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Interocular transfer of visual memory – Influence of visual impairment and abnormalities of the optic chiasm

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ABSTRACT

Due to an increased crossing of the optic nerve fibers at the optic chiasm in albinism, the visual cortex receives largely monocular input from the contralateral eye. Here we investigated whether this obstruction of binocular integration at the cortical input stage also impacts on interocular information exchange at the high processing level of visual memory. Interocular transfer (IOT) of visual memory retrieval was tested psychophysically after monocular encoding in 8 albinotic participants and 24 healthy controls. The retrieval performance (hit rate, reaction time, d') was determined when using the same or different eye at encoding. To assess the effect of reduced visual acuity (VA) on recognition, we simulated interocular acuity differences (IOA) in two healthy control groups (each n = 8), i.e., with large (VA: 0.89 vs. 0.12) and small simulated interocular difference (VA: 0.25 vs. 0.12), with the latter matched to that observed in the albinotic participants (VA: 0.20 vs. 0.15). A significant decrease in retrieval performance was observed in controls with simulated strongly reduced VA in one eye ($p < 0.0001$). For the other conditions and groups, including the albinotic participants, no dependence on VA and no significant difference between using the same or different eye was observed. This indicates interocular transfer and hence interocular information exchange in human albinism. These findings thus provide insights into the scope of plasticity of binocular information processing and inter-hemispherical information flow.

1. Introduction

Information integration is a fundamental feature of the brain, which determines key properties of sensory processing and perception. A powerful model with which to study such integrative processes is binocular vision (Blake, 1989; Freeman and Ohzawa, 1990), as it relies on the integration of the input reaching the primary visual cortex (V1) from both eyes. Conditions obstructing binocular input to the visual cortex thus provide a unique opportunity to investigate the scope and mechanisms of plasticity of binocular integration. Such a condition is encountered in individuals with albinism, an inherited disorder associated with hypopigmentation, foveal hypoplasia, and misrouting of optic nerves.

Normally, only the nasal retinal fibers cross at the optic chiasm and project to the hemisphere contralateral to the eye, while the temporal retinal afferents remain uncrossed and project to the ipsilateral hemisphere. Consequently, each hemisphere receives binocular input from corresponding locations in the contralateral visual field. This input is initially segregated into interleaved ocular dominance columns in the input lamina of V1. From there, the binocular information starts to converge, which yields binocular visual function and stereopsis (Dougherty et al., 2019; Parker et al., 2016; LeVay and Nelson, 1991). In contrast, in albinism, the part of the retina that projects to the contralateral hemisphere extends into the temporal retina, on average by 8° (Hoffmann et al., 2005). As a consequence, in albinism the left hemisphere receives input predominantly from the right eye and vice versa (Hoffmann et al., 2003; Schmitz et al., 2003). This abnormal input to the visual cortex was initially demonstrated with visual evoked potentials (Apkarian et al., 1983) and later cross-validated with fMRI (Von dem Hagen et al., 2008). Due to the enhanced crossing of the optic nerves in albinism, the input to V1 is largely monocular (Fig. 1). Consequently, binocular integration is obstructed, which is associated with

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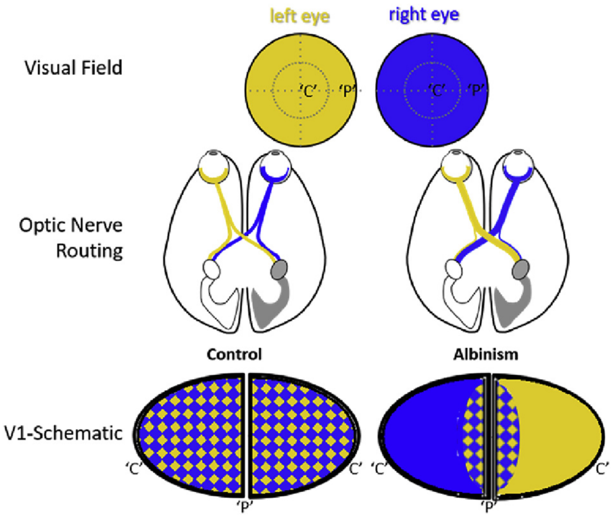

Fig. 1. Schematic illustration of the optic nerve projections and visual field representation in the primary visual cortex (V1) in controls and albinism ('C': central- and, 'P': peripheral visual field). Due to the partial decussation of the optic nerves in controls, V1 receives binocular input that is arranged as interleaved ocular dominance columns. Due to the increased crossing in albinism, each hemisphere receives input from the contralateral eye, and residual binocular input is confined to the representation of the peripheral visual field.

absent or severely reduced binocular and stereoscopic visual perception and with strabismus (Hoffmann and Dumoulin, 2015). Moreover, individuals with albinism typically have reduced visual acuity caused by immature foveal development and nystagmus (Bridge et al., 2014; Hoffmann et al., 2005; Oetting, 1999). Despite this large-scale anatomical abnormality, major aspects of pattern vision remain intact (Hoffmann and Dumoulin, 2015; Hoffmann et al., 2007; Wolynski et al., 2010). This intact pattern vision is taken as evidence for efficient adaptive mechanisms that make the erroneous visual input available for perception and accentuates the importance of albinism as a unique model to assess the scope of plasticity in the human visual system.

Given the obstruction of interocular integration at the level of V1 in albinism, we aimed to test whether this early-stage reduction of interocular integration of information is a general feature in albinotic visual perception and whether such a reduction has an impact on higher level information processing. As an alternative, inter-hemispherical callosal connections might serve to mediate the inter-hemispherical transfer of information for interocular integration (Myers, 1956). We employed a visual memory paradigm, because memory retrieval has been shown to involve reactivation of the brain networks involved at encoding (Rugg et al., 2008), potentially including responses to both external visual stimulation (bottom up) and internally generated signals (top down; Lawrence et al., 2018). If memory encoding takes place only using one eye, one could assume that a reactivation of the encoding networks would be impaired if the retrieval cue were presented only to the other eye, based on a lack of engagement of the same visual cortical networks specifically in albinism. On the other hand, successful memory retrieval would suggest interocular information is transferred at the time of memory encoding, whether in early processing at the level of visual cortex (Dougherty et al., 2019), or at a higher level, via the corpus callosum (Myers, 1956). We note here that while evidence suggests that recall and recognition memory rely on different brain networks (Yonelinas et al., 2005; Aggleton and Brown, 2006; Sauvage et al., 2008; Sweeney-Reed et al., 2016), visual cortical processing is deemed to be similar in both types of memory. Although interocular rivalry paradigms present a potential approach to addressing the issue of interocular information integration (Blake and Logothetis, 2002), it must be noted that albinism is accompanied by strabismus. Therefore, binocular visual perception and eventually stereo vision are suppressed, remaining so even with correction of the strabismus via prismatic lenses in the majority of individuals with albinism (Anderson et al., 2004). As a result, interocular integration is expected to be severely disrupted in interocular rivalry paradigms in albinism (Schmitz et al., 2003; Summers, 2009). Nonetheless, information collected through one eye might be available for processing of information viewed with the other eye. To test this hypothesis, and at the same time bypass the potentially confounding effect of impaired binocular vision, we assessed interocular transfer of visual information without simultaneous binocular stimulation. We tested whether the visual history of one eye is available to the other. Specifically, we developed and applied a paradigm to test the interocular transfer of visual memory.

2. Methods

2.1. Rationale

We investigated binocular integration for higher level visual processing in albinism by determining the interocular transfer (IOT) of visual memory. In the presence of IOT, monocular retrieval of monocularly encoded memory should be identical for encoding and retrieval via the same or different eyes. In the absence of IOT, memory should be better when using the same eye during encoding and retrieval. However, lower visual acuity in albinism may lead to reduced perception of the visual input and consequently reduce encoding and retrieval performance simply due to recognition difficulties. Furthermore, interocular acuity differences (IOA) are prevalent in albinism such that higher retrieval rates might be observed for the better eye compared to the weaker eye. To take these potential confounding effects into account, we tested different groups of participants (controls with different degrees of artificial VA reduction and individuals with albinism), and we tested four experimental conditions for each group: monocular stimulation of the same eye with higher acuity during encoding and retrieval ("HH"), use of the eye with lower acuity for both encoding and retrieval ("LL"), encoding through the eye with lower acuity and retrieval by the eye with higher acuity ("LH"), and the other way around ("HL"). Three hypotheses were developed to describe the influence of IOA on performance: no influence of IOA and present IOT, no influence of IOA and absent IOT, and influence of IOA without any IOT effect (Fig. 2a).

2.2. Participants

Eight participants with albinism (age range: 18–58; decimal visual acuity: 0.06–0.47) and 24 controls (age range: 19–29) with normal visual acuity and no history of ophthalmological or neurological disorders took part in this study. Detailed information about characteristics of the albinotic participants is listed in Table 1. Informed written consent was obtained from all participants prior to the study initiation. The experimental procedures were approved by the Ethics Committee of Magdeburg University and conformed to the Declaration of Helsinki.

2.3. Visual stimuli

Visual stimuli consisted of 240 images of animals and objects that were selected from the 'Bank of Standardized Stimuli' (Brodeur et al., 2010) and the 'Ecological Alternative to Snodgrass and Vanderwart' (Moreno-Martínez and Montoro, 2012). The stimuli were presented monocularly on a monitor with a resolution of 1280 × 960 pixels using Neurobehavioral Systems Presentation (version 17.2). The stimulus (mean luminance: 5.4 cd/m^2 to reduce photophobia in albinism) extended ± 2.9° x ± 4.0° of visual angle from the center of the screen. Each image was shown on a black background with a centered fixation cross for 250 ms to minimize the impact of eye movements (Fig. 3). Participants viewed the display in a dimmed room at 1 m distance and were requested to fixate the cross.

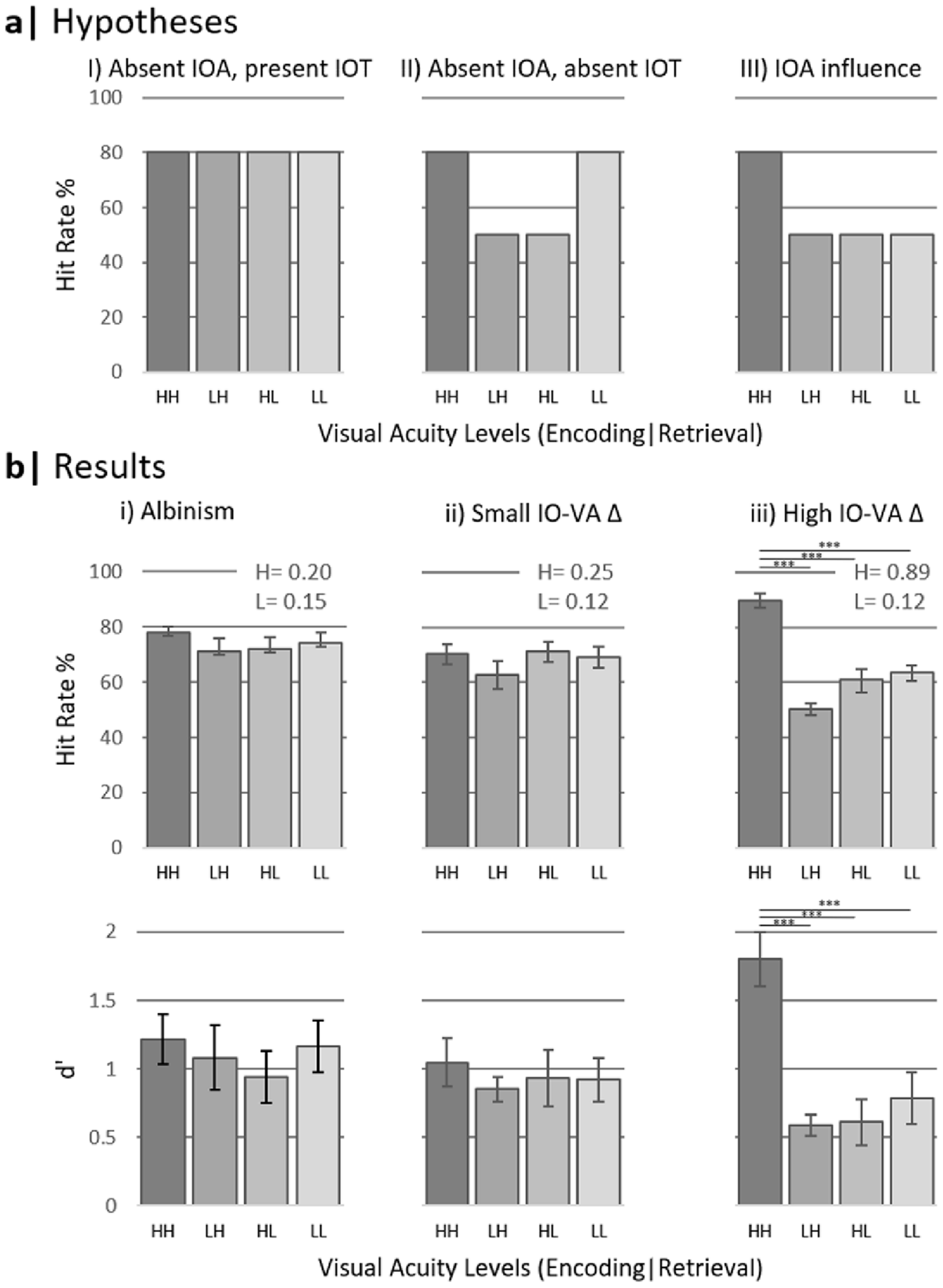

Fig. 2. Hypotheses and results of influence of interocular acuity difference (IOA) conditions ('HH', 'HL', 'LH', 'LL') on IOT of memory: **a)** Hypotheses: (I) no influence of IOA and present IOT, (II) no influence of IOA and absent IOT, (III) only influence of IOA without any IOT effect. **b)** Results of hit-rates (top) and d' values (bottom) (mean and standard error of mean) for the three VA dependent groups: (i) albinism, (ii) controls with small and (iii) high simulated IOA differences. Performance of albinotic and corresponding control group with small IOA differences clearly confirms hypothesis (I), suggesting the presence of IOT of visual memory.

2.4. Design and procedure

All participants underwent the following psychophysical testing: best-corrected decimal visual acuity (VA) was determined with the Freiburg Visual Acuity and Contrast Test (FrACT), which utilizes Landolt-C optotypes with randomized gap orientations (Bach, 1996). Stereopsis was assessed using Lang's stereo-test. Additionally, visual evoked potentials (VEPs) were recorded in albinotic participants and analyzed as described in (Hoffmann et al., 2011) to identify and ensure misrouted optic nerves. Briefly, inter-hemispherical VEP differences were recorded by separate stimulation of the left and right eye with bilateral checkerboard patterns at a viewing distance of 114 cm. Visual stimuli (19° × 15°) were presented in pattern-onset-offset mode (40 bms on, 440 ms off) using three different check sizes (0.5°, 1.0°, 2.0° visual angle) in an interleaved manner. VEPs were measured with gold-cup electrodes at Oz, OL, and OR (4 cm left and right from Oz, respectively), referenced to Fz. The ground electrode was attached to Fpz. The signal was amplified with a physiological amplifier (50,000; Grass Instruments, Quincy, MA), analog filtered in the range of 0.3–100 Hz, and digitized at a rate of 1 kHz with 12-bit resolution. The EP2000 Evoked Potentials System (Bach, 2018) on a G4 Power Macintosh was used for stimulus delivery and electrophysiological recordings. The offline analysis was performed using technical graphing and data analysis software (IGOR 5.0; WaveMetrics, Inc., Lake Oswego, OR). Traces were digitally low-pass filtered (cutoff: 45 Hz) and the difference-VEPs (OL minus OR) were determined for each eye separately to compare the

Table 1
Characteristics of albinotic participants: Listed are the age, dominant eye, corrected visual acuity of the dominant and non-dominant eye, near correction (left | right) if applicable, and stereo vision performance, as tested with the Lang test.

No.	Age	Dominant eye	Corrected visual acuity (dominant | non-dominant)	Near correction (left | right)	Stereo vision
1	34	left	0.47 | 0.32	–	no
2	38	left	0.34 | 0.27	–	no
3	27	right	0.07 | 0.06	–	no
4	27	left	0.26 | 0.20	–	no
5	18	left	0.20 | 0.10	–	no
6	58	right	0.07 | 0.09	1.25 | 1.50	no
7	47	left	0.34 | 0.24	–	no
8	38	right	0.24 | 0.14	1.00 | 1.00	no
mean	36	–	0.20 | 0.15	–	–

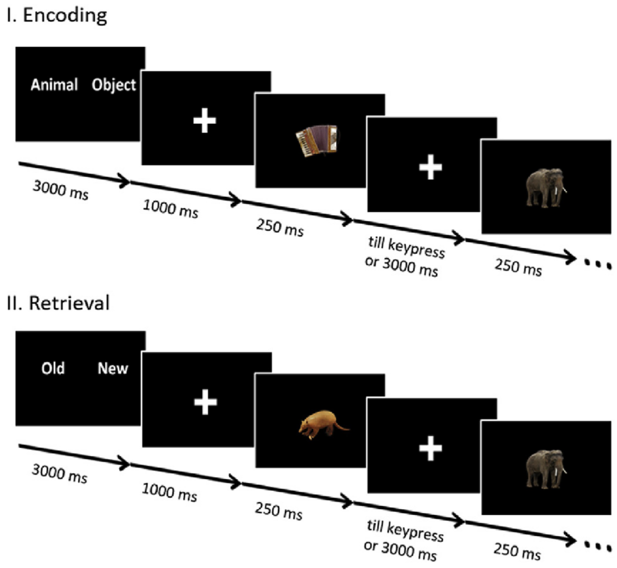

Fig. 3. Schematic sequential representation of the paradigm. Initially the instructions were presented on the screen for 3000 ms, followed by a fixation cross for 1000 ms. Afterwards, each stimulus was shown for 250 ms. Upon receiving feedback from the participant via key press, the next stimulus was presented. The maximum inter-stimulus interval was set to 3000 ms, when the participants provided no response. **(I)** encoding (attention task: object vs. animal) and **(II)** retrieval (discrimination task: old vs. new).

inter-hemispherical activation difference separately for stimulation of each eye. In albinism, monocular stimulation of the central visual field elicits greater VEPs on the hemisphere contralateral to the stimulated eye than on the ipsilateral hemisphere. As a consequence, the polarity of the inter-hemispheric VEP difference is inverted for left compared to right eye stimulation. In contrast, for controls, the polarity does not depend on the stimulated eye. In order to identify inter-ocular differences in these difference-VEPs, we applied a correlation approach, i.e., a correlation of the difference VEP-traces for left and right eye stimulation, that has previously been established and applied in a number of studies (Soong et al., 2000; Van Genderen et al., 2006; Jansonius et al., 2001; Tremblay et al., 1996; Hoffmann et al., 2005, 2006, 2008, 2011, 2015). As opposed to a peak-based analysis, this approach has the benefit that it provides an objective, automated analysis. It is based on the rationale that, due to the polarity inversion of the traces in albinism, the inter-hemispheric activation differences obtained for right and left eye stimulation are negatively correlated, while the absence of such polarity inversion in controls leads to a positive correlation (Pearson's correlation coefficient). In the present study, this correlation approach was applied, following Hoffmann et al. (2005), using a time-window of 50–250 ms was used, reflecting responses from the early visual cortex including V1 (Di Russo et al., 2002). The respective correlation index indicating the lateralization abnormality is termed $I_{\text{VEP-lateralization}}$.

IOT of visual memory was determined using a paradigm comprising an encoding and a retrieval phase (Fig. 3). At encoding, 6 blocks of 10 trials were presented monocularly during a two-choice ‘animal vs. object’ discrimination task. After each block, the viewing eye was alternated by moving an occluder from one eye to the other. A total of 60 images (5 animals and 5 objects per block) were presented for about 6 min. The participants were required to indicate whether the viewed image was an object or an animal and respond as quickly as possible via key press. After a 2-min break, the retrieval phase was initiated. In 6 blocks, a total of 120 images (20 trials per block) were presented, half of which were shown during encoding. Participants judged the stimuli as previously seen (old) or new and responded via key press. The retrieval phase lasted for 9 min, in which each block was presented monocularly and alternated between the eyes. This alternating sequence resulted in four combinations of the eyes (left-left, left-right, right-left, and right-right) in the encoding and retrieval phases.

To probe the effect of IOA differences on performance, the experiment was performed for high (H) and low (L) visual acuity (see Rationale). Controls were divided into three groups of equal size (n = 8 per group), and IOA differences were simulated in two of them using one and two 0.3 Bangerter foils (OPTOTEC GmbH, Seelze, Germany). The first control group was tested without any artificial alteration of their VA during encoding and retrieval (mean decimal VA = 0.89). It should be noted that due to the low luminance of the stimuli, the determined VA was slightly lower than the VA for standard luminance levels, where normal VA is ≥ 1.0. In the second control group, VA was severely reduced in one eye resulting in a strong IOA difference (mean decimal VA for the better | weaker eyes = 0.89 | 0.12). In the third control group, artificially reduced VA with small IOA differences were introduced (mean decimal VA for the better | weaker eyes = 0.25 | 0.12) to equalize the VA-conditions in the controls to those of the fourth group, i.e., the albinotic participants (mean decimal VA for the better | weaker eyes = 0.20 | 0.15). One experiment took approximately 15 min (6 min for encoding and 9 min for retrieval respectively) and was repeated in each participant with a novel set of stimuli after a 15-min break. Reaction times and hit rates, i.e., correct recognition of previously seen (old) objects, were recorded as a measure of memory performance. In addition, the d-prime (d’) discriminability index was calculated to quantify the discrimination between old (hit rate) and new objects (false alarms; Macmillan and Creelman, 1990). The hit rate (HR) was analyzed after arcsine transformation to yield a normal distribution.

3. Results

Two-factor mixed-model ANOVAs (between-subject factor, *group*; within-subject factor, *eye*: same/different eye) were applied to compare HR, d’, and RT for encoding and retrieval with the same eye vs. different eye. Main effects of HR were identified for both factors, i.e., *eye* ($F(1, 28) = 23.59$, $p < 0.0001$, $\eta_p^2 = 0.457$) and *group* ($F(3, 28) = 11.03$, $p < 0.0001$, $\eta_p^2 = 0.542$), and for their interaction ($F(3, 28) = 8.41$, $p < 0.0001$, $\eta_p^2 = 0.474$). The same effects were evident for the d’ values and RTs, as summarized in Supplementary Table 1. Importantly, follow-up post hoc analyses (Holm-Sidak corrected t-tests) showed that significant differences for the factor *eye* were confined to the group of controls with strong IOA (interocular acuity) differences (see Supplementary Table 1 and Fig. 4). In contrast, there was no difference in HR according to the factor *eye* for either controls with normal visual acuity or with IOA differences equalized to those of the albinotic participants. Importantly, also for the albinotic participants, no significant differences in HR between using the same and different eyes were evident.

One-way repeated measures ANOVAs and Holm-Sidak corrected

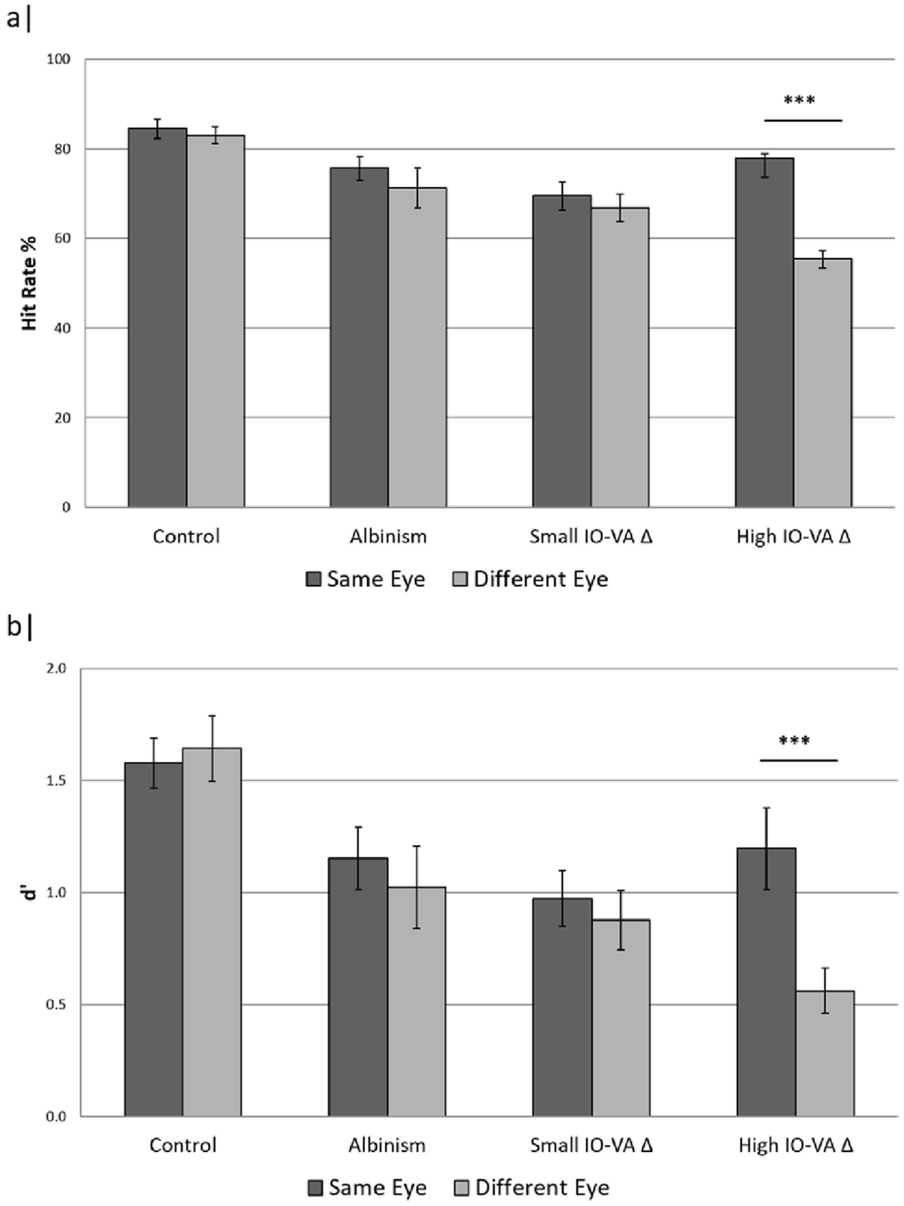

Fig. 4. Comparison of the hit-rates (mean and standard error of mean) for **a)** hit-rate and **b)** d' value between the four experimental groups: control with normal VA, albinism, controls with small simulated IOA differences matched to the level in albinotic group, and controls with strong simulated IOA differences under the two IOT conditions, i.e., retrieval with the same or different eye: Only the performance of the controls with high IOA differences (High IO-VA Δ) depended on the viewing eye, while the albinotic group performed almost equally well during retrieval with the same or different eye, which confirms the presence of IOT of visual memory in albinism.

post hoc tests (t-tests) were applied to compare the IOA combinations ('HH', 'HL', 'LH', 'LL' as detailed in Rationale) within the albinotic group and within the two control groups with simulated IOA differences. Significant effects in HR ($F(3, 21) = 36.83$, $p < 0.0001$, $\eta_p^2 = 0.840$), d', and RT (detailed in Supplementary Table 1) were observed only in controls with strong IOA variations, where the post hoc analysis revealed that it was the condition HH that differed significantly from the other conditions. Importantly, no significant differences in HR, d', and RT were found for the albinotic group and the controls with IOA differences equalized to those in the albinotic group (Fig. 2b).

To evaluate the effect of optic nerve misrouting on performance directly, IOT conditions were compared between the albinotic participants and the corresponding control group with IOA differences equalized to those in the albinotic group using a two-factor mixed ANOVA (between-subject factor, *group*: control and albinotic groups; within-subject factor, *eye*: same and different eye). There was no significant effect of *group* (or *eye* and no interaction between these factors) on hit rate ($F(1, 14) = 1.66$, $p = 0.219$, $\eta_p^2 = 0.106$), d' value, or RT (see Supplementary Table 1), indicating that the misrouted optic nerves in the albinotic participants did not influence their performance.

To exclude the possibility that IOT impairment might be more pronounced in participants with stronger misrouting, we utilized the correlation of the degree of misrouting with the VEP-derived $I_{\text{VEP-lateralization}}$ (Hoffmann et al., 2005). We tested the correlations of IOT with the $I_{\text{VEP-lateralization}}$ for each of the three check sizes tested (see Methods). The IOT-index ($I_{IOT} = [(HR_{HH} + HR_{LL}) - (HR_{LH} + HR_{HL})]/[HR_{HH} + HR_{LL} + HR_{LH} + HR_{HL}]$), i.e., the contrast between responses for the same eye during encoding and retrieval vs. different eye during encoding and retrieval, did not correlate with $I_{\text{VEP-lateralization}}$ [Fig. 5; $p > 0.2$, $r^2 \leq 0.24$]. While this indicates the absence of a strong effect of misrouting strength on IOT, small effects that might become evident for higher sample sizes cannot be fully excluded.

4. Discussion

The current study demonstrates that retrieval of monocularly encoded stimuli in albinism does not differ according to whether retrieval is performed with the same or the different eye to the one used at encoding. This presence of IOT of visual memory highlights the presence of binocular interactions in visual memory, even in the absence of normal binocular input to V1. This finding indicates that the separate monocular input to each V1 is combined at some stage. While it is

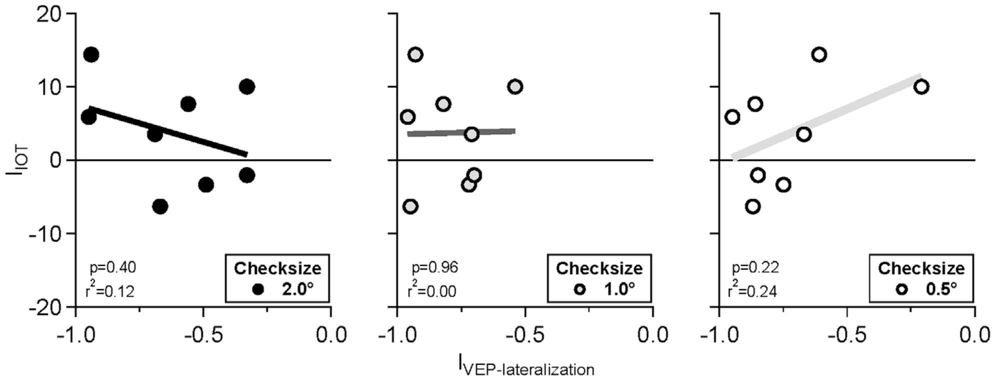

Fig. 5. Correlation between the IOT-index and VEP-lateralization index for increasing checksize from left-to righthand panels. No significant correlations and no common trend across the three checksizes were observed.

highly probable that some information from the two eyes is combined at the level of the corpus callosum (Myers, 1953), more recent evidence in primates suggests that binocular information is actually processed by so-called monocular neurons in layer 4C of V1, as they receive input not only from the retina but, also from cortical neurons, which may contain binocular visual information (Dougherty et al., 2019). Remarkably, IOA differences do not affect the performance of albinotic participants. In fact, the albinotic group had slightly better performance than the two control groups with simulated IOA differences (Fig. 4), suggesting that individuals with albinism might have learned to cope better with reduced vision than controls with simulated reduced vision. By contrast, controls with strong IOA differences displayed a significant decline in performance during retrieval with the different eye. Taken together, these findings imply that in albinism an information exchange between the eyes occurs at a later stage than in the normal system or that, less likely, plasticity of early, striate and extrastriate, visual areas allows for the combination of binocular information.

In albinism, primary visual cortex input from opposing hemifields coexists. Three different cortical organization patterns comprising these opposing hemifields have been inferred from animal models of albinism, termed ‘contiguous representation’, ‘interleaved representation’, and ‘interleaved suppressed representation’ (Hoffmann and Dumoulin, 2015). For the ‘contiguous representation’ (also known as the ‘Boston pattern’), the geniculo-striate projections are reordered, leading to contiguous retinotopic representations of opposing visual hemifields. For the ‘interleaved representation’ (also known as ‘True albino pattern’), conservative and unaltered geniculo-striate projections give rise to hemifield dominance columns that are reminiscent of ocular dominance columns in a normal visual system. For the ‘interleaved suppressed representation’ (also known as the ‘Midwestern pattern’), the same conservative geniculo-striate connections are indicated, but the abnormal input from temporal retinal afferents is suppressed, which results in hemianopia in the ipsilateral visual field (Guillery, 1986; Hoffmann and Dumoulin, 2015). While the ‘contiguous representation’ and ‘interleaved suppressed representation’ are preserved in many albino mammals, in human and non-human primates, only the ‘interleaved representation’ pattern has been reported (Guillery et al., 1984; Hoffmann et al., 2003). This indicates the absence of a profound reorganization in the thalamocortical connections in primates and implies a reassignment of ocular-dominance columns with hemifield-dominance columns in albinism (Guillery et al., 1984). While cross-column integration normally, i.e., across ocular dominance columns, serves to support stereo vision, it might, in the presence of hemifield-dominance columns, lead to major sensory conflicts. In albinism, preservation of such integration would therefore result in perceptual crosstalk between the ipsi- and contralateral hemifields. Interestingly, no evidence for inter-hemifield transfer of adaptation was found in a previous study using the tilt-after-effect (Klemen et al., 2012). Thus, plasticity of intra-cortical mechanisms is required to make the abnormal input available for perception by selective elimination of such integrative processes, while supporting other integrations, such as those required to form monocular spatial receptive field properties (Hoffmann et al., 2012). The present study provides the first evidence for interocular transfer of memory in albinism. As binocular integration in the primary visual cortex is obstructed in albinism, our findings suggest adaptive mechanisms to mediate the integration of the abnormal input for binocular processing. This is in accordance with a previous fMRI study addressing higher-tier plasticity in albinism via the investigation of visuo-motor integration (Wolynski et al., 2010). Here, visuo-motor performance was maintained despite the mismatch of abnormal visual and normal motor (and somatosensory) cortices, which indicates adaptive mechanisms operating at the interface between visual and motor maps.

The successful memory retrieval when the non-encoded eye was used at retrieval in participants with albinism could result from information transfer at different levels in the brain. Memory retrieval involves a hippocampally-coordinated reactivation of cortical patterns present during encoding, and even partial encoding/retrieval overlap can reactivate the whole representation (Rugg et al., 2008). IOT of purely visual information (Mitchell et al., 1975; Mitchell and Ware, 1974) might enable visual cortical representations of encoded stimuli to be reactivated despite the original stimulus having chiefly activated regions of the visual cortex at encoding that were not stimulated during retrieval. On the other hand, given evidence for processing of binocular information by neurons receiving monocular visual input in layer 4C of V1, thought to arise from top-down cortical input of vision-related information from the other eye (Dougherty et al., 2019), a binocular visual cortical representation at the time of encoding is plausible, despite monocular bottom-up visual input. In a recent study using lamina-resolved fMRI, activity associated with visual working memory was observed in different layers of V1 depending on whether it was internally generated or resulted from external visual stimulation (Lawrence et al., 2018), providing further evidence supporting the notion that not only external visual stimulation but rather also internal processes, presumably involving projections from other cortical regions, can trigger activity in the visual cortex associated with visual memory. Indeed, part of the cortical pattern generated at encoding will also have engaged higher processing in other cortical areas, as the participants discriminated between objects and animals, which could have resulted in semantic encoding of the stimuli. A higher-level representation of the image could then lead to cortical reactivation at retrieval that does not actually involve the original visual cortical activation. Future work using functional imaging is required to differentiate between these possibilities.

4.1. Limitations of the study

A few methodological considerations should be addressed. Ideally, the albinotic and control groups would be age-matched. However, higher age within the age range of the participants in the current study is not known to decrease memory performance, especially in immediate picture retrieval (Park et al., 1986; Smith et al., 1990). This supposition was confirmed by a largely indistinguishable performance of the albinotic group compared with the controls with normal visual acuity, i.e., without simulated IOA differences. Furthermore, the study groups of the present study overlapped in their age-ranges. Additionally, due to the low prevalence of albinism, only eight albinotic participants were included, which does not allow assessment of the effect of intersubject variability in albinism. Finally, it must be noted that eye-movements induced by the stimulus presentations are reduced, but not fully excluded by the presentation duration of 250 ms. Future studies should aim to address this issue, either by the use of shorter presentation durations, which, however, reduce performance, or by eye-movement controlled, ideally fundus-controlled, stimulus presentation.

5. Conclusion

We demonstrate here that IOT of information successfully occurs in participants with albinism, who have substantial crossover of optic nerve fibers resulting in chiefly monocular input to the contralateral visual cortex. These findings should guide future research targeting the question of where the initial binocular interaction in albinism arises, by investigating intermediate stages of visual processing. Deciphering the mechanisms underlying human binocular processing provides both fundamental as well as clinically relevant insights and is therefore of importance for our understanding of the human visual system.

Conflict of interest: None

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Appendix A. Supplementary data

Supplementary data related to this article can be found at https://doi.org/10.1016/j.neuropsychologia.2019.03.018.

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