attention, as perceptual alternations tend to cease when attention is diverted away. When this happens, neural oscillations in early visual areas are also suppressed (Zhang et al., 2011), consistent with the notion that attention modulates the strength of early neural representations (Carrasco, 2011). These effects are adequately modelled by assuming that attentional resources are automatically driven to the dominant stimulus unless engaged elsewhere; and that attention provides recurrent excitation of the corresponding monocular input, acting synergically with interocular inhibition to maintain the competition between eyes (Li et al., 2017). Besides diverting attention away from the stimuli, cueing attention to one of the rivalling stimuli can affect binocular rivalry, shifting perceptual dominance in favour of the cued percept (Chong et al., 2005; K. C. Dieter et al., 2016; Hancock & Andrews, 2007; Meng & Tong, 2004; Mitchell et al., 2004; Paffen & Alais, 2011; van Ee et al., 2006). However, the neural underpinnings of cueing effects have been less systematically studied and, to the best of our knowledge, no previous study has tested whether attention cueing affects the strength of early visual representations during rivalry. Interocular competition can sometimes be overcome by pattern-based competition, as in interocular grouping rivalry (Alais et al., 2000), where monocular stimuli are complementary, e.g., two half gratings, and perception alternates between images grouped across eyes (Alais et al., 2000). The role of attention in interocular grouping rivalry has not been investigated. In general, attention cueing has more pronounced effects on more complex types of bistable perception, such as Necker cube or bistable structure from motion (Meng and Tong, 2004; van Ee et al., 2005), which could predict stronger attentional modulations in interocular grouping than in binocular rivalry. Here, we propose pupillometry as a method to indirectly index the

strength of competing visual representations and objectively quantify the effects of attention cueing on binocular and interocular grouping rivalry.

Pupil size is mainly set by retinal illumination through a simple subcortical circuit (Loewenfeld, 1993). However light responses are modulated by saliency, attention, brightness illusions and contextual processing (Binda & Murray, 2015b; Laeng et al., 2012; Mathôt, 2018; Wang & Munoz, 2015) indicating that the subcortical circuit is fed with cortical signals (Binda & Gamlin, 2017) that represent effective stimulus strength. As long as stimuli are tagged with different luminance, pupil diameter can be used to accurately and precisely track attention in space (Binda et al., 2013; Mathôt et al., 2013; Naber et al., 2013) and perceptual alternations over time (Einhäuser et al., 2008; Fahle et al., 2011; LOWE & OGLE, 1966; Naber et al., 2011; Tortelli et al., 2021a; Turi et al., 2018). Here, we exploited this strategy and used luminance to tag pupil responses to stimuli rivalling in perception (for an alternative approach that did not rely on luminance tagging, see Brascamp et al., 2021. We predicted that, if attention cueing enhances the effective strength of the dominant stimulus, pupil modulations should be amplified. The amplification would provide an objective and time-resolved index of how attention affects binocular and interocular grouping rivalry.

3.2 Materials and Methods

3.2.1 Participants

We recruited 38 participants (17 males and 21 females including two authors, mean age 26.5 6 0.69 years). Sample size was based on a power analysis that determined the minimum number of participants required to detect a medium-sized effect (effect size 0.50, two-tailed a 0.05, power 0.8 = 33 participants; we recruited a few more anticipating data losses that fortunately did not occur). Ten additional participants were recruited for the control experiment (nine females and one male, mean age 27.1 6 0.82 years). All participants had normal or corrected-to-normal visual acuity (ETDRS charts), normal stereopsis (TNO test), and normal color vision (Ishihara plates); balanced ocular dominance (excluding participants with ocular dominance higher than 70%); no self-reported history of eye surgery, other active eye diseases or mental illness.

3.2.2 Ethics statement

The experimental protocol was approved by the local ethics committee (Comité d'Éthique de la Recherche de l'Université Paris Descartes, CER-PD:2019–16-LUNGHI) and was performed in accordance with the Declaration of Helsinki (DoH-Oct2008). All participants gave written informed consent and were reimbursed for their time at a rate of 10e/h.

3.2.3 Apparatus, stimuli, and procedures

Experiments took place in a dark and quiet room. Visual stimuli were developed in MATLAB (The MathWorks Inc.) using Psychtoolbox-3 (Brainard, 1997) running on a PC (Alienware Aurora R8) and a NVIDIA graphics card (GeForce RTX2080). Visual stimuli were displayed on a 53.5-cm-wide monitor, driven at a resolution of 1920 x 1080 pixels. The display was linearized by γ-correction; it was seen through a four-mirror stereoscope which enabled dichoptic viewing of two display areas of 12x8° each; a chin rest was used to stabilize head position at 57 cm from the display. In each display area, a central red fixation point (0.15° in diameter) surrounded by a square frame (3.5 x 3.5°) was shown against a uniform grey background (luminance: 152 cd/m^2). The mirrors were carefully adjusted at the beginning of each session to ensure accurate alignment of the dichoptically presented squares. Participants were asked to keep their gaze on the fixation point shown at screen center and to refrain from blinking while the stimuli were on. Dichoptic presentations consisted of two sets of stimuli, designed to elicit two forms of rivalry: binocular rivalry and interocular grouping rivalry. For binocular rivalry, visual stimuli consisted of two disks (Fig. 1A), 3° in diameter, one white (maximum screen luminance 295 cd/m^2) and one black (minimum screen luminance 10 cd/m^2). Given the mid-level grey background, the two stimuli had virtually identical Weber contrast of 0.9, but they differed in terms of Michelson (0.3 for the white disk and 0.9 for the black disk). Perception alternated between exclusive dominance of the white and the black disk, or mixed percepts (either piecemeal or fusion). To discourage fusion, the disks were overlaid with thin orthogonal grey lines (45° clockwise or counterclockwise, one pixel wide, corresponding to 0.033°, and 0.5° apart, with the same luminance as the background).

For interocular grouping rivalry, the same stimuli (white/black disks with thin lines) were split vertically, and the two halves were shown to the two eyes (Fig. 1B). Possible percepts were exclusive dominance of the white or the black disk (grouped interocularly), monocular percepts (half white half black disks, as shown to the left or to the right eye) and fusion or piecemeal percepts. Stimuli were presented continuously for 3-min-long trials. Trials were separated by 60-s-long pauses with only the fixation point shown against the background. During this time, participants reported their perception of afterimages; analyses of this behaviour will be reported in a separate publication. On each trial, a different combination of disk colour and line orientation was presented to each eye; combinations varied pseudo-randomly across trials. Participants continuously reported perception by keeping one of three keys pressed: right or left arrows to report dominance of the stimulus with clockwise or counter-clockwise tilted lines, or the down-arrow key any time dominance of either stimulus was incomplete (i.e., monocular percepts in interocular grouping rivalry, piecemeal and fusion events were not distinguished in our paradigm). We did not exclude data from any trial or participant. We eliminated perceptual phases shorter than 0.3 s (accounting for a total of 1.3% and 0.6% of recording time for binocular rivalry and interocular grouping rivalry, respectively), which we assumed to reflect keypress-errors or very fast switches or return transitions that would not be adequately tracked by the slow dynamics of the pupil. In total, we analyzed ~ 500 perceptual phases per participant and stimulus type (591.23 ± 25.71 for binocular rivalry and 501.78 ± 23.97 for interocular grouping rivalry, mean 6 1 SE across participants). Dominance phase distributions were adequately captured by a typical γ-distribution (LEVELT, 1967) with shape a and scale b parameters for binocular rivalry: a = 2.62; b = 0.32 and for interocular grouping rivalry: a = 2.50 and b = 0.34 in Equation 1. The goodness-of-fit (coefficient of determination R2) was 0.94 for binocular rivalry and 0.97 for interocular grouping:

$$f(x|\alpha,\beta) = \frac{1}{\beta^{\alpha}\Gamma(\alpha)}\, x^{\alpha-1} e^{\frac{-x}{\beta}} \qquad \text{for } x,\alpha,\beta > 0$$

Equation 3-1

Where Γ is the gamma function and x the number of dominance phases.

Binocular rivalry and interocular grouping rivalry were both tested in three conditions: no attentional cue, black percept cued or white percept cued. In the latter, a “D” or a “B” letter was displayed at the beginning of the trial cueing participants to endogenously focus their attention on the black or white disk throughout the rivalrous alternations. We applied a fully randomized factorial design, where each participant completed 32 trials, divided into eight sessions of four trials each, one for each combination of rivalry type and attentional cueing, distributed over two days. We also set up a simulated rivalry stimulus, where a single white, black or half white and half black disk (the latter simulating mixed percepts) was shown monocularly to one eye (right or left in separate trials), alternating with phases of 2.5 ± 0.01 s. Four trials of this stimulus were always run at the beginning of the experiment, to help participants familiarize themselves with the task. Note that this is different from a standard “replay rivalry” as it involved a standardized alternation between stimuli, and it was merely intended to measure pupil modulations produced by the physical alternation of luminance stimuli.

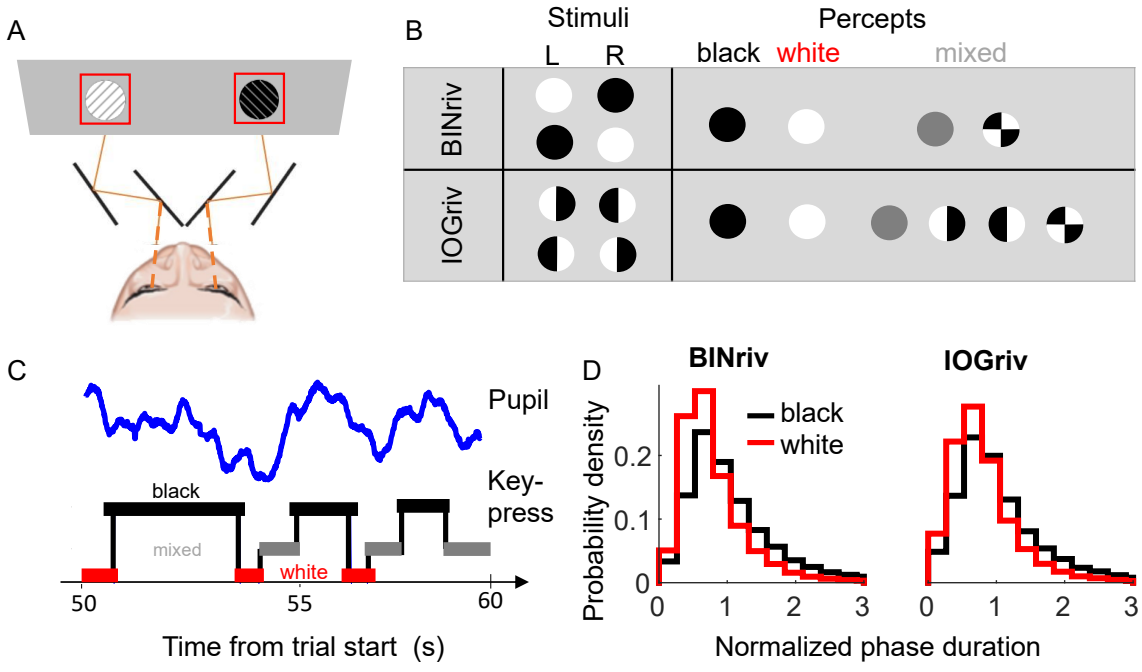


Figure 3-1- Dichoptic stimulation and rivalry dynamics.

A: Schematics of the stimuli (white or black patches overlayed with orthogonal thin lines), presented dichoptically through a four-mirror stereoscope. B: Schematic representation of

the possible stimulus configurations (thin lines omitted) and perceptual outcomes for binocular rivalry (BINriv) and interocular grouping rivalry (IOGriv). C: Example traces from a segment of the experiment, where participants used keypresses to report the dominant percept (square wave) and we recorded pupil size modulations (blue wave). D: Probability density function of the normalized phase durations for exclusive dominance of white or black disk percepts in binocular rivalry and interocular grouping rivalry.

3.2.4 Eye tracking data acquisition and analysis

During rivalry and simulated rivalry, we monitored pupil diameter and two-dimensional eye position with an infrared camera (EyeLink 1000 system, SR Research) mounted below the monitor screen and behind the stereoscope. EyeLink data were streamed to the main computer through the EyeLink toolbox for MATLAB (Cornelissen et al., 2002) and thereby synchronized with participant's keypresses. Pupil diameter measurements were transformed from pixels to millimeters using an artificial 4-mm pupil positioned at the approximate location of the participant's eye Pupil and gaze tracking data consisted of 180 x 100 (180 s at 1000 Hz) time points. These included signal losses, eyeblinks and other artifacts, which we cleaned out by means of the following steps (all implemented with in-house MATLAB software):

- Identification and removal of large artifacts: removal of time-points with unrealistically small or large pupil size (more than 1.5 mm from the median of the trial or <0.2 mm, corresponding to blinks or other signal losses).
- Identification and removal of finer artifacts: identification of samples where pupil size varied at unrealistically high speeds (> 10 mm per second, beyond the physiological range).
- Removal of low-frequency oscillations by subtracting a high-pass Butterworth filter with a threshold frequency of 0.1 Hz from each 180 s-long trial.

After this cleaning procedure was applied, we verified fixation stability by measuring the dispersion of eye position samples around the mean of each trial as the bivariate confidence ellipse area (BCEA), defined as the following:

$$BCEA = 2 * k * \sigma_H * \sigma_V * (1 - \rho)^{0.5}$$

Equation 3-2

Where k is the confidence limit for the ellipse, σH and σV are the standard deviation of eye positions in the horizontal and vertical meridian respectively, ρ is the product-moment correlation of these two position components and k=1.14, implying that the ellipse included 68% (1-e(-k)) of the distribution. To test for possible differences in eye-movement patterns, we averaged the BCEA values across trials and entered these values in a 2x2 repeated measure ANOVA with factors: cueing condition (no cue/cueing) and rivalry type (binocular/interocular grouping rivalry). No main effect or interaction was significant, suggesting that fixation was equally stable across all conditions and rivalry types (main effect of cueing condition: $F(1,37) = .41$, $p = .52$, logBF = –.64; main effect of stimulus type: $F(1,37) = .44$, $p = .51$, logBF = –.69; cueing condition by stimulus type interaction: $F(1,37) = .70$, $p = .41$, logBF = –.54). After cleaning, pupil data and continuous recordings of perceptual reports were down-sampled to 100 Hz, by taking the median of the retained time points in nonoverlapping time windows. If no retained sample was present in a window, that window was set to "NaN" (MATLAB code for "not a number"). Down-sampled pupil traces (to which we re-applied the second step of the cleaning procedure) were finally parsed into epochs locked to each perceptual switch (when the participant changed perceptual report) and labeled according to the color of the dominant stimulus after the switch. Pupil time courses were averaged across epochs for each participant; further averaging across participants yields traces in Figure 2. In order to minimize the impact of pupil size changes unrelated to the perceptual switches, we also analyzed data after subtracting a baseline from each epoch, measured in the -1: 0.5 s interval preceding the switch. To compare pupil size across dominance phases, stimuli and attention conditions, we extracted a pupil size index by averaging baseline corrected pupil size in the -0.5:1 s interval around the switch. Note that shifting the intervals for pupil baseline, or skipping the baseline correction step, affected the size of pupil modulations but it did not change our conclusion on the effects of attention and stimulus type (see Appendix Fig. 7-1); also, we verified that attention cueing did not affect pupil baseline measures (see Appendix Fig. 7-2).

To quantify the effect of attention on both perceptual reports and pupil measurements, we computed indices of attentional modulation (AMI) for comparing perceptual and pupil measures in cueing versus in no-cueing trials. Specifically, we used Eq. 3-4, where PROP is the total dominance time of the white and black disk percepts divided by total testing time and PUPDIFF is the average pupil size difference between black and white disk dominance phases.

$$AMI_{prop} = (PROP\ percept1_{cued} - \ PROP\ percept2_{uncued}) -$$

$$(PROP\ percept1_{nocue} - \ PROP\ percept2_{nocue})$$

Equation 3-3

$$AMI_{pup} = PUPDIFF_{cued} - \ PUPDIFF_{nocue}$$

Equation 3-4

For the sake of clarity, we chose to quantify perceptual reports using dominance proportions; however, the same conclusions could be drawn analyzing mean phase durations instead. To check for possible differences in the reliability of pupillary modulations across conditions, we also evaluated the cross-correlation between pupil size and perceptual reports. Previous studies reported that synchronization with rapid cognitive and perceptual events is more precise for pupil change rate (the first derivative of pupil size) than for pupil (Brascamp et al., 2021; de Gee et al., 2020; Murphy et al., 2021), presumably because of the long temporal impulse-response function of the pupil, which results in a broad autocorrelation of this measure. In line with these studies, we opted to measure the cross- correlation between perceptual reports and the pupil-size change rate. For each participant, we averaged the normalized cross-correlation function across trials and stimulus type. We fit it with a Gaussian function (constrained to peak at lags smaller than 1.5 s and with SD smaller than 0.2 s) and compared its peak amplitude across conditions.

3.2.5 Statistical approach

Significance was evaluated using both p-values and log-transformed JZS Bayes factors computed with the default scale factor of 0.707 (Wagenmakers et al., 2012). The Bayes factor is the ratio of the likelihood of the two models H1/H0 given the observed data, where H1 is the experimental hypothesis (effect present) and H0 is the null hypothesis (effect absent). A base 10 logarithm of the Bayes factor (logBF) larger than |0.5| corresponds to a likelihood ratio larger than 3 in favor of either H1 (when logBF > 0.5) or H0 (when logBF < -0.5) and this value is conventionally used to indicate substantial evidence in favor of either hypothesis (Kass & Raftery, 1995; Keysers et al., 2020). Bayesian ANOVAs were run in JASP, and the corresponding Bayes factors represent the change from before posterior inclusion odds (BFinclusion) computed across matched models. Moreover, following the review reviewed by Richardson (Richardson, 2011), we report partial eta squares (ηp2, computed in JASP) as effect

size estimates for all factors in our repeated measures ANOVAs. We estimated the internal consistency of our parameter estimates by split-half reliability. Each parameter was estimated twice per participant, on half the dataset (odd and even trials) and we evaluated the correlation of the two sets across participants. Finally, we evaluated the significance of behavioral attentional effects at the single participant level with a bootstrapping approach, by resampling (10,000 times, with reinsertion) dominance phases in cueing and no-cueing conditions, applying Equation 3, computing the proportion of samples where the attentional modulation index was larger than 0 or smaller than 0 and assigning the significance for $p < 0.025$.

3.2.6 Control experiment

A control experiment was performed after the end of the study, with the aim of estimating the sensitivity of pupil size measurements to manipulations of stimulus strength. The original set-up was inaccessible at the time of testing, and we replicated the conditions of the main experiment as closely as possible in another set- up, using the same eye-tracker (EyeLink 1000 system, SR Research), similar mirror stereoscope and a computer that ensured equal performance. Specifically, stimuli were generated with the PsychoPhysics Toolbox routines (Brainard, 1997) and MATLAB (MATLAB r2010a, The MathWorks Inc.) housed in a Mac Pro 4.1, and displayed on a 52.5-cm-wide LCD screen with maximum screen luminance of 108 cd/m^2. Instead of using the maximum and minimum screen output, we reduced luminance levels by about a factor of 10 to allow for modulations of stimulus contrast. We set the background luminance to 15 cd/ m^2 grey and tested six conditions: a no cue and white cued condition in which stimuli were 28 and 2 cd/ m^2f or the white and black disk, re-respectively, and four conditions where the Michelson contrast of the white disk stimulus was increased by 25%, 50%, 100% and 150% (luminance values: 33, 40, 63, and 108 cd/ m^2). Each condition was tested in four trials, and all data were collected over a single session.

3.3 Results

We analysed perceptual alternations and the associated pupil modulations during binocular and interocular grouping rivalry, in two conditions: with and without attentional cueing. In no cueing conditions, pupil diameter reliably tracked perceptual alternations between a white

and a black disk presented dichoptically, either one disk per eye generating binocular rivalry, or each disk split vertically between eyes generating interocular grouping rivalry (Figure 1). Despite constant stimulation (hence constant luminance), pupils were relatively dilated when participants reported seeing black, compared to when they reported seeing white (Figure 2A-B, black vs red line), in both types of rivalry.

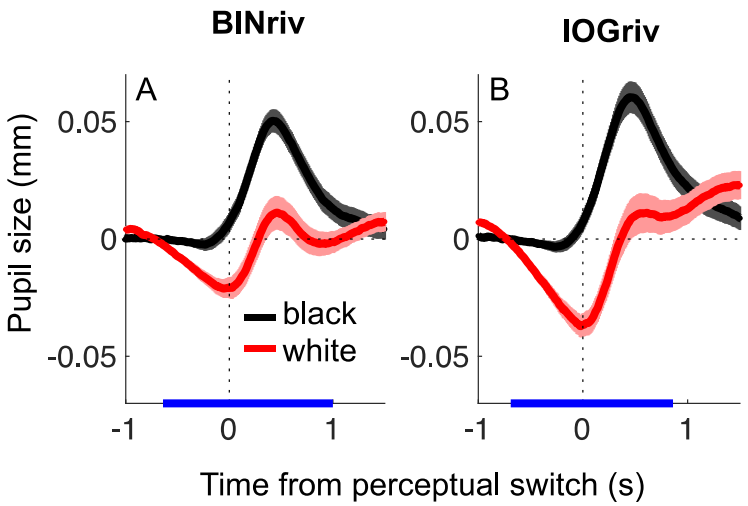


Figure 3-2 Pupil modulations track perceptual alternations.

Baseline subtracted pupil size traces aligned to perceptual switches towards exclusive dominance of a white disk or a black disk percept and averaged across phases, separately for binocular rivalry (A) and interocular grouping rivalry (B). In all panels: shadings report mean ±1 s.e. across participants and the blue marks on the x-axis highlight timepoints where pairwise comparisons between traces are significant (one-tailed t-test, $p < 0.05$ FDR corrected). Observations regarding the latency of the pupillary response and its relative magnitude are reported in Figure 7-1 in the Appendix, where non-baseline subtracted traces are shown.

The analysis of behavioural reports in the no cueing condition (dotted lines in Figure 3) showed a net predominance of black disk percepts with respect to the white ones (binocular rivalry: $t(37) = 8.70$, $p < .001$, logBF = 7.77; interocular grouping rivalry: $t(37) = 12.81$, $p < .001$, logBF

= 12.27). In line with the modified Levelt's propositions and results by Qiu et al., 2020, this can be explained by the higher Michelson contrast of the black disk stimulus (recall that the background was set to mid-grey, resulting in identical Weber contrast but different Michelson contrast for the two disk stimuli). However, dominance of the black percept cannot logically explain the pupil modulations; moreover, while both black dominance and pupil size modulations varied across participants, the two were reliably uncorrelated (binocular rivalry: r = -.09, p = .58, logBF = -.83, interocular grouping rivalry: r = -.20, p = .22, logBF = -.58).

Figure 3A-B also shows that exclusive percepts were much rarer in interocular grouping rivalry compared to binocular rivalry ($t(37) = 12.23$, $p < .001$, logBF = 11.68), reflecting the response mapping we used; for interocular grouping rivalry, mixed reports included epochs where the individual monocular images in the left and right eye dominated.

Having established pupil size as a marker of perceptual dominance in both binocular and interocular grouping rivalry, we proceeded to assess the impact of attention cueing on perceptual alternations and pupil size modulations (continuous lines in Figure 3).

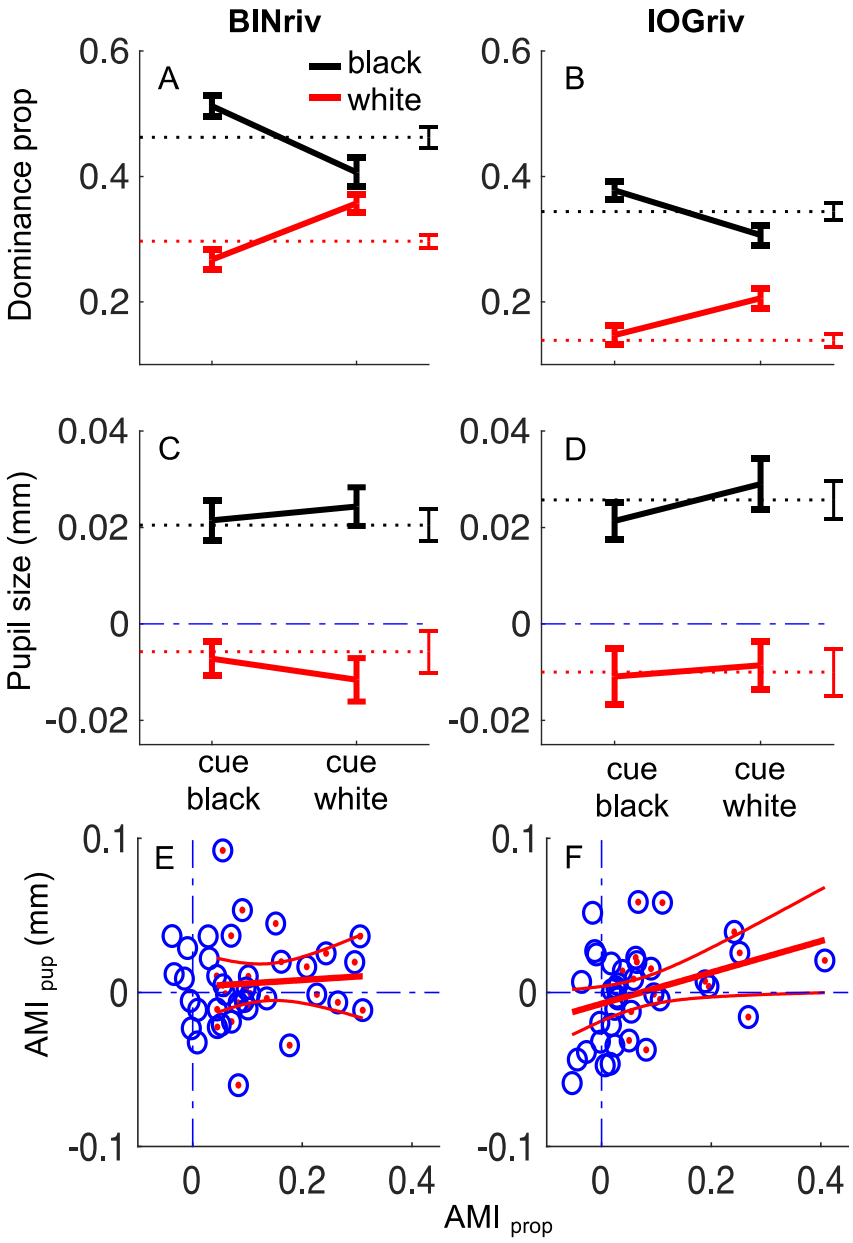


Figure 3-3 Attention cueing affects perceptual alternations but not pupil modulations

A-B: perceptual dominance for exclusive white (red line) or black (black line) disk percepts, without attentional cueing (dashed lines) or when the white or the black disk percept were cued (continuous lines, cueing condition indicated on the abscissa). Error bars report ±1 s.e. across participants.

C-D: baseline corrected average pupil size computed in a fixed temporal window (between -.5 and 1 s from the perceptual transition) during phases of exclusive dominance of the black (black line) and the white disk (red line). Results from the no-cueing condition are reported by

dashed lines. Continuous lines report the results from the trials where the white or the black percepts were cued (separated on the abscissa). Error bars report ±1 s.e. across participants. E-F: individual participants' attentional modulation indices for perceptual dominance (x-axis) and pupil size (y-axis), computed with Equations 3-4. Dash-dot blue lines mark the x=0 and y=0 lines, indicating no effect of attention cueing. Each circle reports results from one participant; red dots highlight participants with a significant attentional modulation index for perceptual dominance. Red lines show the best fitting line and its 95% confidence intervals.
In all panels, the left column reports results for binocular rivalry and the right for interocular grouping rivalry.

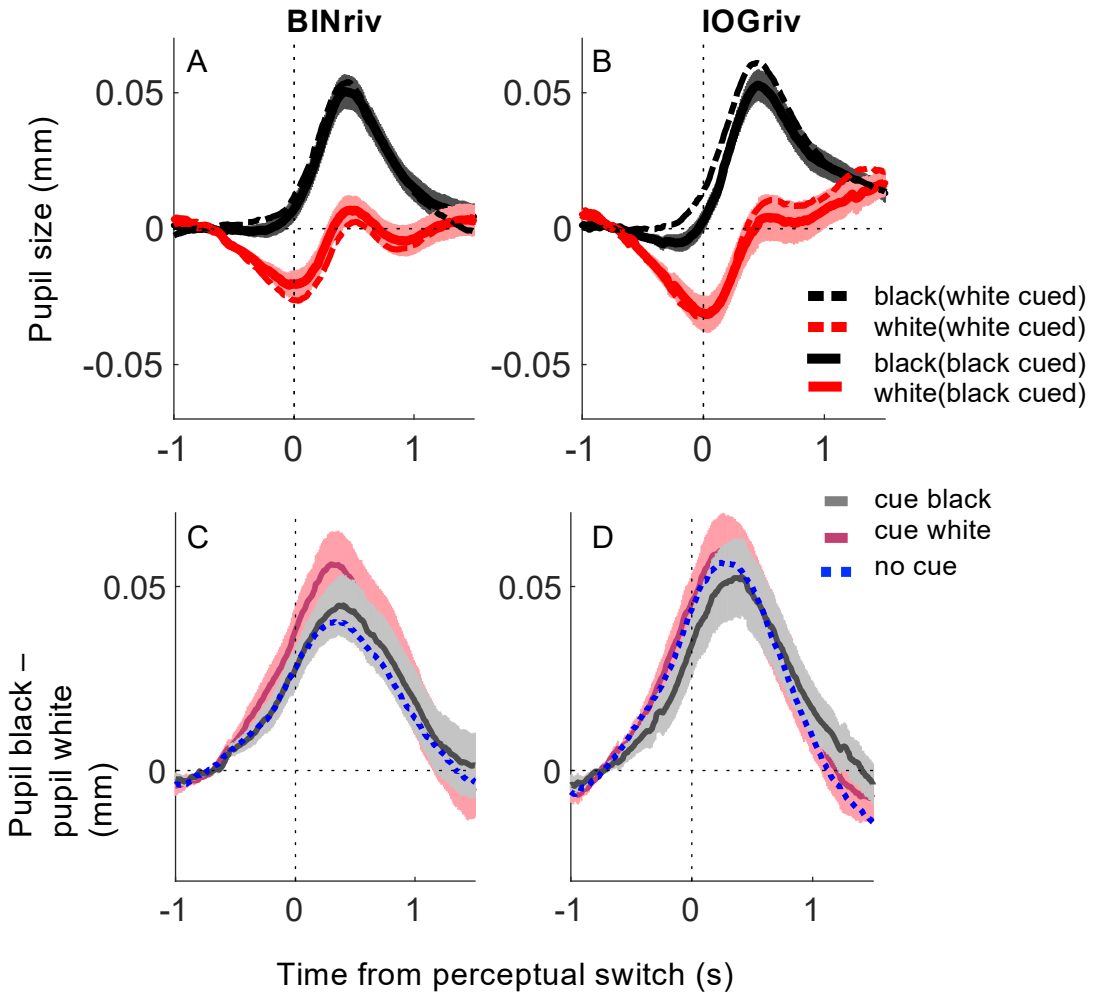
As expected, perceptual dominance of the cued stimulus was enhanced, resulting in a significant interaction between tween dominant percept (white/black) and cued percept (cueing white/cueing black) on the proportion of exclusive dominance phases (Fig. 3A, B; Table 1, middle column). We summarized the effect of attention with an attentional modulation index (Eq. 3 in Materials and Methods), which was in the order of 10% for both types of rivalry (single participant data are shown on the abscissas of Fig. 3E, F). The effect was statistically reliable at the group level and, in most cases, at the individual participant level (boot-strapped attentional modulation indices were significantly higher than zero in 27/38 or 20/38 participants for binocular and interocular grouping rivalry, respectively, highlighted with a red dot in Fig. 3E, F; it was significantly lower than zero in only 2/38 participants for interocular grouping rivalry and in no participant for binocular rivalry). Attentional modulation indices were correlated between binocular rivalry and interocular grouping ($r = 0.61$, $p < 0.001$, logBF = 2.63), suggesting that they measure a relatively stable feature of our participants. In line with this, we found no indication that interocular grouping rivalry was more affected by attention than binocular rivalry; if anything, there was a small effect in the opposite direction (binocular rivalry minus interocular grouping rivalry, $t(37) = 2.33$, $p = 0.02$, logBF = 0.28).

	Proportions	Pupil size
dominant percept	$F_{(1,37)} = 146.46$* $p < 0.001$ logBF = 30.54 $\eta_p^2 = 0.80$	$F_{(1,37)} = 46.09$* $p < 0.001$ logBF = 22.52 $\eta_p^2 = 0.55$
rivalry type	$F_{(1,37)} = 82.62$* $p < 0.001$ logBF = 25.49 $\eta_p^2 = 0.69$	$F_{(1,37)} = 0.12$ $p = 0.73$ logBF = -0.90 $\eta_p^2 = 0.003$
cued percept	$F_{(1,37)} = 5.37$* $p = 0.03$ logBF = -0.82 $\eta_p^2 = 0.13$	$F_{(1,37)} = 1.91$ $p = 0.17$ logBF = -0.78 $\eta_p^2 = 0.05$
dominant percept x rivalry type	$F_{(1,37)} = 0.99$ $p = 0.33$ logBF = -0.62 $\eta_p^2 = 0.03$	$F_{(1,37)} = 0.17$ $p = 0.68$ logBF = -0.72 $\eta_p^2 = 0.005$
dominant percept x cued percept	$F_{(1,37)} = 32.96$* $p < 0.001$ logBF = 11.33 $\eta_p^2 = 0.47$	$F_{(1,37)} = 1.78$ $p = 0.19$ logBF = -0.53 $\eta_p^2 = 0.05$
rivalry type x cued percept	$F_{(1,37)} = 0.08$ $p = 0.77$ logBF = -0.78 $\eta_p^2 = 0.002$	$F_{(1,37)} = 1.92$ $p = 0.17$ logBF = -0.54 $\eta_p^2 = 0.05$
dominant percept x rivalry type x cued percept	$F_{(1,37)} = 5.45$* $p = 0.02$ logBF = -0.11 $\eta_p^2 = 0.13$	$F_{(1,37)} = 0.03$ $p = 0.85$ logBF = -0.41 $\eta_p^2 < 0.001$

Table 3-1 The effects of cueing on proportions and pupil size.

Three-way ANOVA for attention cueing results, with factors: dominant percept (white/black disk), cueing (white/black cued), rivalry type (binocular/interocular grouping rivalry). These results were not affected by skipping this baseline correction step or defining pupil baseline over a wider temporal interval (Table 7-1 in the Appendix).

Based on the assumption that attention cueing boosts perceptual dominance by enhancing the effective strength of the cued percept, we expected to find an enhancement of the pupil responses accompanying perceptual alternations. For example, we predicted that dilations concurrent with black percept dominance would be increased when cueing black. To test for this effect, Figure 3C, D plots the mean baseline-corrected pupil size over a fixed interval [0.5:1s] around the perceptual switch for each percept type and attention cueing condition (the same interval used for computing pupil size in the no-cue condition, shown by dotted lines). Red curves show pupil size during white percepts and black curves during black percepts; the two cueing conditions (white/black percept cued) are separated on the x-axis. The format is the same as that used to expose the effects of attention on the proportions of dominant percepts in Figure 3 A,B. According to our hypothesis, attention should have affected mean pupil size, displacing the continuous curves away from the dashed lines that report the no-cueing results. However, no such systematic displacement was observed. This was confirmed statistically (Table 1, rightmost column, both the main effect of cued percept and the interaction between dominant percept and cued percept are nonsignificant, with log Factors < -0.5). Figure 4 shows the full pupil time courses across cueing conditions, using the same format as in Figure 1, and supporting the same conclusions drawn from Figure 3 and Table 1. The curves are remarkably similar regardless of whether the white or the black percept was cued; as a result, the amplitude of the pupil modulation (computed as the difference between pupil size during black–white disk percepts) was not affected by attention cueing. These figures were computed after baseline correcting pupil traces, i.e., subtracting the average pupil diameter preceding each perceptual switch before averaging traces across switches. We verified that our pupil baseline values were not affected by attention cueing and we checked that skipping this baseline correction step or defining pupil baseline over a wider temporal interval (5:5 s, the whole interval over which we tracked pupil size for each perceptual switch) did not alter our conclusions (Table 7-1; Fig. 7-2 in the Appendix).



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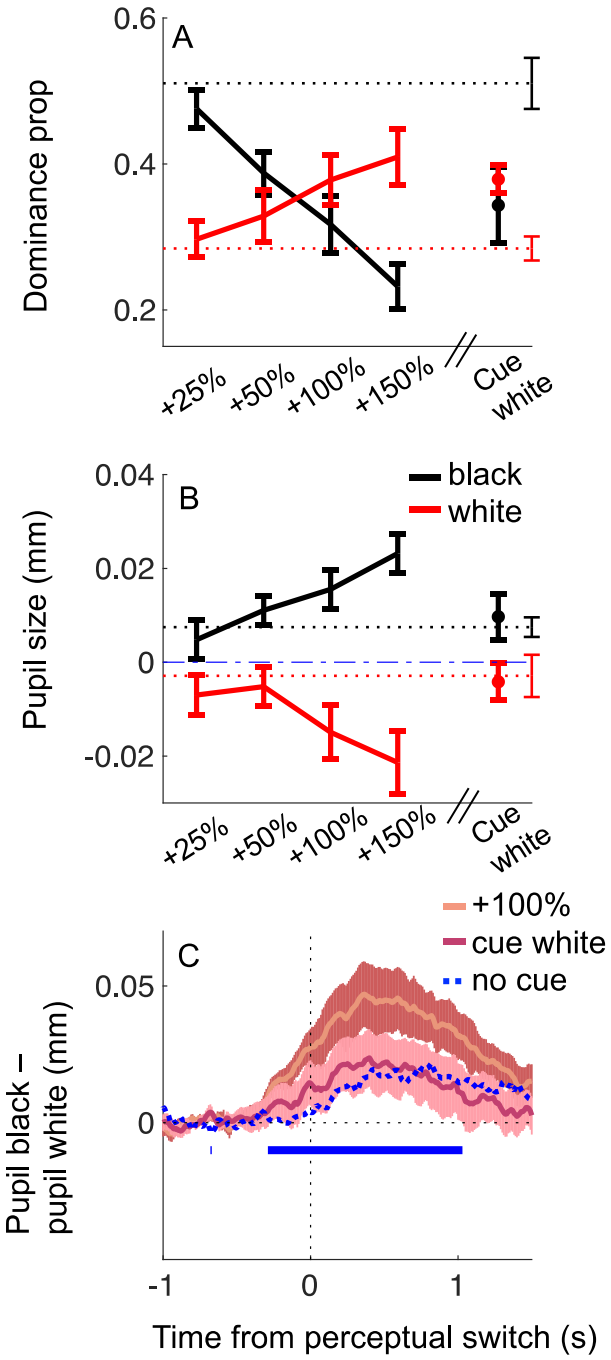
1195 *Figure 3-4 Pupil time courses are comparable across cueing conditions*

1196 *A–B: pupil size traces aligned to perceptual switches towards exclusive dominance of a white*
1197 *disk or a black disk percept computed across phases in individual participants and then*
1198 *averaged for each cueing condition, separately for binocular rivalry and interocular grouping*
1199 *rivalry. C-D: time course of the difference between baseline-corrected pupil size during black*
1200 *and white percepts, computed in individual participants and then averaged for each cueing*
1201 *condition. The resulting traces show no effect of cueing. The same conclusions can be drawn*
1202 *skipping the baseline correction step or defining pupil baseline over a wider temporal interval*
1203 *around perceptual switch, as shown in Figure 7-2 in the Appendix. In all panels: shadings report*
1204 *means ±1 s.e. across participants.*

We computed an attentional modulation index for pupil size (Eq. 4), logically similar to the attentional modulation index computed for perceptual dominance (Eq. 3). Attentional modulation indices for pupil size were distributed around zero for all participants (as shown on the ordinates of Fig. 3E, F). Even selecting the subsample of participants who showed a significant behavioural effect of attention cueing (Fig. 3E, F, red dots), the pupil attentional modulation remained non-significantly different from zero ($t(26) = 1.15$, $p = 0.25$, logBF = –0.42 for binocular rivalry and $t(19) = 1.72$, $p = 0.10$, logBF = –0.09 for interocular grouping rivalry). Thus, our results show disagreement between pupillometric and behavioural measures of perceptual dominance. Only perceptual alternations were affected by attention cueing, not the accompanying pupil modulations. Could this be because of the lack of sensitivity of pupillometry? We gathered several pieces of evidence against this possibility. First, not only we did not find any evidence of an effect of attention, but we also obtained evidence in support of the null hypothesis (no effect of attention) using the Bayes factor (Keysers et al., 2020). Because the log-Bayes factor is defined as the log-likelihood ratio of the experimental and the null hypothesis, a value smaller than 0.5 indicates that the null hypothesis is three times more likely than the experimental hypothesis given the data (conversely, a log-Bayes factor larger than 0.5 implies that the experimental hypothesis is three times more likely than the null hypothesis given the data). As shown in Table 1, the effect of attention was associated with nonsignificant p-values mostly accompanied by log-Bayes factors smaller than 0.5, indicating substantial evidence (Kass & Raftery, 1995) against the hypothesis that attention cueing affects pupil size. Second, we verified that the reliability of pupil measurements was high (test-retest reliability on the pupil size difference: $r = 0.72$, $p < 0.001$, logBF = 4.78 and $r = 0.81$, $p < 0.001$, logBF = 7.11 for binocular rivalry and interocular grouping rivalry, respectively), comparable to the reliability of the behavioural measurements (test-retest reliability for dominance proportions: $r = 0.72$, $p < 0.001$, logBF = 4.84 and $r = 0.79$, $p < 0.001$, logBF = 6.73 for binocular rivalry and inter- ocular grouping rivalry, respectively). Third, we found that pupil measurements were sensitive enough to report the slight imbalance between eyes observed in our set of (nonamblyopic) participants. This was shown by splitting the same set of perceptual phases (binocular rivalry with attention cueing) in two ways: according to whether the reported percept was cued or uncued, and according to whether it matched the stimulus presented in the dominant or nondominant eye. This measure confirmed that pupil size was insensitive to attention cueing (pupil modulations were

not different when the cued or un-cued stimulus was perceived, $t(37) = 1.23$, $p = 0.23$, logBF = –0.46), but it did report eye-dominance (pupil modulations being larger in phases where percepts matched the stimulus in the dominant eye, $t(37) = 2.59$, $p = 0.01$, logBF = 0.51). Fourth, we ruled out the possibility that the amplitude of pupil modulations was already saturated in the no cue condition, by measuring pupil modulations in a simulated rivalry condition. The latter was not intended as a replay-rivalry condition; it was run at the beginning of the experiment, training our participants to report perceptual alternations, and it did not reproduce the dynamics of exclusive dominance and mixed percepts observed during rivalry. However, it did allow us to estimate the pupil modulations elicited by physical alternations of the white and black disk, which measures the maximum modulation possible elicited by perceptual alternations during rivalry. We found that the latter were ~40% of the modulations during simulated rivalry (39.13 ± 8.15 for binocular rivalry and 43.80 ± 10.26 for interocular grouping rivalry, mean ± 1 SE across participants). This implies that there was ample space for the putative boosting effect of attention, ruling out ceiling as an explanation for the lack of such effect. Fifth, and finally, we showed with a control experiment that pupil size modulations reliably track changes in stimulus strength of a size compatible with those simulating the effects of attention cueing on perceptual dominance (Fig. 5). This was tested in a separate cohort of participants and with a different set-up, where we repeated the attentional manipulation (comparing trials where the white disk was cued vs no cue trials) and, in separate no cue trials, we manipulated the physical strength of the white disk increasing it by 25%, 50%, 100%, or 150% (for technical reasons, we had to decrease the average luminance of the stimuli in the equal contrast conditions, which was about 10 times lower than in the main experiment).



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1263 *Figure 3-5 Effects of attention cueing vs. enhancing contrast*

1264 *A-B: perceptual dominance for exclusive white or black disk percepts, in the no cue condition*

1265 *(dashed lines) or when the physical contrast of the white disk was enhanced /cued (continuous*

1266 *lines, contrast or cueing condition indicated on the abscissa). Error bars report ±1 s.e. across*

participants. C: time course of the difference between baseline-corrected pupil size during black and white percepts, computed in individual participants and then averaged for each condition. The blue marks on the x-axis highlight timepoints where pairwise comparisons between the +100% and the no cue condition traces are significant (p < 0.05 FDR corrected). Shadings report mean ±1 s.e. across participants.

A 2x5 repeated measures ANOVA showed that perceptual dominance was affected by the contrast modulation (Fig. 5A), resulting in a significant interaction between dominant percept (white/black) and contrast condition on the proportion of exclusive dominance phases (Table 2). Importantly, the same pattern was found for the pupil modulation (Fig. 5B). Increasing the difference in the physical strength between the two stimuli (i.e., increasing the contrast of the white disk), enhanced the pupil response, resulting in a significant interaction between the pupil response to the dominant percept and contrast condition.

	Proportions	Pupil size
Dominant percept	$F_{(1,9)} = 4.47$ p = 0.06 logBF = 0.19	$F_{(1,9)} = 18.40$* p = 0.002 logBF = 13.99
Contrast increment	$F_{(4,9)} = 4.23$* p = 0.007 logBF = -0.44	$F_{(4,9)} = 1.16$ p = 0.34 logBF = -1.30
Dominant percept x contrast increment	$F_{(4,9)} = 39.75$* p < 0.001 logBF = 12.36	$F_{(4,9)} = 14.11$* p < 0.001 logBF = 3.38

Table 3-2 Contrast enhancement effects.

Two-way ANOVA for contrast enhancement results, with factors: dominant percept (white/black disk) and contrast increment (25, 50,100,150 %). Greenhouse – Geisser corrected values.

However, in line with the results of the main experiment, the effects of attention cueing on perceptual dominance and pupil modulations were very different. While cueing the white disk modulated perceptual dominance in favour of the white stimulus, it did not modulate the

relative pupil response (Fig. 5A, B, rightmost point; Table 3), replicating our main experiment results. These observations were further supported by directly comparing the cueing condition with the contrast condition that better mimicked the effect of attention on dominance proportions: the 100% contrast increase (Table 3), in line with the estimates reported in Chong et al., 2005. Cueing the white disk and increasing its contrast by 100%, despite producing comparable behavioural results, elicited very different pupil responses. While the 100% contrast increase elicited significantly stronger pupil modulations than in the equal contrast (no cue) condition, pupil modulations when the white disk was cued were indistinguishable from those in the no cue condition (Figure 5C).

	MI Proportions	MI Pupil size
Cueing vs. no cue	$t_{(9)} = 5.66$* $p < 0.001$ logBF = 2.04	$t_{(9)} = 0.66$ $p = 0.52$ logBF = -0.43

	Proportions	Pupil size
25% contrast increment vs. cueing	$t_{(9)} = 5.46$* $p < 0.001$ logBF = 1.95	$t_{(9)} = 0.41$ $p = 0.69$ logBF = -0.48
50% contrast increment vs. cueing	$t_{(9)} = 2.43$* $p = 0.04$ logBF = 0.33	$t_{(9)} = 0.52$ $p = 0.61$ logBF = -0.45
100% contrast increment vs. cueing	$t_{(9)} = 0.77$ $p = 0.46$ logBF = -0.40	$t_{(9)} = 3.29$* $p = 0.01$ logBF = 0.81
150% contrast increment vs. cueing	$t_{(9)} = 3.83$* $p = 0.004$ logBF = 1.11	$t_{(9)} = 4.73$* $p = 0.001$ logBF = 1.58

Table 3-3 The effects of cueing on proportions and pupil size in the control experiment. Modulation indices from the control experiment: comparison of attention cueing vs. no cue (first row) and attention cueing vs. contrast enhancement by 25, 50, 100 and 150%.

As a confirmatory analysis, we also checked the cross-correlation between the rate of pupil size change and perceptual reports (see Materials and Methods). The peak cross-correlation

was significantly larger than zero in no-cue conditions ($t(37) = 5.41$, $p < .001$, logBF = 3.70), further confirming that pupil modulations reliably tracked perceptual alternations; and it was higher when the white stimulus contrast was doubled (control experiment +100% contrast, $t(9) = 2.32$, $p = .04$, logBF = .28), indicating that it is indicative of stimulus strength. However, the peak cross-correlation was indistinguishable across cueing conditions (white cued vs. no cue: $t(37) = 1.23$, $p = .22$, logBF = -.45; $t(9) = 0.83$, $p = .42$, logBF = -.39, in the main and the control experiment respectively), confirming that cueing did not alter the reliability of pupil modulations.

3.3.1 Analysis of mixed percepts

All the analyses presented to this point are focused on exclusive dominance phases. In this section we consider perceptual and pupillary reports for the third perceptual state that participants had the option to report: mixed percepts, defined as anything but the exclusive dominance of a white or black disk percept.

Previous work (Brascamp et al., 2006; K. C. Dieter et al., 2017a) highlighted the importance of quantifying the fraction of return transitions, where mixed percepts are interposed between two periods of dominance of the same percept (e.g., black disk percept, followed by mixed percept, followed by another black disk percept). In no-cueing conditions, these return transitions represented a small fraction of all transitions (about 15%) for binocular rivalry and a greater fraction for interocular grouping rivalry (about 40%). Attention cueing dramatically affected the distribution of these transitions, as the proportion of black-mixed-black transitions increased when cueing black and white-mixed-white transitions increased when cueing white. This resulted in a significant interaction between factors “dominance percept after a return transition” and “cued percept” in a 2x2 ANOVA for both binocular rivalry ($F(1,37) = 20.19$, $p < .001$, logBF = 1.75) and interocular grouping rivalry ($F(1,37) = 12.91$, $p < .001$, logBF = 2.94). This indicates that attention cueing also affected the frequency of dominance phases, besides modulating the duration of individual dominance phases.

Figure 6 quantifies the overall percentage of mixed percepts in binocular and interocular grouping rivalry. Attention cueing did not affect the proportion of mixed percepts in binocular rivalry, which averaged .24±.02 and .23±.02 for no cueing and cueing conditions ($t(37) = .80$, $p = .43$, logBF = -.63). In interocular grouping rivalry, the difference was also non-significant

but there was a trend towards reduced mixed reports in the cueing condition (.52±.02 and .48±.02 for no cueing and cueing respectively, $t(37) = 1.71$, $p = .10$, logBF = -.18). Based on this observation, we cannot exclude the possibility that attention cueing may have promoted interocular grouping.

Figure 6 C-D shows pupil traces aligned to the onset of mixed percepts, separately for no cueing and the two attention cueing conditions; note that this is conceptually equivalent to analysing data for exclusive dominance phases aligned to their offset, rather than the onset (same conventions as in Figure 4 C-D). A difference between cueing conditions is apparent for binocular rivalry, suggesting enhanced pupil dilation when the white percept was cued. No such effect is observed for interocular grouping rivalry. This difference between the two rivalry types may suggest that the cueing effect is specifically related to fusion percepts (grey disk percepts), which likely represented a minor percentage of mixed reports in interocular grouping rivalry (the largest majority being monocular half white, half black disk percepts). The relative pupil dilation may indicate that fusion events were perceived as grey disks of a darker shade during white cueing than during black cueing or no cueing. There are at least two reasons why this could happen. One possibility is that white cueing indeed enhanced the effective strength of the white stimulus, implying that the black stimulus strength had to reach a higher threshold before a white-dominance report switched to a mixed report. If this is the case, however, it is unclear why such difference in effective strength should not show in pupil traces during phases of exclusive white dominance (Figures 3 and 4). Another possibility is that cueing may have affected decision criteria so that fusion percepts reported as mixed were generally darker under white cueing (effectively prolonging exclusive white-dominance phases) than under black cueing conditions.

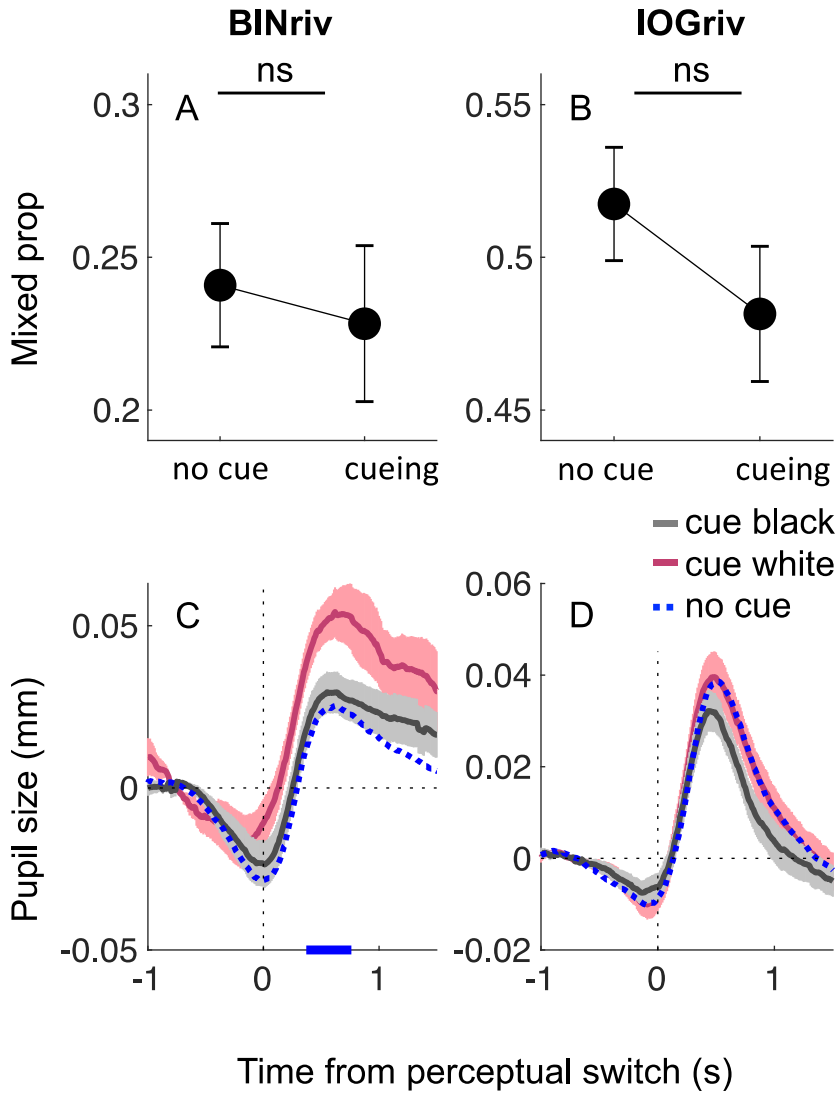


Figure 3-6 Effects of attention cueing on mixed percepts.

A: proportion of mixed percepts in no cueing or cueing conditions (collapsed across white and black cued). Error bars report ±1 s.e. across participants

B: pupil traces during mixed percepts in the three cueing conditions. Shaded areas show ±1 s.e. across participants and blue marks on the x-axis highlight timepoints where pairwise comparisons between the white and black cueing conditions are significant ($p < 0.05$ FDR corrected).

3.4 Discussion

We used pupillometry to investigate the effects of endogenous attention on binocular rivalry and interocular grouping rivalry. We confirmed that pupil size tracks perceptual oscillations during binocular rivalry, despite constant luminance stimulation, and we extended this observation to interocular grouping rivalry. This is consistent with the large body of work suggesting that the subcortical circuit generating the pupillary light response can be modulated by perceptual signals (Binda & Gamlin, 2017; Binda & Murray, 2015a; Mathôt, 2018). Our finding that similar pupillary modulations accompany interocular grouping rivalry constrains the origin of the modulatory signals to visual cortical areas (they must hold a representation of stimulus brightness) with access to binocular information (they must be able to combine information from the two eyes). We found that manipulating endogenous attention reliably affected perceptual alternations, enhancing dominance of the cued percept during binocular rivalry, in line with previous work (Chong et al., 2005; Hancock & Andrews, 2007; Meng & Tong, 2004; Mitchell et al., 2004; Paffen & Alais, 2011). To our knowledge, this is the first study manipulating attention in interocular grouping rivalry. We found that attention cueing had the same or slightly smaller effects on interocular grouping rivalry as on binocular rivalry. This suggests that eye-based and pattern-based competition are similarly permeable to endogenous attention; it also suggests that different degrees of attentional control (as observed, for example, comparing Necker cube vs binocular rivalry; (Meng & Tong, 2004b)) may be related to differences in stimulus complexity rather than to the involvement of different levels (monocular vs binocular) of cortical processing. Many have suggested that attention cueing acts by enhancing the perceptual strength of the cued signals (Carrasco, 2011). This is in line with evidence that focusing attention at a spatial location or feature enhances its representation in early visual cortex, as measured with EEG (F. Di Russo, 2003; Hillyard & Anllo-Vento, 1998; S. P. Kelly et al., 2008; Khoe et al., 2008; Mishra & Hillyard, 2009; J. Wang et al., 2007), fMRI (Boynton, 2009; T. Liu et al., 2005; Pestilli et al., 2011; Saenz et al., 2002), or indexed by enhanced pupillary response to light stimuli at the attended location (Binda & Murray, 2015). Transferring this knowledge to the context of rivalry, we expected that cueing attention to one of the rivalling percepts would enhance its effective strength and thereby increase its dominance. Using pupillometry, we intended to indirectly index this phenomenon. We established that the magnitude of pupil-size modulations accompanying

rivalry is sensitive to effective stimulus strength as set by ocular dominance (control analysis of binocular rivalry data from the main experiment) or physical contrast changes (control experiment). On this basis, we predicted that attention cueing would have a similar effect as physical contrast enhancement, namely an amplification of pupil modulations. However, we obtained evidence against this prediction, as pupil responses during periods of exclusive dominance were reliably unaffected by attention cueing.

The simplest way to explain this negative finding is putting it down to insufficient sensitivity of the pupillometric measurements. However, our reliability analysis, Bayesian statistics and results from a control analysis and a control experiment all coherently speak against this possibility. We therefore speculate on a few logical alternatives.

During binocular rivalry, most of the time is spent in exclusive dominance, where competition between rivalling stimuli is resolved, leaving only one visible stimulus and no distracter. In these conditions, attention may be automatically driven to the dominant stimulus (Li et al., 2017), leaving little space for endogenous re-directing of attention. Although this is consistent with attention affecting early visual processing in markedly different ways at the onset of rivalry vs. for non-rivaling stimuli (Khoe et al., 2008; Mishra & Hillyard, 2009), the model by Li et al., 2017 does not explicitly account for the small but reliable effects of attention cueing on perceptual alternations during rivalry. To account for these, one possibility is assuming that attention cueing primarily affects rivalry when the competition between stimuli is unresolved, namely in the brief times marking transitions between exclusive dominance phases, when the depth of suppression decreases (Alais et al., 2010). This idea has been suggested previously and supported by the observation that exogenous cues are mostly effective when presented near the end of individual dominance periods (K. C. Dieter et al., 2015). In this scenario, we could reconcile our behavioural and pupillometry results by assuming that attention enhances the strength of cued percepts only in short intervals near perceptual switches, not during the entire dominance phases. This could be consistent with our observation that the only effects of cueing over pupil traces were observed in a brief interval during mixed percepts.

An alternative possibility is that attention cueing affects rivalry dynamics by acting on a stimulus representation that is not represented in pupil dynamics. Available evidence is consistent with pupil size integrating a cortical representation of stimulus brightness (e.g., one that oscillates, tracking rivalry dynamics), but we lack direct knowledge on the level at which such visual representation is generated and fed into the pupil control circuit (Binda & Gamlin,

2017). On the other hand, evidence indicates that rivalrous perception is orchestrated by the interplay of fronto-parietal and occipital regions, which participate in different degrees depending on the details of the stimulus and task (Logothetis et al., 1996; Sterzer et al., 2009; Sterzer & Kleinschmidt, 2007). It is possible, then, that attention affects competition after the stage where visual representations are fed to pupil control – whether this needs to be a decisional stage or still a sensory representation cannot be determined based on the available research.

This is not the first case where we find that the pupillary responses are independent of physical luminance and yet inconsistent with perceptual judgments (Pomè, Binda, et al., 2020; Tortelli et al., 2021a, 2021b; Turi et al., 2018). These inconsistencies were generally explained by calling decisional factors into the picture, as these may bias or add variability to perceptual reports while leaving pupil size unaffected (Tortelli et al., 2021b). That contextual factors other than physical luminance affect pupil size and perception similarly but independently – if it proves recurrent and reliable across paradigms – might call for an updated model of pupil control. It might suggest that separate processing pathways support perception and pupil control, in analogy (or perhaps in overlap) with the separate pathways supporting vision for perception and vision for action (Goodale & Milner, 1992).

In conclusion, we find that pupil size oscillates in phase with perceptual oscillations during binocular and interocular grouping rivalry, implying cortical control. Despite this, and despite the reliable effects of attention cueing on behavioural reports, pupil size during periods of exclusive dominance does not show any modulation with attention. This introduces new constraints for models of attention in rivalry and pupil control: either attention cueing affects perception without enhancing the dominant percept, or we hold multiple representations of the dominant percept that independently regulate behavioural reports and pupil size and are differentially affected by attention cueing.

4 Chapter 4 – Pupil size as an index of ocular dominance plasticity

4.1 Introduction

When incompatible images are simultaneously presented to the eyes, perception alternates between the two, even though the visual input remains constant. This phenomenon is known as 'binocular rivalry' and has a long tradition as an experimental model for investigating the neural mechanisms of conscious perception (LEVELT, 1966; Bartels & Logothetis, 2010; Blake & Logothetis, 2002).

Perceptual dominance in binocular rivalry is a reliable index of ocular dominance (Acquafredda et al., 2023). At any given moment, the reported perceptual dominance during binocular rivalry mirrors the fluctuating contribution of each eye to conscious visual perception. While ocular dominance is typically established during the critical period (Hensch and Quinlan, 2018; Hubel & Wiesel, 1965), recent studies have shown that a form of homeostatic plasticity of ocular dominance is retained throughout adulthood (see Castaldi et al., 2020). The first study to describe this phenomenon was published by Lunghi and colleagues in 2011 and showed that patching one eye for two hours transiently restores ocular dominance plasticity in the adult brain (Lunghi et al., 2011); following deprivation, the deprived eye dominates rivalrous perception for twice as long as the nondeprived eye, indicating a strong shift of ocular dominance in favour of the deprived eye. The boost of the deprived eye was associated with an enhancement of the perceived contrast, as assessed through a contrast discrimination task (Lunghi et al., 2011). This counterintuitive effect has been related to a compensatory homeostatic response of the visual system to the temporary reduction in monocular visual input, mediated by mechanisms of contrast gain control (Binda et al., 2017; Binda & Lunghi, 2017; Lunghi, Berchicci, et al., 2015; Lunghi, Emir, et al., 2015; Lunghi et al., 2011, 2013, 2019; Lunghi & Sale, 2015; Steinwurzel et al., 2020; Zhou et al., 2013, 2014) This hypothesis is supported by electrophysiological and imaging techniques that showed how, following short-term monocular deprivation, visual evoked responses were enhanced in the deprived eye and reduced in the non-deprived eye (Lunghi, Berchicci, et al., 2015b)

However, it is interesting to note that these physiological indices of the boost of the deprived eye are not directly related to the behavioural effect, because they were acquired in

conditions that are very different from those used in behavioural testing. Visual evoked responses (EEG or fMRI) were recorded by presenting stimuli passively, in absence of any perceptual report; in addition, stimuli for EEG and fMRI measurements were delivered monocularly, i.e., separately to each eye (Binda et al., 2018; Lunghi, Berchicci, et al., 2015b). All this contrasts with the conditions of the behavioural experiments, where participants were continuously engaged in reporting their perception, which tracked the competitive interactions between the stimuli presented to the two eyes. In the present work, we aimed at tracking the effective strength of monocular signals during the behavioural assessment of the effect (based on binocular rivalry), using an objective physiological index: pupil size.

The perceptual alternations that occur during binocular rivalry can be accompanied by changes in pupil size, which are triggered by oscillations in the perceived brightness of the competing stimuli (Acquafredda et al., 2022; Einhäuser et al., 2008; Fahle et al., 2011; LOWE & OGLE, 1966; Naber et al., 2011) et al., 2022). Because the dominant percept influences the direction of pupil size changes, the oscillations in pupil size during binocular rivalry provide a continuous and objective physiological measure of the effective stimulus strength of the two eyes. Increased effective strength should lead to more significant fluctuations in pupil size (as directly tested through contrast manipulations in Acquafredda et al., 2022). It follows that, if monocular deprivation modulated the effective strength of the monocular stimuli, enhancing the deprived eye and suppressing the fellow eye, this should impact the size of pupil oscillations. This should make for a combined experimental paradigm, integrating perceptual reports during binocular rivalry with pupillometry, to provide simultaneous behavioural and physiological measures of ocular dominance plasticity. Given the potential implications of short-term monocular deprivation for the treatment of amblyopia in adults ((Lunghi et al., 2019); for reviews, see: (Baroncelli & Lunghi, 2021; Castaldi et al., 2020) evaluating the effectiveness of this combined experimental approach holds significant methodological and translational relevance.

4.2 Methods

4.2.1 Subjects

We recruited 10 participants (6 females, mean age 26.9 ± 0.77 years). These had normal or corrected-to-normal vision and normal color vision, no known history of amblyopia, eye surgery, or other active eye diseases (such as keratoconus) and balanced ocular dominance (we included all participants with a ratio of mean phase durations of the dominant over the nondominant eye smaller than 0.2 log units). Sample size was based on our previous study (Acquafredda et al., 2022), where we showed with the same set-up and the same stimuli, a detectable effect of contrast on pupil size across 10 participants.

4.2.2 Apparatus, stimuli and procedures

Experiments took place in a dark and quiet room. Visual stimuli were developed in Matlab (MATLAB r2010a, The MathWorks Inc., Natick, MA) using PsychoPhysics Toolbox routines (Brainard, 1997)housed in a Mac Pro 4.1, and displayed on a 52.5 cm-wide LCD screen, driven at a resolution of 1920 x 1080 pixels. The display was seen through a four-mirror stereoscope which enabled dichoptic viewing of two display areas of 12 x 8 deg each; a chin rest was used to stabilize head position at 57 cm from the display. In each display area, a central red fixation point (0.15 deg in diameter) surrounded by a square frame (3.5 x 3.5 deg) was shown against a uniform grey background (luminance: 12.3 cd/m^2). The mirrors were carefully adjusted at the beginning of each session to ensure accurate alignment of the dichoptically presented squares. Participants were asked to keep their gaze on the fixation point shown at screen center and to refrain from blinking while the stimuli were on. Dichoptic presentations consisted of two disks, 3° in diameter, one white (maximum screen luminance 28.9 cd/m^2, Michaelson contrast: 0.31) and one black (minimum screen luminance 1.7 cd/m^2, Michaelson contrast: 0.8). Perception alternated between exclusive dominance of the white and the black disk, or mixed percepts (either piecemeal or fusion). To discourage fusion, the disks were overlaid with thin orthogonal grey lines (45° clockwise or counterclockwise, 1 pixel wide, corresponding to 0.033 deg, and 0.5 deg apart, with the same luminance as the background). Participants were tested in two sessions, performed on two separate days. In each experimental session, binocular rivalry was measured in one block (comprising four 3 3-minute-long trials) before monocular patching and one immediately after (Figure 1-A). On each trial, a different combination of disk colour and line orientation was presented to each eye; combinations were varied pseudo-randomly across trials. The first trial was discarded

from both sessions, because of the poor signal-to-noise ratio of the pupil responses in the post-deprivation session, so we included in the analysis three trials per block per participant (repeated in two sessions, so six trials in total). During the trial, participants continuously reported perception by keeping one of three keys pressed: right or left arrows to report dominance of the stimulus with clockwise or counterclockwise tilted lines, or the down-arrow key any time dominance of either stimulus was incomplete (we considered piecemeal and fusion events as "mixed"). Dominance phase distributions were adequately captured by a typical gamma distribution (LEVELT, 1966b), with shape α and scale β parameters: α = 2.98; β = 0.26 (Equation 1; Figure 1-C). The goodness-of-fit (coefficient of determination R2) was 0.95.

$$f(x|\alpha,\beta) = \frac{1}{\beta^{\alpha}\Gamma(\alpha)}\, x^{\alpha-1}e^{\frac{-x}{\beta}} \qquad \text{for } x,\alpha,\beta > 0$$

Equation 4-1

Where Γ is the gamma function and x the number of dominance phases.

4.2.3 Monocular deprivation

Monocular deprivation was achieved by patching the dominant eye, defined as the eye with longer mean phase duration in binocular rivalry, for 2 hours.

As in previous studies (Binda et al., 2017; Binda & Lunghi, 2017; Lunghi et al., 2011, 2013; Steinwurzel et al., 2020) we used a translucent plastic material that allowed light to reach the retina (attenuation 15%), but no pattern information, as assessed by the Fourier transform of a natural world image seen through the eye patch. During the 2 hours of monocular deprivation, participants were free to read, work at the computer, or walk around the laboratory (but not to eat or sleep).

To quantify the plasticity effect elicited by monocular deprivation, we defined a deprivation index (DI) as the ratio between the deprived and non-deprived eye mean phase durations, before(pre) and after(post) deprivation:

$$DI = \frac{\frac{DepPost}{NDepPost}}{\frac{DepPre}{NDepPre}}$$

Equation 4-2

Note that Equation 2 can be rewritten using log-transformed mean phase durations, becoming a linear combination.

$$lgDI = \left(lg_{DepPost} - lg_{NDepPost}\right) - \left(lg_{DepPre} - lg_{NDepPre}\right)$$

Equation 4-3

A deprivation index > 1 (or logDI > 0) implies a shift of ocular dominance in favour of the deprived eye (the expected effect).

4.2.4 Eye tracking data acquisition and analysis

During rivalry, we monitored pupil diameter and two-dimensional eye position with an infrared camera (EyeLink 1000 system, SR Research, Canada) mounted below the monitor screen and behind the stereoscope. EyeLink data were streamed to the main computer through the EyeLink toolbox for Matlab (Cornelissen et al., 2002)and thereby synchronized with participant's keypresses. Pupil diameter measurements were transformed from pixels to millimeters using an artificial 4 mm pupil positioned at the approximate location of the subject's eye.

Data were analysed as in Acquafredda et al., 2022. Pupil and gaze tracking data consisted of 180 x 1000 (180 seconds at 1000 Hz) time points. These included signal losses, eyeblinks and other artifacts, which we cleaned out by means of the following steps (all implemented with in-house Matlab software):

- Identification and removal of gross artifacts: removal of time-points with unrealistically small pupil size (<0.2 mm, corresponding to blinks or other signal losses).
- Identification and removal of finer artifacts: identification of samples where pupil size varied at unrealistically high speeds (larger than 10 mm per second) and removal of the possible resulting isolated data points.
- Removal of any linear trend by fitting a linear function to pupil data from each 180 s-long trial.

After this cleaning procedure was applied, we verified fixation stability by measuring the dispersion of eye position samples around the mean of each trial as the bivariate confidence ellipse area (BCEA), defined as:

$$BCEA = 2 * k * \sigma_H * \sigma_V * (1 - \rho)^{0.5}$$

Equation 4-4

Where k is the confidence limit for the ellipse, σH and σV are the standard deviation of eye positions in the horizontal and vertical meridian respectively, ρ is the product-moment correlation of these two position components and k=1.14, implying that the ellipse included 68% (1-e(-k)) of the distribution.

Cleaned pupil data and continuous recordings of perceptual reports were down-sampled to 100 Hz, by taking the median of the retained time-points in non-overlapping time windows. If no retained sample was present in a window, that window was set to "NaN" (MATLAB code for "not a number"). Down-sampled pupil traces were finally parsed into epochs locked to each perceptual switch (when the subject changed perceptual report) and labelled according to the color of the dominant stimulus after the switch. Pupil time courses were averaged across epochs for each participant; further averaging across participants yields traces in Figure 1-B. In order to minimize the impact of pupil size changes unrelated to the perceptual switches, we also analyzed data after subtracting a baseline from each epoch, measured in the [-1 -0.5] s interval preceeding the switch – again, adopting the same conventions as in Acquafredda et al. (2022). To compare pupil size across dominance phases and conditions (pre vs. post deprivation), we extracted an index of pupil size in each epoch by averaging its value in the [-0.5 1] s interval around the switch. Note that shifting the intervals for pupil baseline, or skipping the baseline correction step, affected the size of pupil modulations but it did not change our conclusion on the effects of monocular deprivation.

4.2.5 Statistical approach

Significance was evaluated using both p-values and log-transformed JZS Bayes Factors computed with the default scale factor of 0.707 (Wagenmakers et al., 2012). The Bayes Factor is the ratio of the likelihood of the two models H1/H0, where H1 is the experimental hypothesis (effect present) and H0 is the null hypothesis (effect absent). By convention, a base 10 logarithm of the Bayes Factor (logBF) > 0.5 is considered substantial evidence in favor of

H1, and logBF < −0.5 substantial evidence in favor of H0. Bayesian ANOVAs were run in JASP, and the corresponding Bayes Factors represent the change from prior to posterior inclusion odds (BFinclusion) computed across matched models.

4.3 Results

In 10 adult observers, we measured perceptual alternations and pupil oscillations during binocular rivalry before and after monocular deprivation. Our primary aim was to establish whether the increase in perceptual dominance of the stimulus shown to the dominant eye induced by monocular deprivation, would yield a measurable effect on its pupil response.

The analysis of behavioural reports before monocular deprivation showed a clear predominance of black percept over to the white one, consistent with its higher Michelson contrast (in turn implied by the identical Weber contrast of the white and black disks). The average phase durations across subjects were 2.00 ± 0.33 seconds (mean ± standard error of the mean) for the black percept and 1.26 ± 0.16 seconds for the white one. Dominance proportion, computed as the time during which one percept dominated over the total trial time, was 0.47 ± 0.03 for the black percept and 0.25 ± 0.03 for the white one.

These perceptual alternations were reliably tracked by pupil size. Despite constant stimulation, participants' pupils were relatively dilated when they reported seeing black, compared to when they reported seeing white (Figure 1-B).

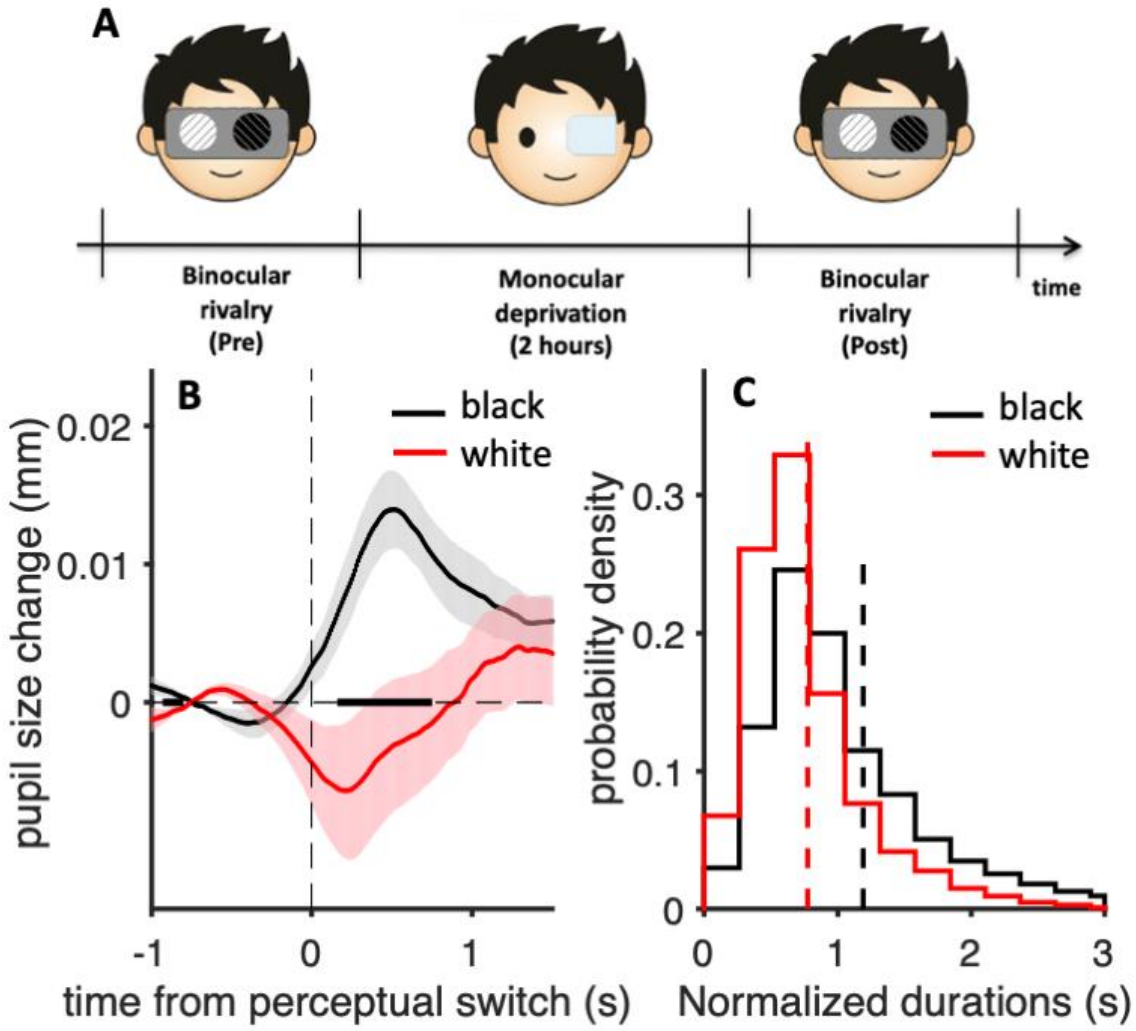


Figure 4-1 Experimental procedure and indices of perceptual alternations before monocular deprivation.

A: Time course of the experiment, where binocular rivalry dynamics were measured before and after deprivation. Short-term monocular deprivation was achieved by applying a translucent patch over the dominant eye for 2 hours. B: Baseline subtracted pupil size traces aligned to perceptual switches toward exclusive dominance of a white disk or a black disk percept and averaged across phases. Shadings report mean ± SE across participants and the black mark on the x-axis highlights time points where the pupil difference is significantly different from zero (one-tailed paired t-test, $p < 0.05$ FDR corrected). C: Probability density function of the normalised phase durations for each stimulus (black and white), measured before deprivation and pooled across conditions and participants. The function conforms to the typical gamma distribution.

Having established the perceptual and pupil size oscillations before monocular deprivation ("pre" condition), we proceeded to assess the impact of monocular deprivation upon the two measures ("post" vs. "pre" conditions).

Following patch removal, we tested four blocks of binocular rivalry (3 minutes each). Across blocks, we alternated the eye to which the black and white disks and the associated oriented lines were delivered – as customarily done to minimize the impact of adaptation and astigmatism. Each participant took part in two monocular deprivation sessions with swapped color-eye assignments. Results were analysed after pooling data from blocks where the white disk was delivered to the deprived eye and blocks where the black disk was delivered to the deprived eye. The effect of deprivation was tested using a one-way ANOVA with factor time at three levels: "pre" deprivation, "post: white" and "post: black" meaning post-deprivation blocks with the white or black disk delivered to the deprived eye.

Behavioral results were consistent with previous studies, in that monocular deprivation shifted ocular dominance in favour of the deprived eye, irrespectively of the color-eye assignment. The ANOVA revealed a significant effect of patching on perceptual dominance (Figure 2A; $F= 15.77$, $p < .001$), and post-hoc tests showed that it is due to an increase of the black-white perceptual dominance when the black stimulus was shown to the deprived eye ($|t(9)| = 2.81$, $p_{holm} = 0.02$) and a decrease when the white stimulus was given to the deprived eye ($|t(9)| = 2.80$, $p_{holm} = 0.02$; t-test between the two levels: $|t(9)| = 5.61$, $p < .001$).

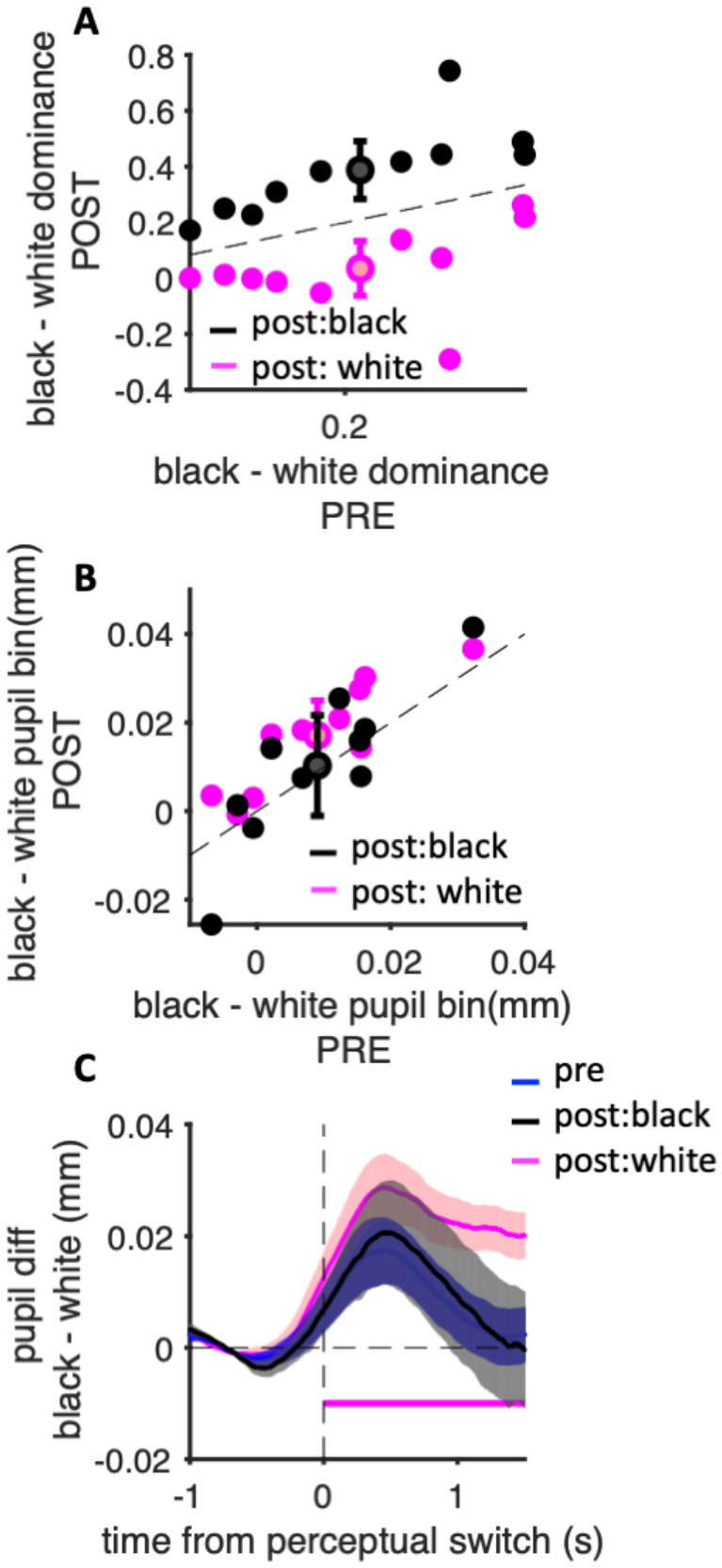
Based on the assumption that monocular deprivation boosts perceptual dominance by enhancing the effective strength of the percept shown to the deprived eye, we anticipated that the pupil oscillations accompanying perceptual alternations would be amplified. We predicted that constrictions concurrent with white percept dominance would be increased when the white stimulus was delivered to the deprived eye, and that dilations elicited by the black percept would be increased when the black stimulus was delivered to the deprived eye. This would result in larger differences in pupil size during black vs. white percepts after deprivation, as compared to before deprivation. We tested for this effect by looking at the

average pupil-size difference in the usual [-.5 1] s interval relative to perceptual switches and analysing it with the same ANOVA used for perceptual reports.

This revealed a significant effect of patching on the pupil modulation ($F = 4.99$, $p = 0.02$). In addition, post-hoc tests showed that this effect was selective due to an increase in pupil modulations when the white stimulus was shown to the deprived eye ($|t(9)| = 2.94$, $p_{holm} = 0.03$), while the "post – blackdep" condition was not significantly different from the "pre" condition ($|t(9)| = 0.45$, $p_{holm} = 0.65$; t-test between the two "post" conditions: $|t(9)| = 2.48$, $p = 0.05$).

We verified that the deprivation effects could not be explained by differences in eye-movements patterns by averaging the BCEA values across trials and comparing them across conditions ($F = 1.24$, $p = 0.31$).

We also analyzed mixed percept phases, where participants reported fusion-derived (or piecemeal) percepts as dominating perception. We found no effect of monocular patching, neither on their proportion ($F = 0.92$, $p = 0.41$) nor on the evoked pupil response ($F = 0.10$, $p = 0.90$).



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1745 *Figure 4-2 Monocular deprivation effects on perceptual dominance and pupil modulations.*

A: Difference between white and black dominance proportions measured before (x-axis) and after (y-axis) monocular deprivation. Single dots report individual values when the white (magenta dots) or the black stimulus stimulus (black dots) was shown to the deprived eye, after monocular deprivation. Error bars indicate mean ± S.E. across participants.

B: Difference between baseline-corrected pupil size (in time bin -.5:1 s around perceptual switch) in black and white dominance phases measured before (x-axis) and after (y-axis) monocular deprivation. Single dots report individual values when the white (magenta dots) or the black stimulus stimulus (black dots) was shown to the deprived eye, after monocular deprivation. Error bars indicate mean ± S.E. across participants.

C: Time course of the difference between baseline-corrected pupil size during black and white percepts computed before (blue trace) and after monocular deprivation (black trace for blackdep condition, magenta trace for whitedep condition). Shadings report mean ± SE across participants; marks on the x-axis highlight time points where the pupil difference after deprivation (magenta for "post-whitedep" and black for "post-blackdep") is significantly different from the "pre" condition (paired t-tests, $p < 0.05$ FDR corrected).

4.4 Discussion

In this study, we investigated the effects of short-term monocular deprivation on the pupil response evoked by rivalling visual stimuli.

We successfully replicated the effects of short-term monocular deprivation on perceptual dominance during binocular rivalry, which consisted of a clear bias in favour of the eye that had been deprived of visual input (Lunghi et al., 2011, 2013).

We also confirmed that pupil size tracks perceptual oscillations during binocular rivalry, despite constant stimulation, consistently with a large body of work suggesting that the subcortical circuit generating the pupillary light response is modulated by perceptual signals (Binda & Gamlin, 2017; Binda & Murray, 2015a; Mathôt, 2018). In line with our predictions, we found that these pupil size changes during rivalry were modulated by monocular deprivation, and increased after patch removal. This effect is in line with the hypothesis that monocular deprivation boosts the effective strength of the deprived eye.

Surprisingly, the effect on pupil modulations differed depending on which stimulus, white or black, was delivered to the deprived eye. When the white stimulus was shown to the deprived eye, it elicited significantly larger pupil modulations, whereas the effect was non-significant when the black stimulus was delivered to the deprived eye.

This asymmetry in our results may be explained by considering that black stimuli generally drive a much weaker pupillary response than bright stimuli, implying weaker modulations thereof (e.g., Binda & Murray, 2015).

It is interesting to compare these results with those in Acquafredda et al., 2022, where we used the same technique to measure the effects of attention during rivalry. Voluntary attention to one of the rivalry stimuli and short-term deprivation of one eye produced similar effects on perceptual reports – a modulation of about 10-20% dominance. However, the effects on pupil oscillations differed. Only monocular deprivation, not voluntary attention, modulated pupil responses. This suggests that these two factors affect rivalry at very different levels; as suggested in Acquafredda et al., 2022), attention could alter rivalry dynamics by acting at a higher level than monocular deprivation; it could affect perceptual decisions, rather than sensory representations. Of course, this suggestion requires further experimental tests.

Our findings attest to the sensitivity of the pupillometric technique for tracking perceptual modulations; they also suggest that similar perceptual effects can be accompanied by very different modulations on effective strength, likely implicating distinct neural underpinnings. There is increasing evidence on the relevance of pupillometry in investigating a variety of neural phenomena, including neuroplasticity (Binda & Lunghi, 2017; Viglione et al., 2023). For the first time, we were able to integrate the pupillometric technique into one of the standard tests for revealing short-term monocular deprivation effects – binocular rivalry. Our results indicate that enhanced pupil modulations serve as an objective, automatic and unconscious index of the increased dominance of the deprived eye following patch removal.

5 Chapter 5 - Short-term monocular deprivation in adult humans alters functional brain connectivity measured with ultra-high field Magnetic Resonance Imaging

5.1 Introduction

Monocular deprivation is the classical paradigm to investigate ocular dominance plasticity. During development, closing one eye for a prolonged period of time leads to amblyopia, a permanent loss of the deprived eye representation in the visual cortex, producing a shift of ocular dominance in favour of the non-deprived eye (HENSCH & QUINLAN, 2018; Hubel & Wiesel, 1965; Wiesel & Hubel, 1963). In adult humans, a shorter period of monocular patch (only two hours) leads to a paradoxical shift of ocular dominance: temporary and opposite to that produced during development, consisting of a transient boost of the deprived eye (Bai et al., 2017; Binda & Lunghi, 2017; Castaldi et al., 2020; Chadnova et al., 2017; Lunghi, Berchicci, et al., 2015b; Lunghi, Emir, et al., 2015; Lunghi et al., 2011, 2013, 2019; Lunghi & Sale, 2015; Lyu et al., 2020; Min et al., 2018; Schwenk et al., 2020; M. Wang et al., 2020; J. Zhou et al., 2013, 2014, 2015). This phenomenon was interpreted as a form of homeostatic plasticity (Turrigiano, 2012). The effects of short-term monocular deprivation have been extensively studied with electrophysiological and imaging techniques, which have consistently shown a change in the ocular drive of cortical visual evoked responses in favour of the deprived eye (Binda et al., 2018; Lunghi, Berchicci, et al., 2015b). Crucially, these effects were found not only in the visual cortex, but also in a key nucleus of the visual thalamus: the ventral Pulvinar (Kurzawski et al., 2022). The same study failed to find any effect of deprivation in the lateral geniculate nucleus (LGN) (Kurzawski et al., 2022). This suggests that the primary visual cortex (V1) modulation is not inherited from LGN, since the former was reliably observed in a dataset where the latter was absent.

this observation also opens the possibility that the pulvinar plays an important role in mediating the effect of monocular deprivation.

The pulvinar is the largest nucleus in the primate thalamus and it is anatomically and functionally heterogeneous (Bridge et al., 2016). Functional connectivity analyses have revealed two distinct subregions, namely the ventral (vPulv) and dorsal (dPulv) regions (Arcaro et al., 2015, 2018). While dPulv exhibits stronger connections with the parietal and frontal cortex, the vPulv region is primarily connected with the occipital cortex, particularly with areas

along the ventral pathway. This finding aligns with similar results observed in other primates (Kaas & Lyon, 2007).

Unlike the first-order thalamic relay nuclei, including the LGN, which receive their driving input from subcortical sources and project to layer 4 of the corresponding unimodal cortical area, most of the pulvinar neurons receive driving input from layer 5 of the cerebral cortex and project to layer 4 of a higher cortical area. These connections give rise to a cortico-thalamo-cortical route for both feedforward and feedback corticocortical communication (Arcaro et al., 2018; Benarroch, 2015; Sherman, 2005; Shipp, 2003).

It is thanks to its recurrent connectivity with the cortex that this thalamic nucleus is receiving more and more attention for its involvement in a variety of brain functions, including attention (Kaas & Lyon, 2007; Purushothaman et al., 2012; Saalmann et al., 2012; Sherman & Guillery, 2002; Shipp, 2003; H. Zhou et al., 2016), sensory-motor integration in the context of eye movements (Miura & Scanziani, 2022) and modulation of bottom-up and top-down cortical pathways (Bridge et al., 2016; Galuske et al., 2019; Jaramillo et al., 2019; Kanai et al., 2015; Z. Liu et al., 2012).

Recently, Ziminski and colleagues (Ziminski et al., 2023) have also shown its involvement in plasticity mechanisms, demonstrating that learning-dependent changes in thalamocortical connectivity, gate sensory processing through GABAergic inhibition in the visual cortex. The idea that experience-dependent changes in the adult brain can be modulated by top-down gating mechanisms has been also proposed in (Steinwurzel et al., 2023), which shows that de-synchronization of visual information and voluntary actions is sufficient to trigger ocular dominance plasticity, suggesting that homeostatic plasticity is gated by circuits integrating visual inputs and actions outcomes.

Here, we hypothesise that the effects of monocular deprivation might extend beyond modulations of visual evoked responses to a (temporary) reorganization of thalamo-cortical circuits.

To test this hypothesis, we investigate the effects of short-term monocular deprivation on the resting state functional connectivity of two thalamic nuclei: the ventral Pulvinar and the LGN.

5.2 Materials and Methods

5.2.1 Participants and ethics statement

Experimental procedures are in line with the declaration of Helsinki and were approved by the regional ethics committee [Comitato Etico Pediatrico Regionale—Azienda Ospedaliero-Universitaria Meyer—Firenze (FI)] and by the Italian Ministry of Health, under the protocol 'Plasticità e multimodalità delle prime aree visive: studio in risonanza magnetica a campo ultra alto (7T)' version #1 dated 11/11/2015. Written informed consent was obtained from each participant, which included consent to process and preserve the data and publish them in anonymous form. Twenty-five healthy volunteers with normal or corrected-to-normal visual acuity were examined (13 females including one author, mean age ± S.E.M.= 26.6 ± 3.7). We analyzed data from two fMRI sessions, acquired before and after 2 hours of monocular deprivation.

5.2.2 Short-term monocular deprivation

Monocular deprivation was achieved by patching the dominant eye for 2 hours. The operational definition of dominant eye applied to the eye showing the longer phase durations during the baseline binocular rivalry measurements. Like in previous studies (Lunghi et al., 2011, 2013), we used a translucent eye-patch made of plastic material allowing light to reach the retina (attenuation 0.07 logUnits, at least 3 times smaller than the threshold for discriminating a full-field luminance decrement (Knau, 2000) and more than ten times smaller than the minimum photopic luminance decrement required for shifting the spatial (Van Nes & Bouman, 1967) or temporal contrast sensitivity function (D. H. Kelly, 1961). The patch prevents pattern vision, as assessed by the Fourier transform of a natural world image seen through the eye-patch. During the 2 hours of monocular deprivation, participants were free to walk, read and use a computer.

5.2.3 Binocular rivalry

Binocular rivalry was measured in two short sessions (each comprising two runs of 3 min each), immediately before each fMRI session to estimate the transient ocular dominance shift (pre- vs. post deprivation). Stimuli were presented on a 15-inch LCD monitor, placed at a 57 cm distance, and were viewed through anaglyph red-blue goggles (right lens blue, left lens red). Stimuli were composed of two oblique orthogonal red and blue gratings (orientation:

±45°, size: 3°, spatial frequency: 2 cpd, contrast 50%), surrounded by a white smoothed circle, presented on a black uniform background in central vision. Peak luminance of the red grating was reduced to match the peak luminance of the blue one using photometric measures. During stimulus presentation, participants were asked to respond with the computer keyboard and report which grating (red or blue or a mixture of the two) they perceived as dominant by continuous keypresses.

We defined ocular dominance as the proportion of dominance time spent seeing through either eye.

$$ODI = \frac{TimeDE - TimeNDE}{TimeDE + TimeNDE}$$

Equation 5-1

Where DE stands for Dominant Eye and NDE stands for Non-dominant Eye. From this, we derived an index of ocular dominance shift by taking the difference between ocular dominance indices acquired before and after the 2h monocular deprivation.

The ocular dominance shift following monocular deprivation (mean ± S.E.M: 0.18 ± 0.02) was significant across participants (one sample t-test: $|t(24)| = 7.36$, $p < 0.001$, lgBF = 5.06), validating the efficacy of monocular deprivation paradigm in triggering ocular dominance plasticity in our dataset.

5.2.4 MR system and sequences

Scanning was performed on a Discovery MR950 7 T whole body MRI system (GE Healthcare, Milwaukee, WI, USA) equipped with a 2-channel transmit driven in quadrature mode, a 32-channel receive coil (Nova Medical, Wilmington, MA, USA) and a high-performance gradient system (50 mT/m maximum amplitude and 200 mT/m/ms slew rate).

Anatomical images were acquired at 1 mm isotropic resolution using a T1-weighted magnetization-prepared fast Fast Spoiled Gradient Echo (FSPGR) with the following parameters: TR = 6 ms, TE = 2.2 ms. FA = 12 deg, rBW = 50 kHz, TI = 450 ms, ASSET = 2. Two different sets of functional images were acquired. One with spatial resolution 1.5 mm and slice thickness 1.4 mm with slice spacing = 0.1 mm, TR = 3 s, TE = 23 ms, rBW = 250 kHz, ASSET = 2, phase encoding direction AP-PA. The other with spatial resolution 1.5 mm and slice

thickness 1.4 mm with slice spacing = 0.1 mm, TR = 1 s, TE = 23 ms, rBW = 250 kHz, ASSET = 2, phase encoding direction AP-PA. For the first four participants, these scans were acquired at a TR of 0.8 s. For each EPI sequence, we acquired an additional volume with the reversed phase encoding direction (Posterior-to-Anterior), used for distortion correction.

We acquired each set of functional images (the acquisitions at TR = 3s first, followed by acquisitions at TR = 1s) in a resting state condition, before and after monocular deprivation. During the acquisitions, that lasted respectively 8 and 4 minutes, subjects were in the dark, instructed to keep their eyes closed and not to fall asleep.

5.2.5 fMRI preprocessing

Analyses were performed mainly with Freesurfer v6.0.0, with some contributions of the SPM12 and BrainVoyager 20.6 and FSL version 5.0.10 (Jenkinson et al., 2012) packages. Anatomical images were corrected for intensity bias using SPM12 (Friston et al., 2007) and processed by a standard procedure for segmentation implemented in Freesurfer (recon-all: Fischl et al., 2002). Functional images were corrected for subject movements (Goebel et al., 2006) and undistorted using EPI images with reversed phase encoding direction (Brain Voyager COPE plug-in (Jezzard & Balaban, 1995)). We then exported the preprocessed images from BrainVoyager to NiFTi format.

Each individual participants' first functional acquisition (acquired right after the anatomical images), was aligned to the corresponding T1 images using ANTs, by means of an affine registration matrix and a warp field (AVANTS et al., 2008; Avants et al., 2011)For all subsequent functional acquisitions, a rigid transformation matrix was computed to align them to the first acquisition. All transformation matrices were applied to align each individual participants' preprocessed BOLD data (which had been slice-time, motion, and distortion corrected) through the antsRegistrationSyN.sh routine (Tustison & Avants, 2013), so that all functional acquisitions were aligned to the T1 anatomical image and to the reference functional image. Functional images were then projected to the cortical surface of each hemisphere. Each hemisphere was then aligned to a left/right symmetric template hemisphere (fsaverage_sym Greve et al., 2013) and data were smoothed with an isotropic Gaussian kernel (FWHM= 5 mm).

5.2.6 ROI definition

Thalamic ROIs (vPulv, LGN and dPulv) were defined in the MNI space based on the recently published NSD dataset, for which they were defined based on a combination of functional data (retinotopic mapping experiments) constrained with anatomical features (Arcaro et al., 2015). Each subject's T1 image was aligned to the MNI template available in (Collins et al., 1995; Mazziotta et al., 2001), and the resulting transformation matrices were applied to the thalamic ROIs to align them to each subject's anatomy through ANTs functions. BOLD time series were averaged across voxels within each ROI, resulting in one time series per each participant, ROI, and condition.

Cortical ROIs were defined based on the cortical parcellation atlas by Glasser et al. (Glasser et al., 2016). Area MT+ was obtained by combination of areas MT and MST. BOLD time series were averaged across vertices within each ROI, resulting in one time series per each participant, ROI, and condition.

5.2.7 Analysis performed on data acquired at TR = 3s

5.2.7.1 Functional connectivity analysis

After slice-time, motion correction and alignment, additional steps were performed on the resting state data: band-pass temporal filtering retaining frequencies in the 0.01– 0.1 Hz band; removal by regression of several sources of variance (Arcaro et al., 2018) : (1) the six motion-parameter estimates and their temporal derivatives, (2) the signal from ventricular and white matter regions (derived for each subject from the recon-all segmentation procedure after subtracting the thalamic rois of interest), (3) physiological parameters (respiration and cardiac pulsation preprocessed with the PhysIO Toolbox (Kasper et al., 2017)). To minimize the effects due to the filtering procedure, the initial 10 TRs and the last 10 TRs were removed from each scan.

We generated super-subjects functional connectivity maps for each condition by concatenating for each vertex, the z-scored individual participant's BOLD signals and then computing the Pearson's correlation between each voxel and the super-subjects thalamic ROIs (derived from concatenating the average individual time courses).

Next, we compared the cortical connectivity patterns in the two conditions by computing vertex-wise differences in Person's r values (post– pre deprivation), resulting in maps of functional connectivity differences.

To evaluate the effect across subjects for the individual cortical ROIs, we complemented these analyses with a within-subjects analysis. We computed the Pearson's correlation between the averaged time courses of the thalamic seeds and the cortical ROIs for each condition for each subject and assessed the statistical significance by paired t-tests.

5.2.7.2 Statistical analysis

To evaluate the statistical significance of the functional connectivity maps, we transformed the individual Pearson's correlation values into t values with the following formula (Cohen et al., 2003):

$$t = \frac{r}{\sqrt{\frac{1 - r^2}{n - 2}}}$$

Equation 5-2

Where r is the Pearson's correlation value and n is the degrees of freedom (n = number of time points * number of subjects). The p-value is calculated as the corresponding two-sided p-value for the t-distribution with n-1 degrees of freedom.

For the maps of functional connectivity differences, in a first step the correlation coefficients r for pre and post deprivation conditions were transformed using Fisher z transformation:

$$z = \frac{1}{2} ln \frac{1 + r}{1 - r}$$

Equation 5-3

Then the relative standard error was computed as following:

$$se_{post-pre} = \sqrt{\frac{1}{n_{pre} - 3} + \frac{1}{n_{post} - 3}}$$

Equation 5-4

And used to compute the z-score of the functional connectivity differences (Witz et al., 1990):

$$z_{diff} = \frac{z_{post} - z_{pre}}{se_{post-pre}}$$

Equation 5-5

The associated p-value was calculated as the corresponding two-sided p-value for the z-distribution. Using an alpha of 0.05, p-values were assessed for significance following False Discovery Rate (FDR) correction (Benjamini & Hochberg, 1995) and used to mask the connectivity maps.

Moreover, a cluster threshold was applied to all connectivity maps using the FreeSurfer function mri_surfcluster. The cluster threshold area was set to 200 mm^2, which was designed to exclude small clusters but include MT, the smallest area of interest.

5.2.8 Analysis performed on data acquired at TR = 1s

After slice-time, motion correction and alignment, similar steps were performed: high-pass temporal filtering retaining frequencies higher than 0.01 Hz; removal by regression of several sources of variance: (1) the six motion- parameter estimates and their temporal derivatives, (2) physiological parameters (respiration and cardiac pulsation preprocessed with the PhysIO Toolbox (Kasper et al., 2017).

On this set of functional images, we measured the effective connectivity between two thalamic ROIs (vPulv and LGN) and the primary visual cortex (V1). We extracted the mean time course across voxels for each of the three ROIs (defined as described above) and performed: (1) dynamic causal modeling, using the rDCM toolbox (Frässle et al., 2017, 2018), available as part of the TAPAS software collection (Frässle et al., 2021) and (2) a cross-correlation analysis using the xcorr built-in MATLAB function.

The DCM routine provides an estimated connectivity pattern described with parameter estimates for each connection. To compare the effective connectivity before and after deprivation, we applied a 3x2 ANOVA to the connectivity parameters, with factors: nodes (LGN-V1 vs. vPulv-V1 vs. LGN-vPulv), condition (pre vs. post deprivation) and directionality (feedforward vs. feedback). A further 2x2 ANOVA was run separately for each seed together with post-hoc t-tests.

Moreover, paired t-tests were applied to cross-correlation values to assess any changes following monocular deprivation at different lags.

5.2.9 Diffusion tensor imaging preprocessing and analysis

Diffusion data was first formatted according to BIDS standard (Gorgolewski et al., 2016)and

further preprocessed with QSIprep (Cieslak et al., 2021). Preprocessing involved distortion correction, denoising using MP-PCA, motion correction and registration to the anatomical template. Tensor fitting and reconstruction of the whole brain tractogram were performed with pyAFQ. Tractogram was generated with 1500000 seeds using a CSD model and was limited by a white matter mask. We segmented three bundles. LGN to V1, vPulv to V1 and one summary bundle – the Optic radiations. To delineate LGN and vPulv bundles, we used the same ROIs as in the functional analysis. To map optic radiations, we use predefined ROIs available in pyAFQ. After successfully labelling tracts that belong to each bundle the outlier tracts were removed. A single tract was considered an outlier if it was 4 SD away from the mean length of the bundle or 3 SD away from the mean location of the bundle. Fractional Anisotropy (FA) tract profiles of clean bundles were generated after resampling the tract length to 100 points.

For each participant, we estimated the tract profiles of FA values before and after monocular deprivation and compared them with paired t-tests. Using an alpha of 0.05, p-values were assessed for significance following Bonferroni-Holm correction for multiple comparisons (Holm, S. (1979)).

5.3 Results

In 25 adult participants, we measured the resting state brain functional connectivity in two conditions, before and after 2 hours of monocular eye patching (Figure 1A).

Pooling data across participants, we computed seed-based functional connectivity maps for two thalamic seeds: ventral Pulvinar and LGN (shown in the MNI space in Figure 1B).

The functional connectivity maps show Pearson's correlation indices for each vertex, following FDR correction and cluster threshold (see Methods).

Before monocular deprivation, the functional connectivity maps of the two thalamic regions were similar, as both vPulv and LGN were strongly functionally connected to the visual cortex, as shown in Figure 1C.

After two hours of monocular deprivation however, the functional connectivity of the ventral Pulvinar with the visual cortex decreased (i.e. the magnitude of Pearson's correlations decreased – Figure1 - D). The LGN connectivity pattern, on the other hand, did not change.

Pearson's correlation differences are shown in the rightmost part of Figure 1 (E) which shows the extent of the decrease, that includes most part of the visual cortex.

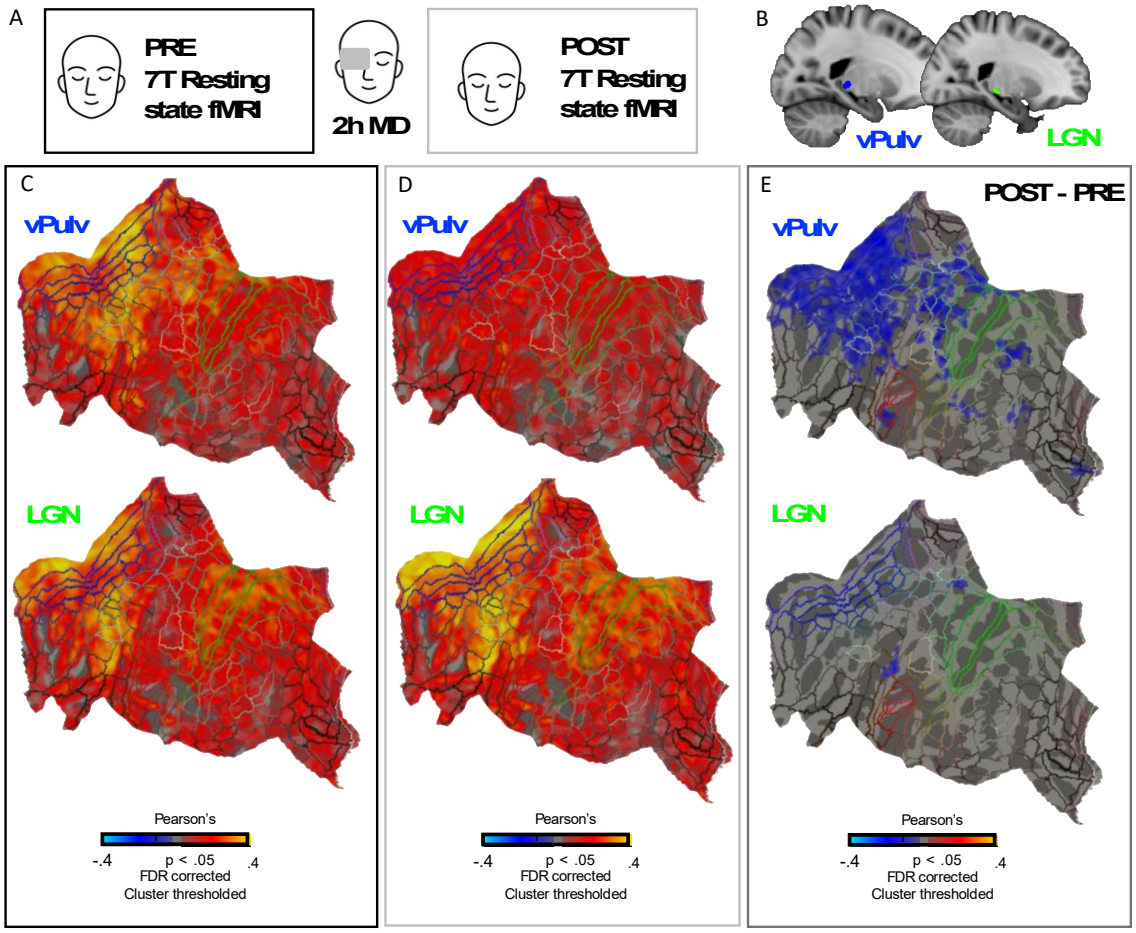

Figure 5-1 vPulv and LGN functional connectivity patterns

A – Experimental design. Resting state functional images were acquired before and after two hours of monocular deprivation. Participants were instructed to keep their eyes closed for the entire duration of the acquisitions. B – Sagittal view of the thalamic ROIs mapped on the 1 mm^3 MNI template. C -D Super-subjects correlation maps computed before (C) and after (D) monocular deprivation for the two thalamic seeds: vPulv and LGN. E- Maps of super-subjects correlation differences (post–pre deprivation) for vPulv and LGN.

All maps are thresholded by False Discovery Rate (FDR) corrected p values (alpha = 0.05) and cluster size (threshold = 200 mm^2).

These observations were replicated with a within-subjects approach. For each participant, we correlated the average time courses of the cortical areas of interest with the average time course of each thalamic seed. Figure 2 shows the individual correlation values of vPulv (A) and LGN (B) with the primary visual cortex, before and after monocular deprivation.

Both thalamic regions were positively and significantly correlated with V1 both before (vPulv: $|t(24)|=6.19$, $p<0.001$, lgBF: 3.94; LGN: $|t(24)|=10.87$, $p<.001$, lgBF: 8.02), and after monocular deprivation (vPulv: $|t(24)|=3.87$, $p<.001$, lgBF: 1.65; LGN: $|t(24)|=9.70$, $p<.001$, lgBF: 7.10). The correlation values in the two conditions were also significantly correlated across subjects, suggesting a good reliability for both vPulv and LGN functional connectivity measures (vPulv: $r = 0.65$, $p <.001$, lgBF = 1.87; LGN: $r = 0.42$, $p=0.04$, lgBF = 0.13).

After monocular deprivation however, only the correlation of V1 with the vPulv decreased ($|t(24)|=2.47$, $p=0.02$, lgBF: 0.41), leaving the correlation with LGN unaffected ($|t(24)|=1.08$, $p=0.29$, lgBF = -0.45).

After investigating V1 connectivity with vPulv and LGN, we quantified the effect of monocular deprivation on neighbouring visual regions, namely V2, V3, V4 and area MT+. Similarly to V1, all these areas showed a significant and positive correlation with vPulv and LGN in both conditions (one sample t-tests: all $|t| > 5$, all $p_{FDRcorrected} < .001$) and decreased connectivity with the ventral Pulvinar (one sample t-tests: all $|t| > 2$, all $p_{FDRcorrected} < .05$), but not with LGN (all $|t| < 1$, all $p_{FDRcorrected} > .05$).

We also investigated the functional connectivity of these cortical visual regions with the primary visual cortex and the dorsal Pulvinar. We found no effect of monocular deprivation across subjects (see Appendix).

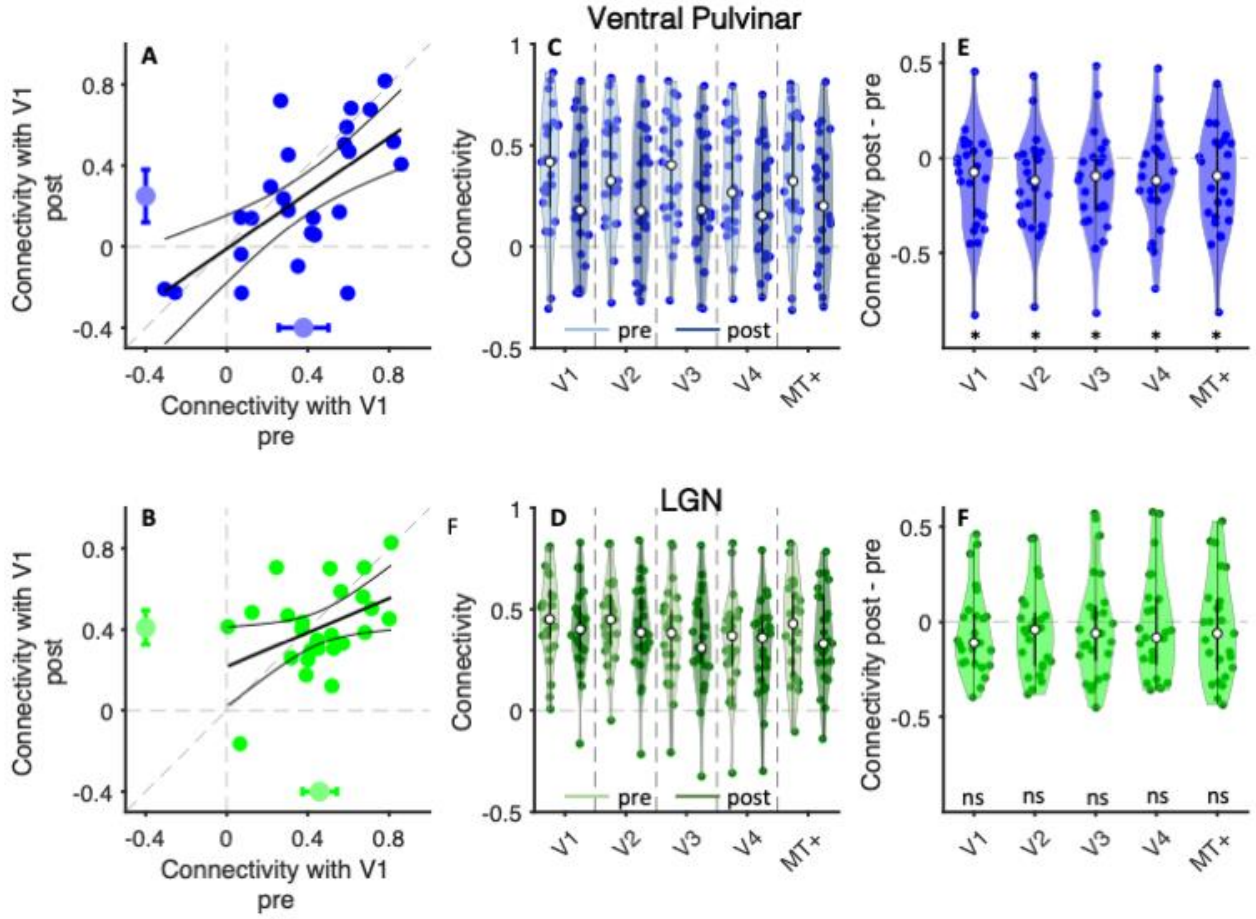

Figure 5-2 vPulv and LGN functional connectivity with the visual cortex.

A –B: Individual correlation values of vPulv (A) and LGN (B) with the primary visual cortex (V1). The x-axis reports values before monocular deprivation, the y-axis reports values after monocular deprivation. Error bars show mean ± 1 S.E.M. across subjects. The continuous black lines show the best-fitting line and its 95% confidence intervals.

C-D: Violin plots report, for each cortical region (shown on the x-axis), the Pearson's correlation with vPulv and LGN before and after monocular deprivation. E-F: Violin plots report for each cortical region (shown on the x-axis) the correlation values difference (post – pre), with vPulv (E) and LGN (F). From C to H, thick black error bars indicate the ends of the first and third quartiles, and thin black bars indicate 95% confidence intervals. The white circle indicates the median across subjects. Single points indicate individual values. In-text values correspond to FDR corrected p -p-values for one sample t-tests against zero ($p_{FDR} < .05$; ** $p_{FDR} < .01$; *** $p_{FDR} < .001$, $^{ns}p_{FDR} > .05$).*

Notably, functional connectivity changes induced by monocular deprivation occurred in absence of any variations in signal-to-noise ratio or amplitude spectra in either of the seed regions (see Table 7-2 and Figure 7-4 in the Appendix).

These results were replicated and expanded on another dataset, acquired right after, at a higher temporal frequency (TR = 1 second). We applied the rDCM (regression dynamic causal modelling, see methods) to examine the bidirectional connections among our nodes, namely V1, vPulv and LGN. We then compared the parameter estimates for each connection with ANOVAs.

Figure 3 A-B shows the parameter estimates for each connection (i.e. the relative weight of each connection in the network) for the two conditions, averaged across participants.

A 3x2 ANOVA with factors: nodes (LGN-V1 vs. vPulv-V1 vs. LGN-vPulv), condition (pre vs. post deprivation) and directionality (feedforward vs. feedback), showed a significant interaction between all factors ($F(1,24) = 4.62$, $p = 0.04$). A further 2x2 ANOVA was run separately for LGN and vPulv. Direct LGN-vPulv negligible connections, shown in grey in Figure 3 A-B, were not investigated further. The two 2x2 ANOVAs showed that, while for LGN there was only a main effect of directionality ($F(1,24) = 17.10$, $p < 0.001$) and no interaction with the conditions ($F(1,24) = 0.27$, $p = 0.61$), for vPulv there was a significant interaction between directionality and condition ($F(1,24) = 11.48$, $p < 0.01$).

A post-hoc analysis revealed that, as reported in Figure 3C-D, monocular deprivation affected selectively the vPulv-V1 connection (paired t-test pre vs. post: $|t(24)| = 3.8$, $p < .001$, lgBF = 1.60), leaving the reciprocal unaffected (paired t-test pre vs. post: $|t(24)| = 1.71$, $p = 0.1$, lgBF = -0.12).

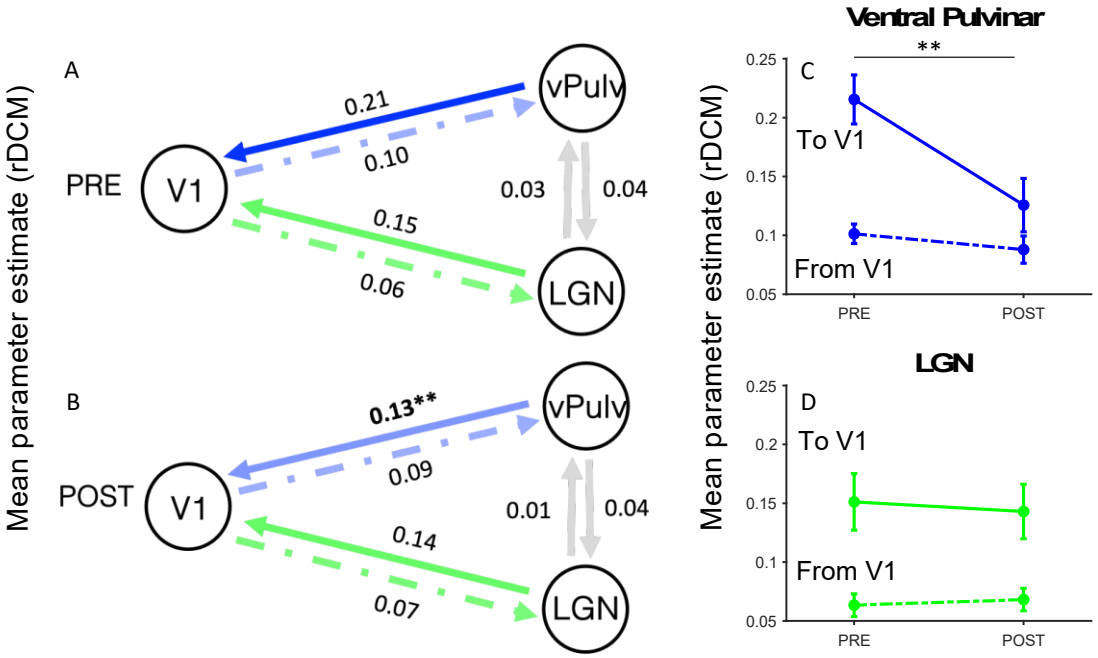

Figure 5-3 vPulv and LGN effective connectivity with V1 assessed with Dynamic Causal Modeling

*A-B: Scheme of nodes and connections considered in our network. In-text values are group-average parameter estimates obtained from rDCM, indicating the contributions of each connection, pre (A) and post(B) deprivation. C-D: Parameter estimates obtained from rDCM averaged across subjects for the two conditions (pre and post-monocular deprivation). The continuous lines report the connections leaving the vPulv (C) and LGN (D) to reach the primary visual cortex. Dashed lines report the opposite directionality (from V1 to thalamus). Error bars show mean ± 1 S.E.M. across subjects. Asterisks report significance for the 2x2 interaction; (*p < .05; ** p < .01; *** p < .001).*

These observations on effective connectivity were complemented by a cross-correlation analysis (Figure 4). We computed the cross-correlation between the average V1 time courses and each thalamic ROI, and evaluated the effect of monocular deprivation at different lags: At negative lags (from -3 to -1), where correlation values measure the similarity between the thalamic time course and shifted (delayed) copy of the V1 time course, thus the strength of the thalamus --> V1 directionality.

At positive lags (from 1 to 3), where the thalamic time course is correlated with an anticipated copy of the V1 time course, thus correlation values measure the strength of the V1 à thalamus directionality.

We also investigated the zero-lag range (lags from -1 to +1), which corresponds to Pearson's correlation between two time courses, with no shift between the two. By doing so, we aimed at verifying the replicability of our main findings (at TR=3seconds) on a dataset with different temporal characteristics.

These analyses show that the average cross-correlation around zero between V1 and vPulv decreased after monocular deprivation ($|t(24)| = 2.22$, $p < .05$, lgBF= 0.22), replicating our main findings.

A significant effect of deprivation for vPulv was found at negative lags ($|t(24)| = 3.11$, $p < .01$, lgBF= 0.95), replicating the rDCM results: a decrease of connectivity in the vPulv à V1 direction.

No significant effect was found for positive lags ($|t(24)| = 1.14$, $p = .27$, lgBF= -0.42), nor for LGN cross-correlation values (at 0: $|t(24)| = 1.26$, $p = .22$, lgBF= -0.37; negative lags: $|t(24)| = 0.10$, $p = .91$, lgBF= -0.67; positive lags: $|t(24)| = 0.43$, $p = .67$, lgBF= -0.63)

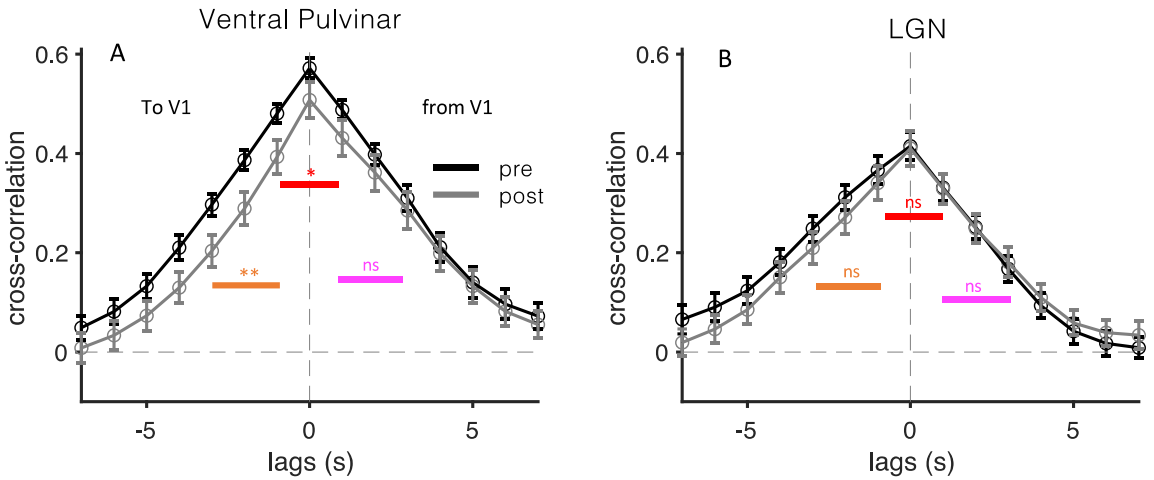

Figure 5-4 vPulv and LGN effective connectivity with V1 assessed with a cross-correlation analysis

*A-B: Normalized cross-correlation values between vPulv (a) or LGN (b) and V1, as a function of temporal lags, measured before (black symbols) and after monocular deprivation (grey symbols). Error bars show mean ± 1 S.E.M. across subjects. At negative lags, correlation values quantify the connectivity in the thalamus à V1 directionality. At positive lags, correlation values quantify the connectivity in the V1 à thalamus directionality. Asterisks and bars report significance of one sample t-tests performed across subjects against zero. The red ones report significance for the average of the three time points around zero (lags from -1 to +1); orange symbols report significance for the average of the three time points before zero (lags from -3 to -1); magenta symbols report significance for the average of the three time points after zero (lags from 1 to +3); (*p < .05; ** p < .01; *** p < .001).*

Finally, we checked whether monocular deprivation had any effect on the anatomical connections giving rise to the optic radiation, the bundle of projection fibres that link the thalamus with the visual cortex (Moini & Piran, 2020). For each participant, we estimated the Fractional Anisotropy tract profiles, before and after monocular deprivation, for the LGN-V1 tract and the vPulv – V1 tract. As shown in Figure 5 for the two tracts, the group averages computed for the two conditions fully overlap. Paired t-tests excluded any effect of monocular deprivation on the optic radiation fibres in our dataset (all $p_{FDRcorrected} > .05$).

We further investigate the diffusivity properties of our regions of interest to check for any changes in structural integrity following monocular deprivation. We did not find any pre-post deprivation differences in any of them (paired t-tests: vPulv: |t (24)|= 0.04, p=0.97, lgBF = -0.67; LGN: |t(24)|=0.25, p=0.81, lgBF = -0.66; V1: |t(24)|=0.28, p=0.78, lgBF = -0.66).

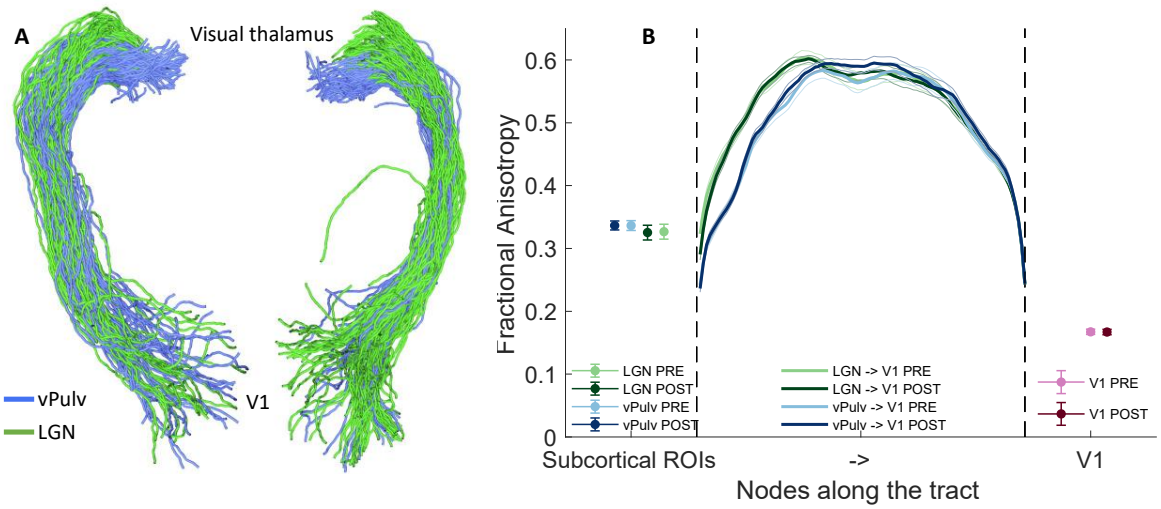

Figure 5-5 Mean optic radiation profiles

A: Cleaned bundles of LGN - V1 (green) and vPulv - V1 (blue) for a representative subject generated with DSI-STUDIO. B: Fractional anisotropy values as a function of nodes along the thalamus – V1 tract, measured before and after monocular deprivation, reported with the brighter and darker plots respectively. Thick continuous lines show mean values, shaded areas report mean ± 1 S.E.M. across subjects. Error bars show mean fractional anisotropy values for the three ROIs of interest ± 1 S.E.M. across subjects. Using an alpha of 0.05, p-values were assessed for significance following Bonferroni-Holm correction for multiple comparisons.

5.4 Discussion

Our research investigated the impact of monocular deprivation on the communication between the visual cortex and the visual thalamus. What we discovered was that only two hours of monocular deprivation led to a significant decrease in functional connectivity between the visual cortex (V1 and extra striatal areas) and the ventral Pulvinar. The functional connectivity patterns of LGN and dPulv were unaffected, consistently with the results from Kurzawski et al., 2022 on visual evoked responses.

These findings were replicated and further expanded on a second dataset, acquired at a higher temporal resolution, which allowed us to specifically examine how monocular deprivation affected each direction of the reciprocal thalamo-cortical connections.

Our results indicate that the decline in functional connectivity selectively affected the connections originating from the ventral Pulvinar and heading towards the primary visual

cortex. The effects of monocular deprivation exclusively involved functional connectivity, without any accompanying anatomical reconfiguration. These negative results were in line with our expectations, given that our manipulation was very brief. However, we predict that after repeated monocular deprivation sessions (see Lunghi et al., 2019), the reported visual acuity improvement (Lunghi et al., 2019) might be supported by functional changes as well as anatomical reconfigurations. We are currently testing this hypothesis on a population of amblyopic patients, replicating Lunghi et al., paradigm (short-term inverse occlusion, combined with moderate physical exercise).

A recent study by Kurzawski and colleagues (Kurzawski et al., 2022)showed that the effects of monocular deprivation on the ocular drive of visual evoked responses extended from the visual cortex to the ventral Pulvinar, but not to LGN. This led them to suggest that monocular deprivation effects do not stem from modulations at the level of monocular cells that are inherited by the primary visual cortex, but instead, they might be modulated by the cortical connections with the ventral Pulvinar.

We support this hypothesis and further speculate that the role of the ventral Pulvinar in mediating this short-term plasticity phenomenon might be related to predictive coding mechanisms.

Predictive coding is a theoretical framework proposing that the brain processes sensory information by making predictions about incoming sensory inputs. It would use prior knowledge to build hierarchical internal predictions, which are compared with incoming information to continuously adapt these internal models and minimize prediction errors (Clark, 2013; Friston, 2005, 2010; George & Hawkins, 2009; Hohwy Jakob, 2013; Huang & Rao, 2011; Mumford, 1992; Rao & Ballard, 1999), predictive coding suggests that the brain constantly generates and compare predictions on how the world should look like, based on prior experiences, with incoming visual information.

Recent work has proposed the Pulvinar (and its ventral portion in the context of visual processing) as the perfect candidate for gating bottom-up information and its integration with high-level predictions. Through modulation of cortical oscillatory activity and modulation of prediction error units in the superficial layers via diffuse projections, the Pulvinar would regulate the integration between ascending prediction errors and descending expectations (Bridge et al., 2016; Galuske et al., 2019; Jaramillo et al., 2019; Z. Liu et al., 2012).

In light of our results, we hypothesise that depriving one eye of visual input, as in monocular deprivation, would lead to a mismatch between the brain's predictions based on the participant's interactions with the environment and the actual sensory input. The deprived eye's inability to transmit visual changes produced by the participant's actions could result in an increased discrepancy between what the brain predicts (based on priors, actions, and input from the open eye) and what it perceives.

To reduce prediction errors and improve the accuracy of perception, the brain may undergo a reconfiguration of cortical circuits. This reconfiguration could involve adjusting the relative contributions of bottom-up sensory evidence (actual sensory input) and top-down predictions (what the brain expects to see). Crucially, this reconfiguration would involve the thalamo-cortical reciprocal connections, hence the effect of monocular deprivation on the vPulv -> V1 connectivity.

This idea is supported by a recent study conducted by Steinwurzel and colleagues (Steinwurzel et al., 2023) showing that de-synchronization of visual information and voluntary actions (achieved by introducing a visual delay in one eye while participants actively performed a visuomotor task) triggers ocular dominance plasticity, comparably to monocular contrast deprivation.

The contribution of sensory-motion integration circuits to monocular deprivation effects is also coherent with our results on V1 functional connectivity. Although this aspect might need further investigation, we found that, following deprivation, V1 connectivity decreases selectively with intraparietal areas, which are thought to be involved in the transformation of sensory information into motor output (reaching, grasping, eye movements, processing of multimodal motion (for a review see Konen & Kastner, 2008). We speculate that this dissociation between V1 and intraparietal areas might be a result of the reconfiguration of the thalamo-cortical circuits mediating cortico-cortical communications.

Altogether, these findings align with the growing body of evidence indicating that the Pulvinar is not merely a passive relay nucleus but plays a role in a variety of mechanisms regulating information transmission to the cortex and between cortical areas (Purushothaman et al., 2012; Saalmann et al., 2012; Sherman & Guillery, 2002; Shipp, 2003; H. Zhou et al., 2016). These include mediating learning-dependent changes in sensory processing through GABAergic inhibition in the visual cortex (Ziminski et al., 2023).

In conclusion, the present study shows that the effects of monocular deprivation in adult humans are not limited to a gain change of visual evoked responses, but also involve a global system reconfiguration, with the ventral Pulvinar as a focal point. These results are in line with previous studies showing its involvement in sensory-motor integration and learning, and overall point towards a new model for experience-dependent changes in the visual system, which include short–term adjustments in the way the brain processes sensory information and integrates them with prior expectations.

6 Chapter 6 – General discussion

My thesis aimed to assess contextual effects on visual perception, with a focus on binocular vision. After exploring the potentialities of binocular rivalry as a tool for studying experience-dependent changes on perceptual dominance (Chapter 2), I focused on two experimental manipulations: endogenous cueing of attention (Chapter 3), and short-term monocular deprivation (Chapter 4 and 5).

Across the projects presented here, I exploited binocular rivalry as the main behavioural paradigm.

In accordance with an extensive body of prior research, we showed that rivalry is a versatile experimental tool, which provides a controlled but dynamic context for studying the mechanisms that govern our visual perception. The multi-level competition that underlies this phenomenon allows for investigating both perceptual phenomena related to the stimulus, like attention, and to the eye-of-origin, like ocular dominance. In Chapter 2, we contributed substantial evidence for the reliability of binocular rivalry, based on a conspicuous amount of data collected in four different setups and with three different sets of stimuli. A thorough statistical approach allowed us to indicate that not all parameters that can be extracted from binocular rivalry have the same stability. Ocular dominance was found to be a trait-like characteristic stable over time; this confirms that binocular rivalry is a valid tool to follow short-term changes of sensory eye-dominance. Switch rate and mixed percepts, however, were sensitive to state-related changes; for example, day-by-day fluctuations in the speed of rivalry alternations could not be explained by the internal noise of the measure. This suggests that internal states can drive systematic changes in the dynamics of perception. This raises the question: Are these changes in perception itself, or are they related to participants' decision-making processes?

The work presented in Chapter 3 is broadly related to this question. We focused our efforts on attention, a modulatory factor of binocular rivalry dynamics (Chong et al., 2005; K. C. Dieter et al., 2016; Hancock & Andrews, 2007; Meng & Tong, 2004a; Mitchell et al., 2004; Paffen et al., 2006; van Ee et al., 2005). We investigated the effects of endogenous cueing on rivalry dynamics, as indexed by both perceptual reports and the associated pupil responses. We

expected that more attended stimuli would generate stronger pupil responses, as observed in non-rivalry-based paradigms. Quite surprisingly, our results showed that attention biased the perceptual dominance of the cued stimulus without boosting the associated pupil response. These results suggest two possible answers to our experimental question.

One possibility is that attention, the state-dependent variable of interest, does affect the strength of the representation of the cued stimulus, but it does so only when both stimuli are comparable in strength, so during fusion-derived perceptual phases. This outcome can be predicted by the attentional model of binocular rivalry (Li et al., 2017). In this model, the two rival stimuli continuously compete for attentional resources and attention is modelled as multiplicative gain. At any given moment, the stimulus associated with stronger sensory responses attracts a larger share of attention. This model predicts that, during dominance phases (i.e., when competition between rivalling stimuli is resolved in favour of one or the other stimulus/eye), attention is automatically driven to the dominant stimulus, leaving little space for endogenous re-directing of attention. However, during periods of unresolved competition (i.e., mixed percepts, when the two stimuli are equally represented in perception), endogenous attention might act by selecting the cued stimulus and increasing its perceptual strength (K. C. Dieter et al., 2015). This interpretation could be consistent with our observation of a mild pupil modulation during phases of mixed perception. Selective attention is often described as the ability to focus on and prioritize relevant information while filtering out irrelevant information (Plebanek & Sloutsky, 2019). In this description of the mechanisms of attention, the competition among inputs seems to be crucial. Supporting the idea proposed by (K. C. Dieter et al., 2015), we hypothesise that attention is effective in producing changes in the stimulus appearance only when this competition is not completely resolved. This observation also raises interesting questions on the contribution of a suppressed stimulus, the inhibition of which is amplified by bottom-up exogenous attention, to perception, and whether awareness of the competing stimuli is necessary for selective attention (Mack et al., 2002; Norman et al., 2015).

Another possibility is that attention does not act on the effective strength at all, but rather biases decision towards the cued stimulus. This would suggest that internal states, like endogenous attention, can favour one stimulus in perception without altering its appearance. In this picture, when reality is stable (retinal stimulation does not change in binocular rivalry) and low-level perception is mediated by the sensory responses evoked by the visual input, the

brain would comply to the goal (attending one stimulus), by changing the internal decision thresholds, causing the same perceptual outcome to be labelled differently based on attentional demands. According to this hypothesis, perceptual reports and pupil size measurements can be dissociated and provide two reliable measures of two different neural representations that correspond to the same physical input but are differentially affected by attention. Perceptual reports would be guided by a visual representation that is further shaped by decision criteria; pupil responses would more directly track the effective content of perception.

In Chapter 4 we report, with the use of the same combined paradigm, the perceptual outcome of sensory deprivation: monocular contrast deprivation. This paradigm has been extensively employed to investigate short-term ocular dominance plasticity, described as a form of homeostatic plasticity (Turrigiano, 2012). In line with previous studies, we found that following monocular deprivation, the deprived eye dominance was boosted (Binda et al., 2018; Lunghi, Berchicci, et al., 2015a; Lunghi et al., 2013; J. Zhou et al., 2013, 2014). Unlike the attentional effect, this perceptual boost was accompanied by a measurable change in the relative pupil responses, which we used as an index of effective stimulus strength. Our findings suggest that this manipulation of sensory history was effective in triggering a change in the content of perception, making the deprived eye stronger in the competition for awareness, thus increasing the perceived strength of the stimulus shown to it.

What are the mechanisms underlying this perceptual change? Previous studies proposed an up-regulation of the contrast gain-control mechanisms, boosting the neuronal responses to compensate for the reduced incoming signal in the deprived eye (Castaldi et al., 2020). An alternative proposal is that increased inhibition of the non-deprived could be responsible for the effect (Gong et al., 2023; Lyu et al., 2020). Our work, presented in Chapter 5, suggests that contrast-gain control may not be the only or the main mechanism supporting the perceptual consequences of short-term monocular deprivation. In a series of fMRI experiments, we moved away from measuring contrast-gain and from visually evoked responses, and simply looked at brain activity in resting state conditions. We found that this was strongly and systematically affected by the 2h-long monocular deprivation. Specifically, functional connectivity between the visual cortex and the visual thalamus was affected; even more specifically, the modulation was selective for one thalamic sub-nucleus (ventral pulvinar) and

spared the others (including the LGN). Our interpretation of this result is inspired by the "predictive coding" literature, whereby the pulvinar has been implicated in relaying signals related to "a priori" information and predictions to the visual cortex, where they are combined with incoming sensory information (Kaas & Lyon, 2007; Purushothaman et al., 2012; Saalmann et al., 2012; Sherman & Guillery, 2002; Shipp, 2003; H. Zhou et al., 2016) and modulate learning-dependent changes (Ziminski et al., 2023). We suggest that the temporary disconnection between the pulvinar and the visual cortex following monocular deprivation reflects the mismatch between incoming sensory input and top-down predictions. We propose that this reconfiguration could allow for adjusting the relative contributions of bottom-up sensory evidence (sensory input) and top-down predictions (what the brain expects to see). This hypothesis represents a radical shift compared to the standard "homeostatic plasticity" model and clearly, it will require further experimental and theoretical efforts to be validated.

6.1 Conclusions and future direction

The ability to adapt to varying task requirements and changes in the external environment is a distinctive feature of our brain. Understanding this flexibility is not only crucial from a theoretical perspective. It also holds strong applicative potential in the context of pathological conditions, where re-opening windows of plasticity could foster functional recovery. For example, the treatment of adult amblyopic patients could be directly impacted by a firmer understanding of homeostatic plasticity. I am currently hoping to extend my investigations in this direction, testing the possibility that the transient functional reorganization observed after monocular deprivation could evolve into enduring neuroplastic changes, which could lead towards the amelioration of visual function in adult amblyopic individuals.

7 Appendix

7.1 Extended data from Chapter 3

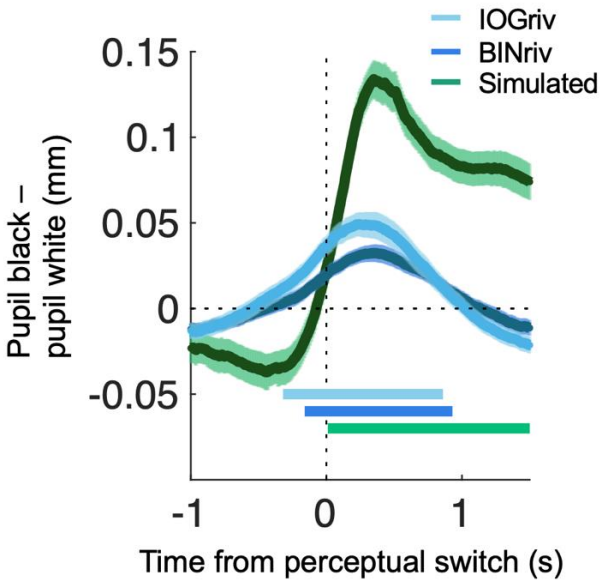

Figure 7-1 Pupil size modulations in rivalry and simulation conditions.

Time course of the difference between pupil size during black and white percepts, computed in individual participants and then averaged for binocular rivalry (dark blue curve), interocular grouping rivalry (light blue curve) and simulation (green curve). In all panels: shadings report mean ±1 s.e. across participants and the marks on the x-axis highlight timepoints where each trace is significantly different from 0 (one-tailed t-test, $p < 0.05$ FDR corrected).

Pupil modulations during binocular and interocular grouping rivalry averaged respectively $39.14 \pm 8.15\%$ (mean $\pm$ 1 s.e. across participants) and $43.80 \pm 10.26\%$ of the pupil size modulations observed during simulated rivalry, as previously reported by Binda and colleagues (Binda et al., 2013a) in a different spatial-attention task.

Moreover, they consistently started before the perceptual switch, and this was more pronounced in the rivalry conditions than in the simulated rivalry (significant pupil difference started 160 ms before the switch in binocular and 320 ms in interocular grouping rivalry,

compared with almost no latency for simulated rivalry). This finding, in line with (Fahle et al., 2011; Naber et al., 2011) may reflect the graded nature of rivalry transitions, which may delay change detection in rivalry compared with the sharp transitions used in the simulated rivalry condition.

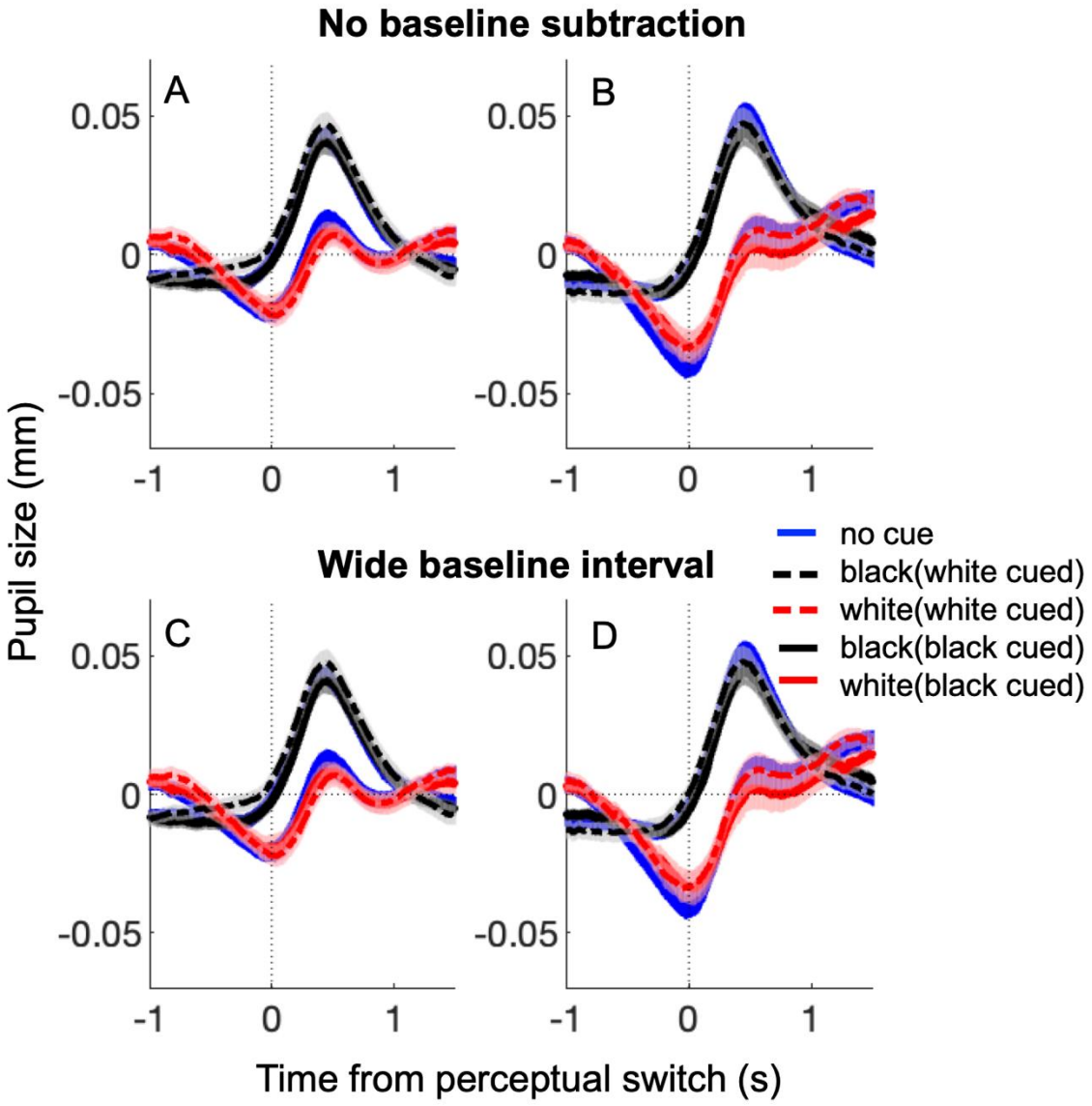

Figure 7-2 Pupil modulations track perceptual alternations comparably across cueing conditions irrespectively of whether and how pupil traces are baseline corrected.

Pupil size traces aligned to perceptual switches towards exclusive dominance of a white disk or a black disk percept and averaged across phases, separately for binocular rivalry (A) and interocular grouping rivalry (B) and separately for the two cueing conditions: cueing the white percept (dashed lines) or the black percept (continuous lines). Shading report ± 1 s.e. across participants.

These traces are computed without subtracting any baseline correction (A-B) and after subtracting a baseline computed as average pupil size in the [-5:5] s interval around perceptual switch (C-D). Note how the resulting traces are virtually indistinguishable: in both cases, pupil size still allows to discriminate white and black percepts (red and black curves are clearly separated) but shows no effect of cueing (dashed and continuous lines are virtually superimposed, together with the blue traces).

Coherently, we found that cueing did not affect pre-switch pupil baseline used for the main Figures, which was computed in the [-1:-.5] s interval from the perceptual switch (main effect of cued percept: $F_{(1,37)} = 1.51$, $p = 0.23$, logBF = -0.60; dominant percept x cued percept interaction: $F_{(1,37)} = 0.14$, $p = 0.71$, logBF = -0.74).

	No bsl sub	Bsl sub [-5 5]
dominant percept	$F_{(1,37)} = 40.09$* $p < 0.001$ logBF = 22.35	$F_{(1,37)} = 38.61$* $p < 0.001$ logBF = 21.73
rivalry type	$F_{(1,37)} = 2.17$ $p = 0.15$ logBF = -0.52	$F_{(1,37)} = 2.12$ $p = 0.15$ logBF -0.54
cued percept	$F_{(1,37)} = 2.58$ $p = 0.12$ logBF = -0.61	$F_{(1,37)} = 2.72$ $p = 0.11$ logBF = -0.57
dominant percept x rivalry type	$F_{(1,37)} = 1.10$ $p = 0.30$ logBF = -0.52	$F_{(1,37)} = 0.99$ $p = 0.32$ logBF = -0.52
dominant percept x cued percept	$F_{(1,37)} = 1.00$ $p = 0.32$ logBF = -0.50	$F_{(1,37)} = 0.98$ $p = 0.33$ logBF = -0.63
rivalry type x cued percept	$F_{(1,37)} = 0.04$ $p = 0.85$ logBF = -0.77	$F_{(1,37)} = 0.05$ $p = 0.82$ logBF = -0.79
dominant percept x rivalry type x cued percept	$F_{(1,37)} = 1.67$ $p = 0.20$ logBF = -0.51	$F_{(1,37)} = 1.77$ $p = 0.19$ logBF = -0.49

Table 7-1 Three-way ANOVA for attention cueing results

Three-way ANOVA for attention cueing results, with factors: dominant percept (white/black disk), cueing (white/black cued), rivalry type (binocular/interocular grouping rivalry).

We confirmed our results on cueing with a three-way ANOVA entered with the average pupil size in the interval [-.5:1] s (the same interval used for Table 1 in the main text) but now skipping the baseline correction step (first column) or subtracting a baseline computed as the average pupil size in the [-5:5] s interval around perceptual switch (second column). In both cases, we confirm the main effect of dominant percept type and the absence of any reliable effect of attention cueing, suggesting that our results are not limited to the specific window we used to compute the baseline pupil size.

7.2 Extended data from Chapter 5

ROI	Pre	Post	Paired t-test pre vs. post
vPulv	44.70 ± 0.77	44.00 ± 0.77	|t(24)| = 1.20 p = 0.25 lgBF = -0.41
LGN	42.97 ± 0.64	42.94 ± 0.42	|t(24)| = 0.08 p = 0.94 lgBF = -0.67
dPulv	41.61± 1.67	39.80 ± 1.98	|t(24)| = 0.64 p = 0.53 lgBF = -0.60
V1	121.54± 9.03	120.60± 8.54	|t(24)| = 0.09 p =0.93 lgBF = -0.67

Table 7-2 Signal-to-noise ratios for the seed regions of interest

Signal-to-noise ratio (SNR) of the BOLD activities in the four seed regions of interest. For each condition, SNRs were computed as the voxel-wise ratio between the average activity across time and its standard deviation, then averaged across voxels and across subjects. Reported values are mean ± S.E.M.

Paired t-tests, reported in the leftmost column, show that the SNR for each region did not change after monocular deprivation.

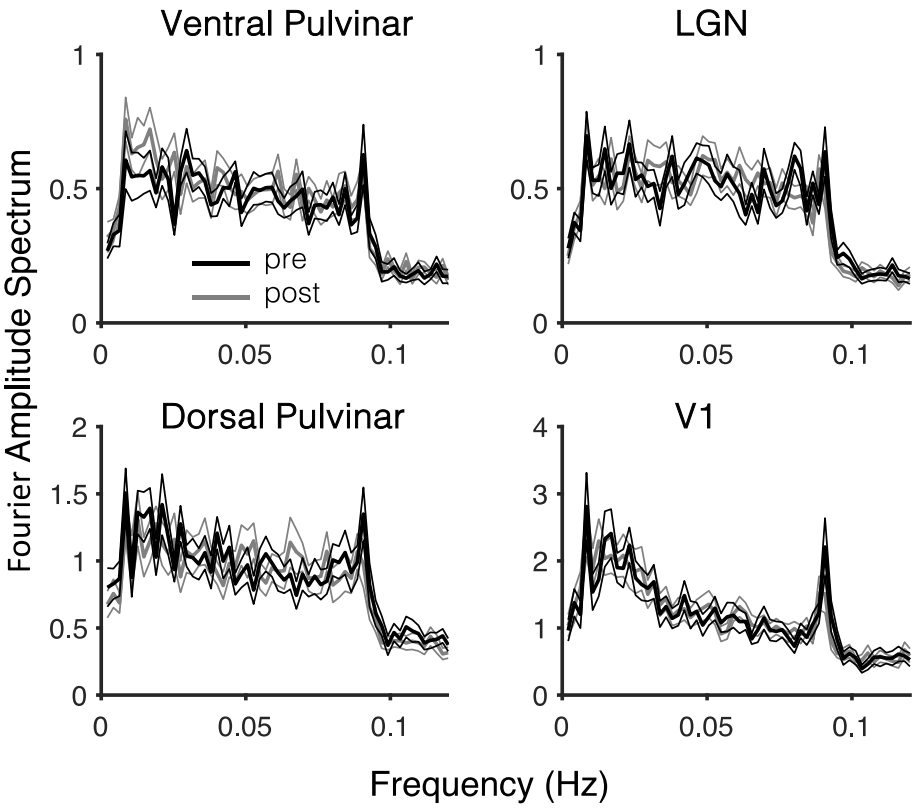

Figure 7-3 Fourier amplitude spectra for the seed regions of interest

Group-average Fourier amplitude spectra for the four seed regions of interest before (black plot) and after (grey plot) monocular deprivation. Reported values are mean ± S.E.M. Paired t-tests showed no changes after monocular deprivation at any temporal frequency (all $p_{FDRcorrected} > 0.05$*).*

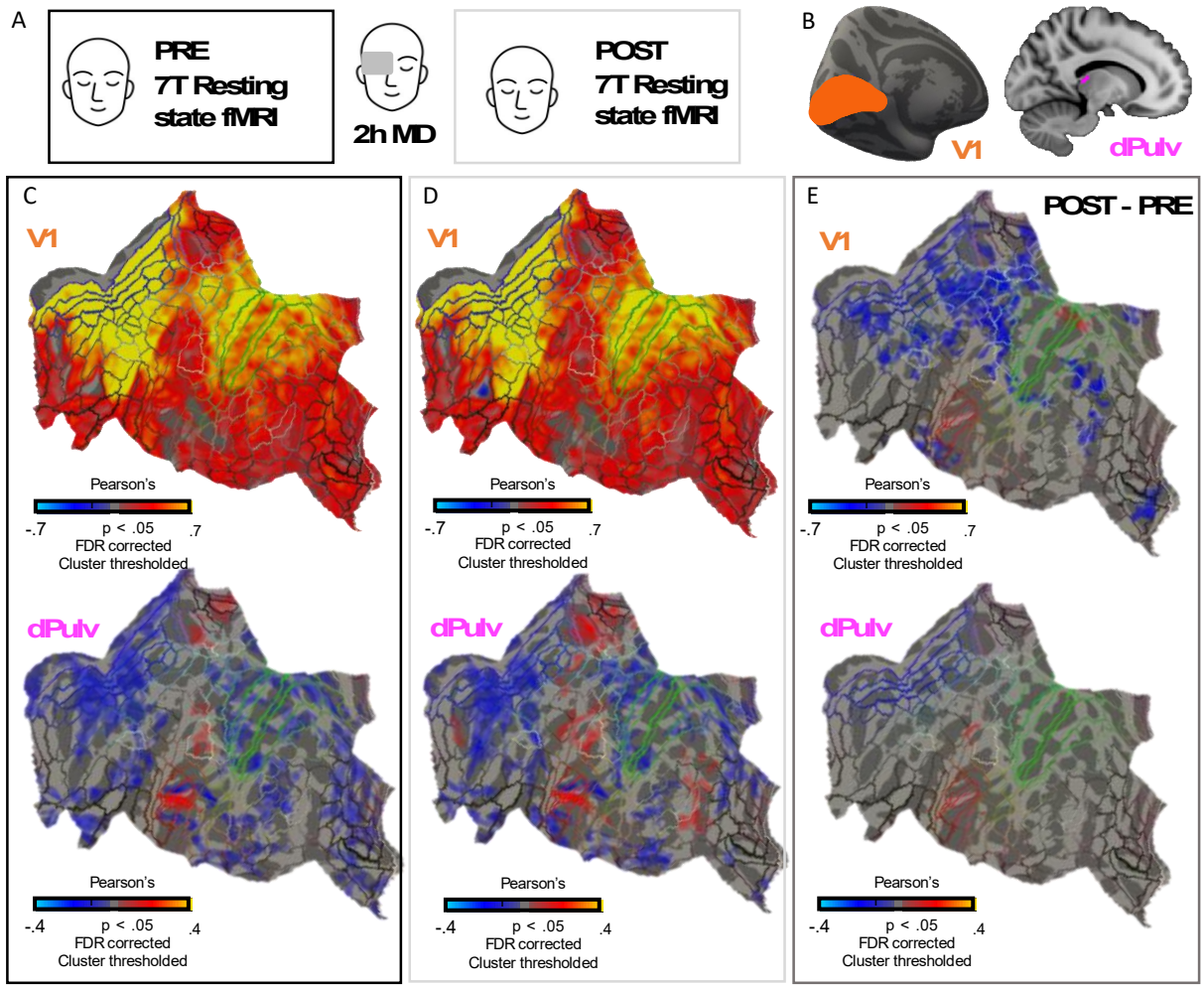

Figure 7-4 V1 and dPulv functional connectivity patterns

A – Experimental design. Resting state functional images were acquired before and after two hours of monocular deprivation. Participants were instructed to keep their eyes closed for the entire duration of the acquisitions. B – Sagittal view of the V1 ROI mapped on the fsaverage_sym surface template and dPulv mapped on the 1 mm^3 MNI template. C -D Super-subjects correlation maps computed before (C) and after (D) monocular deprivation for the two seeds: V1 and dPulv. E- Maps of super-subjects correlation differences (post–pre deprivation) for V1 and dPulv. All maps are thresholded by False Discovery Rate (FDR) corrected p values (alpha = 0.05) and cluster size (threshold = 200 mm^2).

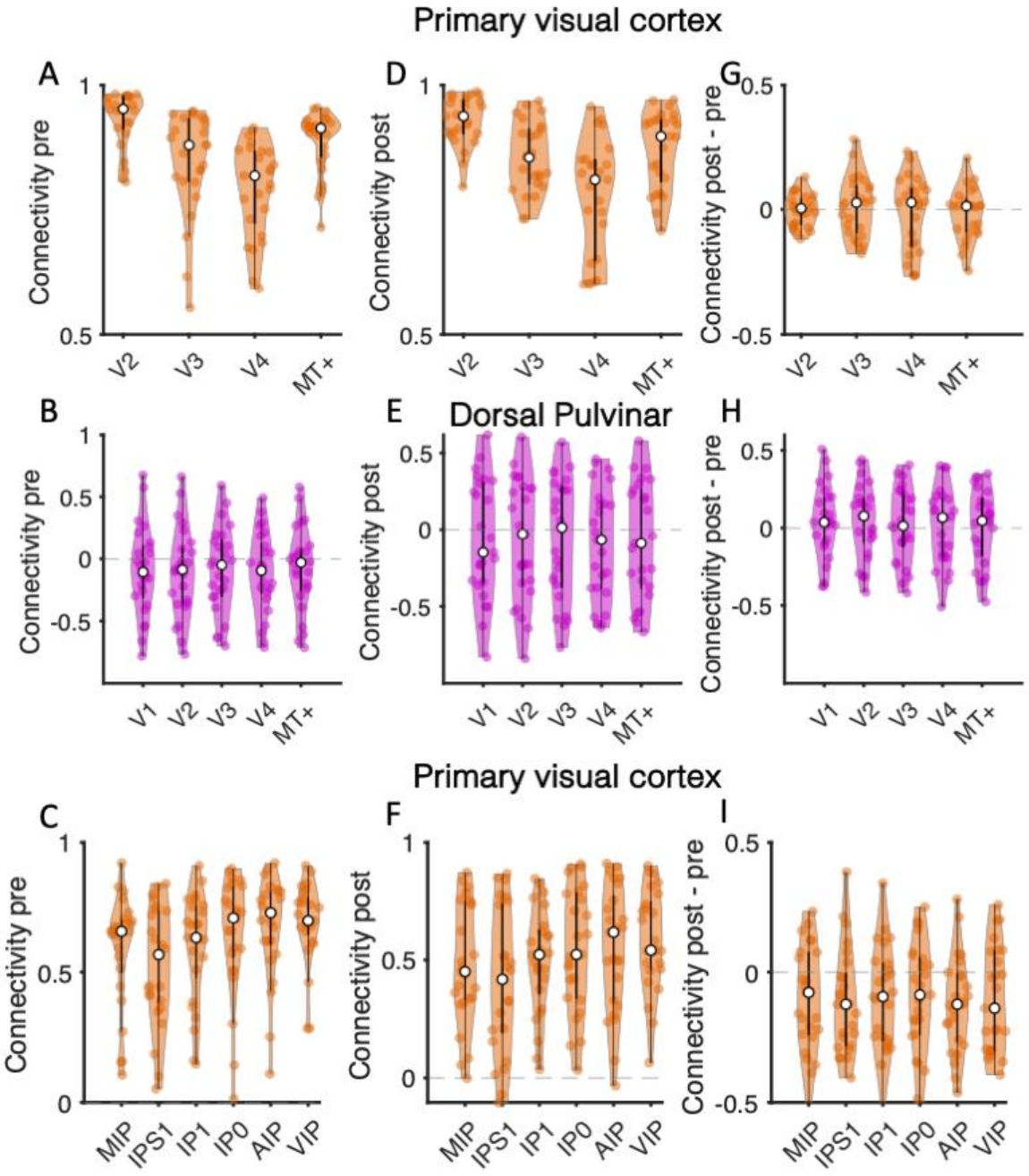

Figure 7-5 V1 and dPulv functional connectivity with visual and intraparietal regions

A-F: Correlation between the cortical regions of interest (on the x-axis) and V1 (A,C,D,F) or dPulv (B,E) before and after monocular deprivation. G-I: Differences in correlation values (post – pre deprivation) between the cortical regions of interest (on the x-axis) and V1 (G,I) or dPulv (H). From A to I, thick black error bars indicate the ends of the first and third quartiles, thin black bars indicate 95% confidence intervals. The white circle indicates the median across subjects. Single points indicate individual values.

Figures 7-4 and 7-5 show the effects of monocular deprivation on two supplementary seed regions, the primary visual cortex and the dorsal pulvinar.

These correlation maps show no effect of monocular deprivation on the functional connectivity pattern of the dPulv, which remained uncorrelated with the visual cortex (Figure 7-4), as confirmed by the within-subjects analysis (Figure 7-5; one sample t-tests: all $|t(24)| > 1$, all p FDRcorrected > .05).

V1 functional connectivity showed a different outcome. The super-subjects maps show a decrease in functional connectivity between V1 and the intra-parietal cortex (Figure 7-4). We confirmed this observation by performing one-sample t-tests across subjects on the post-pre differences, that showed a significant connectivity decrease with the Intraparietal Areas (Figure 7-5 bottom panel: all $|t(24)| > 2.5$, all $p_{FDRcorrected} < .05$). No effect of monocular patching was found on the connectivity between V1 and extra striatal areas (Figure 7-5; one sample t-tests on post-pre differences: all $|t(24)| > 0.4$, all $p_{FDRcorrected} > .05$).

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