



Mechanisms underlying simultaneous brightness contrast: Early and innate

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ABSTRACT

In the phenomenon of simultaneous brightness contrast, two patches, one on a dark background and the other on a light one, appear to have different brightness despite being physically equi-luminant. Elucidating the phenomenon's underlying mechanisms is relevant for the larger question of how the visual system makes photometric judgments in images. Accounts over the past century have spanned low-, mid- and high-level visual processes, but a definitive resolution has not emerged. We present three studies that collectively demonstrate that the computations underlying this phenomenon are low-level, instantiated prior to binocular fusion, and available innately, without need for inferential learning via an individual's visual experience. In our first two studies, we find that strong brightness induction is obtained even when observers are unaware of any luminance differences in the neighborhoods of the probe patches. Results with dichoptic displays reveal that eye of origin, although not evident consciously, has a marked influence on the eventual brightness percept of the probe patches, thereby localizing brightness estimation to a site preceding binocular fusion. The third study uses conventional simultaneous brightness contrast displays, but an unusual group of participants: Congenitally blind children whom we were able to treat surgically. The results demonstrate an immediate susceptibility to the simultaneous brightness illusion after sight onset. Together, these data strongly constrain the search for mechanisms underlying a fundamental brightness phenomenon.

1. Introduction

The mechanisms of brightness estimation need to do more than simply measure image luminance values, since the perceived brightness of a region does not necessarily correspond to its luminosity. The classical illusion of simultaneous brightness induction (Fig. 1a), embodies the challenges inherent in this task. The small gray discs appear to have different brightness despite having identical luminance. Notwithstanding this phenomenon's long historical roots (Chevreul, 1839; Kuehni, 2002), and extensive study in human as well as non-human observers (Kinoshita, Takahashi, & Arikawa, 2012; Agrillo, Miletto Petrazzini, & Bisazza, 2016), fundamental questions about its underlying mechanisms are still open. The proposals regarding the broader question of how we perceive lights and darks in the world have spanned multiple levels of processing in the visual system. 'Low-level' accounts have suggested that this illusion results from simple filters that

implement lateral inhibition at early stages of the visual system (Hering, 1874; Wallach, 1948, 1963; Land & McCann, 1971; Blakeslee and McCourt, 1999, 2004; Dakin & Bex, 2003; Blakeslee, Cope, & McCourt, 2015). These accounts have been challenged by explanations that draw upon more sophisticated analyses of image structure. 'Mid-level' proposals suggest that the eventual brightness percepts rely upon grouping processes of the kind highlighted by the Gestaltists (Benary, 1924; Kardos, 1934; Koffka, 1935; Agostini & Proffitt, 1993; Gilchrist, 2006; Economou, Zdravkovic, & Gilchrist, 2007; Boyaci, Fang, Murray, & Kersten, 2010). Taking the analysis a step further, 'high-level' accounts maintain that brightness computations depend upon a sophisticated understanding of the scene and illumination layout depicted in the image (Helmholtz, 1867; Knill & Kersten, 1991; Adelson, 1993, 2000; Bloj, Kersten, & Hurlbert, 1999). The teleological motivations for all of these accounts are similar – they are meant to explain how the visual system can disentangle surface albedo, illumination and

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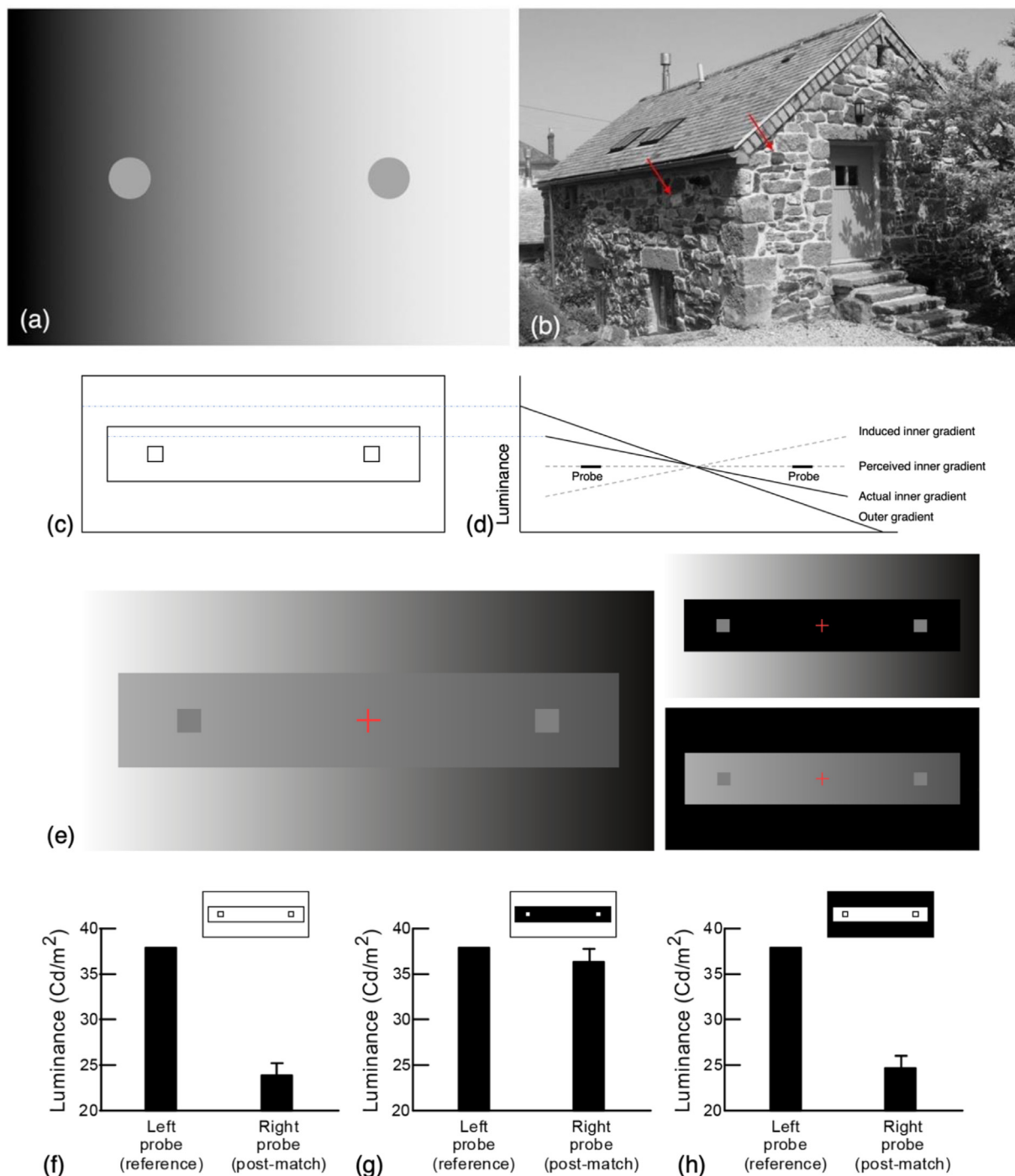


Fig. 1. (a) A simultaneous brightness contrast display. The two small discs appear to have different brightness despite having identical luminance. (b) Simultaneous brightness contrast in a real-world setting. The two stones indicated, one in shadow and the other in light, have the same mean luminance, but appear to have different brightness. (c) Display design used in experiment 1. Both rectangles have linear luminance gradients. The magnitude of the outer gradient is fixed (0–76 cd/m²) but the inner gradient is under experimental control. The outer gradient induces a change in the brightness profile of the inner strip, with the more luminous side of the outer gradient leading to a perceived darkening of the inner strip. This design of nested rectangles allowed control of the appearance of the inner one. Specifically, the physical gradient of the inner rectangle could interact with the induced gradient from the outer rectangle. We could then study how the brightness of the probe patches was determined by the appearance/physical gradient of the inner rectangle. (d) By setting the inner gradient to precisely null the induced gradient from the surrounding rectangle, the inner strip was made to appear homogenous throughout its length. (e) (Left panel) Two identical probe squares placed within the perceptually uniform strip appear to have very different brightness. (Right panels) Two variations of the display, one with the inner strip removed and the other with the outer enclosing rectangle removed. (f) Results from brightness matching experiments performed with the display shown in the left panel of (e). (g) Results with inner strip removed. (h) Results with outer enclosing rectangle removed. Error bars represent ± 1 standard error.

transparency in varied real settings. However, they differ in the level of sophistication of their underlying neural mechanisms (Gilchrist, 2007).

Deepening this debate is the unresolved question of whether visual

experience contributes to the genesis of this percept. The ‘empirical’ account maintains that this illusion arises from perceptual exposure to surfaces of different geometries and reflectances under varying

illumination conditions (Helmholtz, 1867; Williams, McCoy, & Purves, 1998; Lotto & Purves, 2000); through ontogenetic and/or phylogenetic learning, these experiences lead to the development of priors that influence how image data are interpreted, consistent with the aforementioned ‘high-level’ proposals. For instance, an image with bright and dark sections, may have occurred most frequently when a figure was partly in shadow. This experience-derived interpretation has consequences for explaining the equi-luminance of the inner patches: the patch in shadow needs to be inherently lighter than the one in illumination to emit the same luminous flux, leading to the illusion (Fig. 1b shows a real-world instance of this illusion, with background darks and lights interpretable as illuminated and shadowed regions). Serving as a counterpoint to empiricism is the nativist perspective, dating back historically to Plato (translation 1981), Descartes (1648), Leibniz (1704) and Kant (1781). A ‘nativist’ account denies a role for experience, suggesting instead that the neural circuitry already in place from the first moments of sight leads to this phenomenon. This is most compatible with low and mid-level explanations of the simultaneous brightness illusion.

Our goal here is three-fold: First, we seek to dissociate low- and high-level factors in the simultaneous contrast display. This has been difficult thus far because both factors are present simultaneously in the conventional display and make predictions in the same qualitative direction. Second, we attempt to more precisely constrain the locus of processing, and thereby the nature of admissible circuitry. Finally, we address the empiricist versus nativist debate to further define the space of likely mechanisms responsible for the simultaneous brightness illusion.

We emphasize that the focus of this work is the perception of brightness (perceived luminance), rather than lightness (perceived surface reflectance). This is an important distinction because the notion of multiple levels of explanation (low, mid and high) has typically been applied in the context of lightness, while brightness, as a low-level image attribute is assumed to admit only low-level accounts (Schirillo, Reeves, & Arend, 1990; Gilchrist, 2007). However, here we adopt the perspective that the treatment of brightness perception as an exclusively low-level process and lightness perception as spanning low/mid/high levels merits reconsideration. When an observer is asked to report their percept, they cannot necessarily distinguish between the two terms. The example of visual angle and visual size is a good case in point. Consider the Ponzo illusion (Ponzo, 1911). Two bars that subtend the same visual angle nevertheless appear to have different extents. An observer would not say that the perceived visual angles are identical but perceived sizes different. The illusion changes both attributes. Hence, even the ‘low-level’ attribute of visual angle is impacted by factors that can have low/mid/high level origins. Pupillary constriction, and changes in brightness ratings, in response to high-level cues such as having an image appear to be of the sun rather than the moon (Binda, Pereverzeva, & Murray, 2013), or perception of edges in Kanizsa figures all underscore similar points. Even though the attribute being reported is ostensibly low-level (here, brightness), the factors causing deviations from veridicality can span a range of complexity.

2. Methods & results

2.1. Study 1: Brightness induction by unseen causes

In order to disentangle low- and high-level factors in the simultaneous contrast display, we designed variations which allowed independent manipulation of the two kinds of causes and thereby permitted an assessment of their individual sufficiency to account for the observed phenomena. Fig. 1c shows the general structure of the display used in the first experiment. It comprised a rectangle nested in a larger one, and both rectangles could be assigned precisely controlled luminance gradients along their lengths. In this display, the perceived brightness profile of the inner rectangle is governed by two factors: its

actual luminance gradient and the gradient induced by the spatially varying luminance profile of the enclosing rectangle. To create our experimental display, we assigned the inner rectangle a luminance gradient having a magnitude and direction such as to precisely null the induced gradient from the surround. As a consequence, the inner rectangle perceptually appeared to have uniform brightness throughout its extent, even though it actually possessed a non-zero luminance gradient (Fig. 1d). This nulling of the inner rectangle’s gradient was performed individually by each of five subjects, naive as to the purpose of the study, by pressing one of two keys on the keyboard to swing the gradient in either direction in small steps. Following this nulling, our experiments involved placing two small horizontally separated probes with identical luminance within the inner rectangle. The subjects were asked to adjust the brightness of one of the probes to have it match the other. All experiments were performed in a darkened room. Participants were graduate students (age range 23–25 years). They viewed the displays on a CRT monitor from a distance of 40 cm. Displays subtended approximately 18 degrees of visual angle horizontally. Studies were approved by MIT’s IRB and informed consent was obtained from all participants.

As is evident in Fig. 1e, a strong brightness induction effect is obtained despite the perceptual homogeneity of the probes’ background. The two physically identical probes embedded in a seemingly uniform field are nevertheless perceived as having very different brightnesses (Fig. 1f).

For this display, there are four causes that can, in principle, yield the observed brightness induction effect: the perceived or actual gradients of the outer rectangle and the perceived or actual gradients of the inner one. By the nulling procedure described above, we have effectively dispensed with the perceived gradient of the inner rectangle as a cause. We tested the contribution of the gradients of the outer rectangle in two ways – first by examining the effects of removing the outer rectangle on the perceived brightness of the probe squares and second by removing the inner rectangle (replacing it with a uniform black area) and thus exploring whether induction from the outer rectangle on its own could account for the observed brightness difference. As the results in Fig. 1g and h demonstrate, removal of the outer rectangle does not significantly alter the perceived brightness difference between the two probe squares. Furthermore, the outer rectangle on its own is inadequate to induce a substantial brightness difference between the two probes. Taken together, these data establish that the observed brightness difference between the two probe patches is due to the actual gradient in the inner strip, although it is perceptually non-apparent. Thus, brightness induction is obtainable even without any perceptible luminance gradient.

Although perceptible gradients, which can serve as cues regarding illumination or transparency distributions, appear not to be necessary for inducing brightness differences, can they, when present, modulate the influence of the actual luminance gradients? We examined possible interactions between the inner strip’s perceived and actual gradients with an additional experiment. The experiment makes use of the fact that small changes in the magnitude of the outer gradient around the ‘equilibrium’ state (when the inner strip appears perceptually uniform) can be used to induce marked changes in the appearance of the inner strip. Depending on whether the outer gradient is made slightly steeper or shallower relative to the equilibrium state, the inner strip is imparted a perceptual gradient in one or the other direction (Fig. 2a) while keeping the actual luminance profile constant. We find that these reversals of perceived gradient direction in the inner strip (and corresponding changes in the inferences regarding illumination or transparency gradients) do not alter the perceived brightness of the probe squares (Fig. 2b).

It can be argued that the reason for the observed lack of influence from inferences regarding illumination or transparency distribution in the scene is that this display may not be readily interpretable in terms of factors such as illumination gradients or three-dimensional structure.

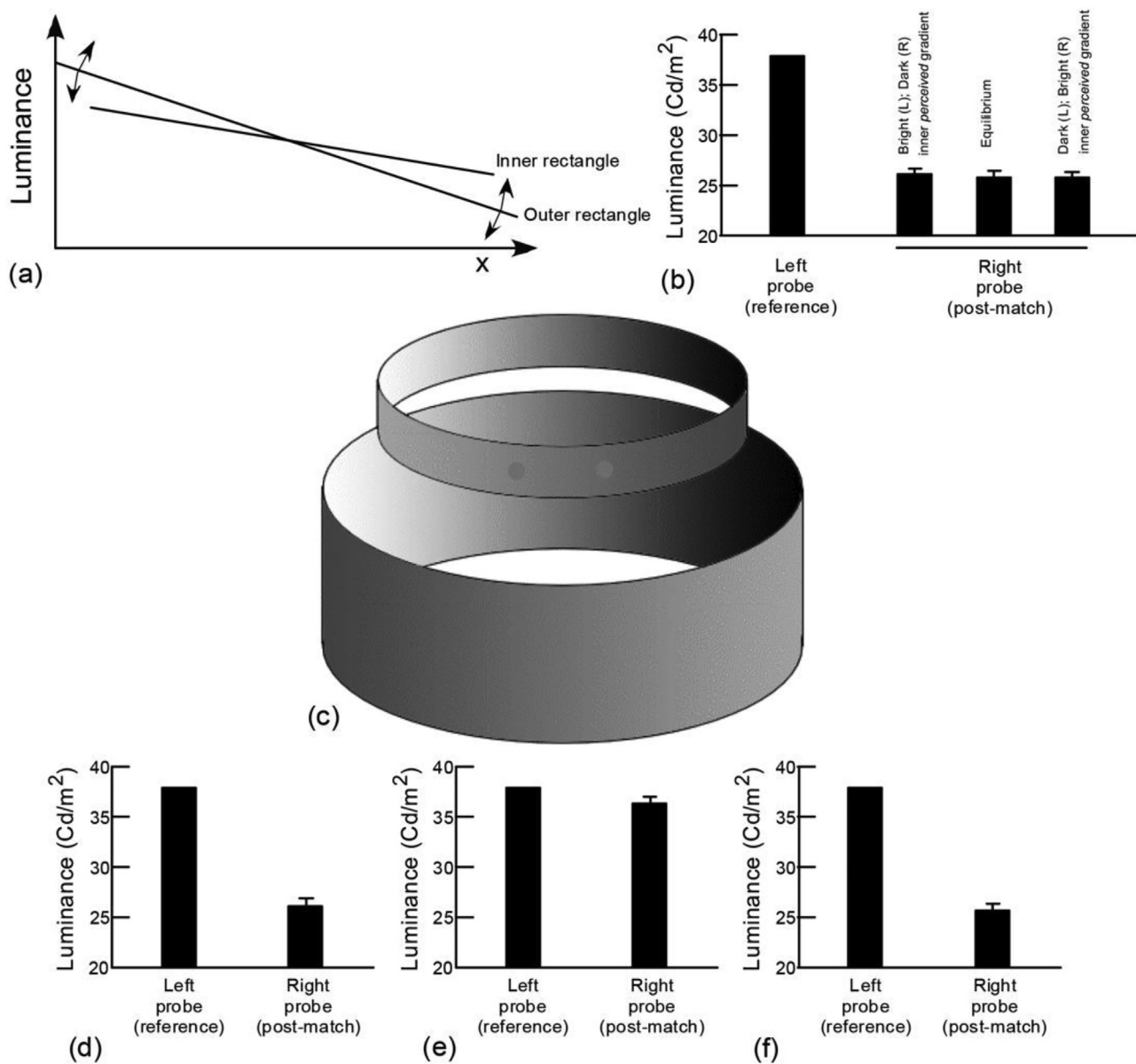


Fig. 2. (a) Approach for assessing trade-off between perceived and actual gradients. By changing the gradient magnitude in the enclosing rectangle about the equilibrium state, the inner rectangle can be imparted perceptual brightness gradients in opposite directions while leaving its physical luminance values unchanged. The end points of the gradient were shifted through ± 7.5 cd/m². (b) Results from brightness matching experiments under three appearances of the inner rectangle: 1. Gradient that is brighter on the left, 2. Perceptual uniformity, and 3. Gradient that is brighter on the right. Brightness matching results stay unchanged across the three conditions. (c) A variant of the display shown in Fig. 1e. The gradients are now readily interpretable as gradual illumination changes with the light source positioned on the right. The brightness percepts of the two probe dots are unchanged relative to Fig. 1e. (d) Brightness matching results with the display shown in (c). (e) Matching results after making the outer surface of the top ring black (f) Results after removal of lower ring. Error bars represent ± 1 standard error.

To address this issue, we created a variant designed to permit an easy interpretation of the display in terms of the scene's three-dimensional characteristics and illumination distributions (Fig. 2c). However, notwithstanding the inclusion of additional cues for aiding scene analysis, we find that the brightness percepts obtained with this display (Fig. 2d–f) are unchanged relative to those from the original one, and appear to be determined entirely by the perceptually non-apparent luminance gradient.

To further validate these findings, we devised an additional variant of the simultaneous-contrast display using the Craik-O'Brien-Cornsweet (COBC) effect (Cornsweet, 1970; Craik, 1966; O'Brien, 1959). Unlike a conventional COBC display where the physical luminances of the regions a little distance from the central wedge are identical (Fig. 3a), we created a version where the side that was actually of higher luminance

was perceived as being darker and vice-versa (Fig. 3b). Two probes were placed in the center of the outer flanks and initially had luminance corresponding to middle gray (Fig. 3c). Subjects had to adjust the brightness of one of the probes to match the other.

A high-level account, which would attribute the perceived darkness to shadow or attenuating transparency, would predict that the probe on the perceptually darker side would appear lighter than the other one (as in a conventional simultaneous contrast display, Fig. 1a). A low-level account would predict an effect in the other direction. The experimental results, shown in Fig. 3d, are consistent with the prediction of the low-level account. All subjects perceived the probe on the perceptually darker (but physically more luminous) side as being darker than the other one. In order to quantitatively assess potential trade-offs between low and high-level factors, we investigated whether scene-level analysis

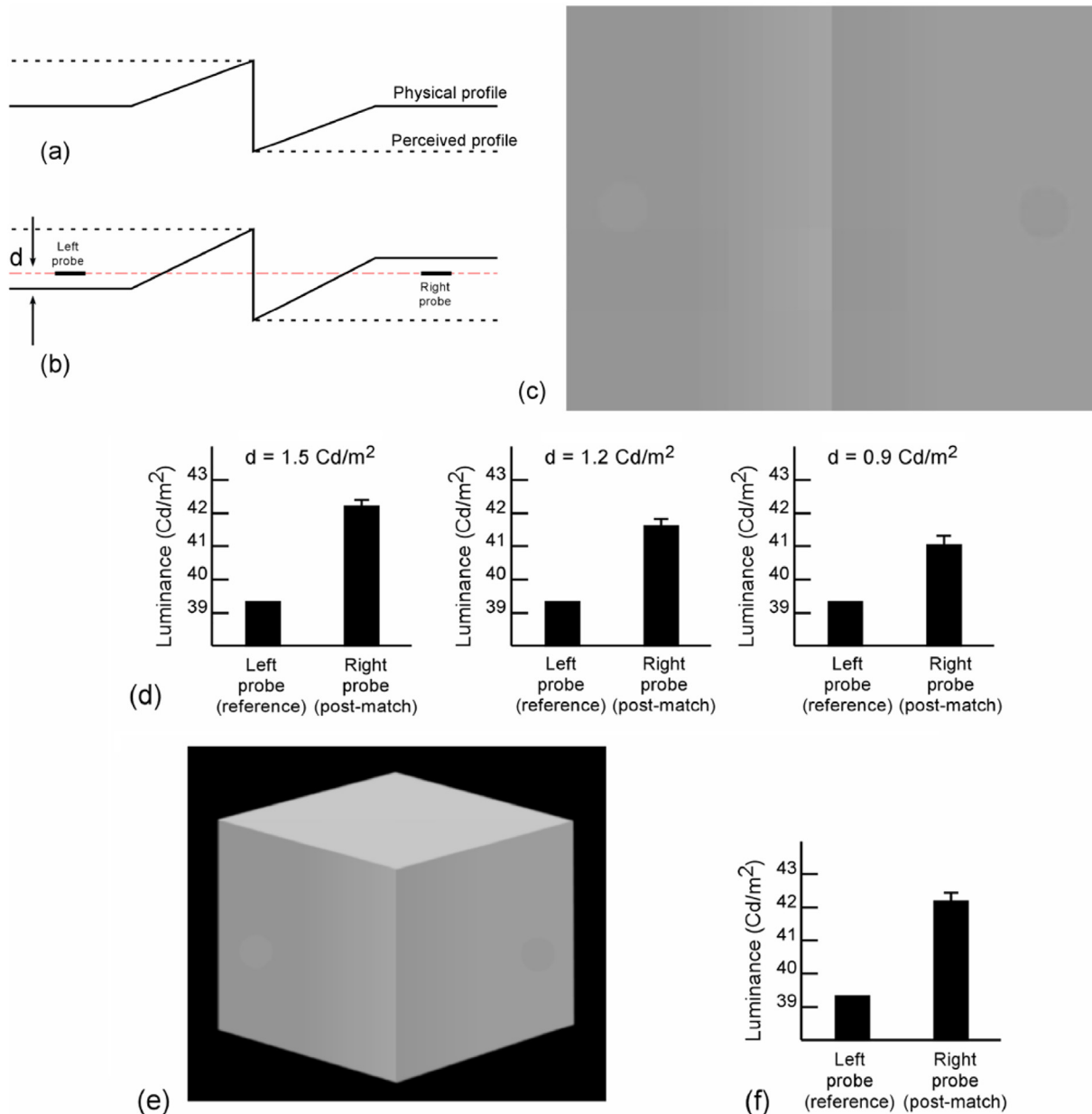


Fig. 3. (a) Intensity profile across a conventional Craik-O' Brien-Cornsweet (COBC) display. (b) The flanks in our display differed from each other so that the side perceived as dark actually had higher luminance than the other. Two identical probes with their luminance set at the mean value of the flanks' luminances were placed one on each flank. (c) The appearance of the display used in our experiments. The probe on the seemingly lighter flank is perceived as being lighter than the one on the darker flank. (d) Brightness matching results from five participants for three values of inter-flank luminance difference. (e) A variant of the modified COBC display shown in (c). The two fields are now interpreted as differently illuminated faces of a three-dimensional cube. The probe on the right face, which is perceived to be in shadow, is seen as being darker than the other – a result that runs counter to predictions from high-level accounts. (f) Brightness matching results with the COBC display shown in (e). Error bars represent ± 1 standard error.

could overwhelm the low-level influences if the latter were weakened by reducing the luminance difference between the flanks. As Fig. 3d shows, for all values of luminance difference tested, the perceived brightness of the probe squares remained consistent with low-level factors. The results stayed unchanged even with variants of the display in Fig. 3a, designed to permit an easy interpretation in terms of the scene's three-dimensional characteristics and illumination distributions (Fig. 3e and f).

Taken together, results from study 1 establish the role of low-level factors in determining brightness percepts. Study 2 sought to more precisely localize these processes.

2.2. Study 2: Constraining the locus of processing underlying simultaneous brightness contrast

We used dichoptic presentations to determine whether brightness in our displays was computed prior or subsequent to binocular information fusion. The logic of the experiment was as follows: Subtly different images were presented to the two eyes, leading to a fused non-rivalrous cyclopean percept that was different from the image in either eye individually. Pairs of equi-luminant probe discs were flashed transiently in one or the other eye. In this setting, we determined whether the brightness percept of the disc pair was consistent with the cyclopean view (which would indicate that the underlying brightness computation happens after information-fusion from the two eyes) or with the

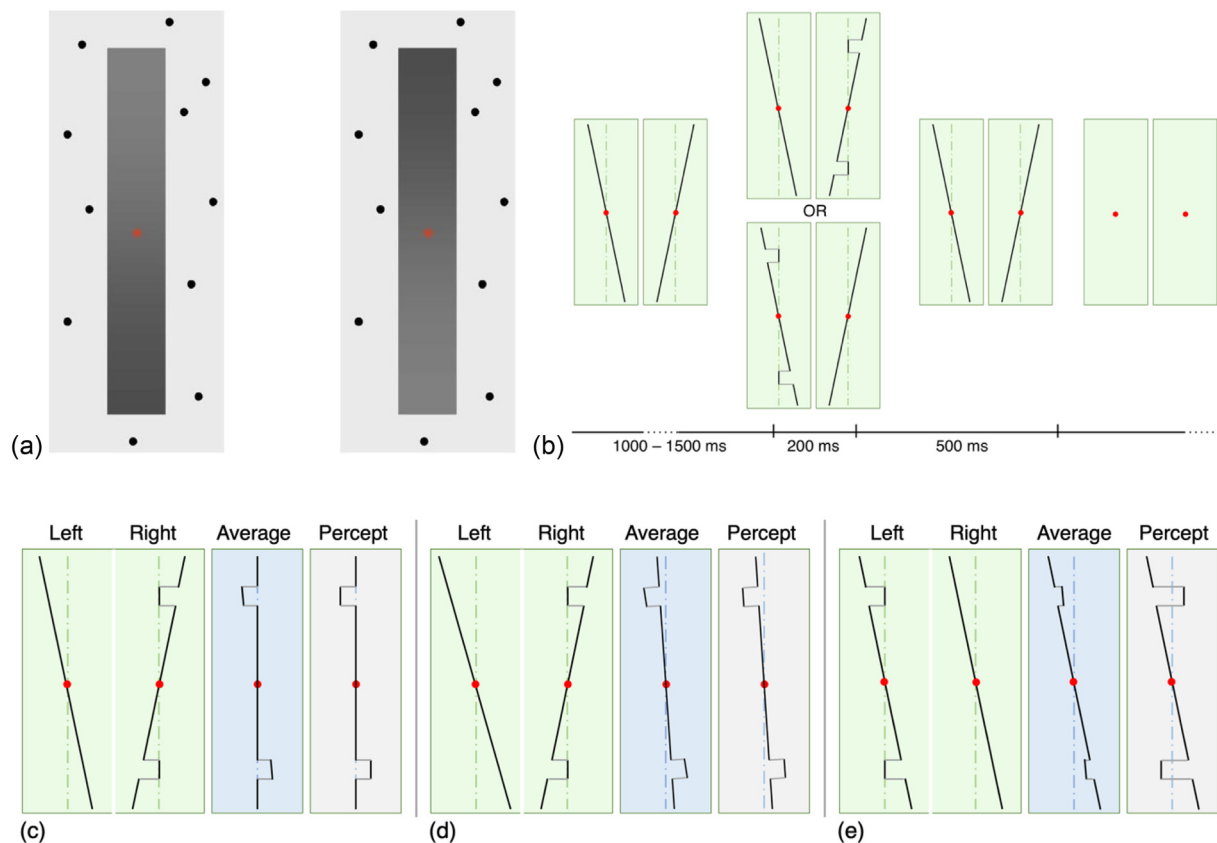


Fig. 4. (a) General appearance of the stereo display used in our experiments. A stereo function allowed a different gradient to be presented to each eye while a subject was wearing NVIDIA 3D Vision stereo goggles. The stimulus was shown to subjects on an ASUS VG278He monitor from a distance of 60 cm. The counter-aligned gradients spanned a luminance range from 33 cd/m² to 43 cd/m². The probes had a luminance of 38 cd/m². The display vertically subtended 10 degrees of visual angle. Subjects were asked to fixate on the red cross. The luminance gradients in this image have been enhanced for the purpose of exposition. (b) Temporal structure of each trial. The solid black lines in each panel represent image intensity profiles. A trial began with the basic stereo display showing the two strips. Next, a pair of equi-luminant probe discs were transiently superimposed on one of the stereo-half images. (c, d) Percepts obtained with oppositely directed luminance gradients equal (c) or unequal (d) in magnitude are qualitatively consistent with binocular averaging accounts. (d) With two *iso*-directed gradients, the binocular averaging account predicts brightness percepts that are at odds with the actual percept obtained. As shown in the schematic profiles, the averaging account predicts the relative brightness of the two probes to be in the opposite direction from what is actually perceived. (Note that in the schematic for the obtained percept in panels c and d, we have not indicated a gradient within the probes because the subjects' task was simply to report the relative brightness of the two probes.) (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

monocular image on which the disc-pair was superimposed (indicating that brightness computation precedes binocular fusion). The latter possibility is especially interesting since an observer, while experiencing the cyclopean percept, would not be aware of monocular image content of either eye, or even know in which eye the disc-pair had been flashed (Baker, 2017).

Fig. 4a depicts the experimental display. Each of the left and right stereo-halves comprised a rectangular strip surrounded by an identical pattern of dots, which facilitated steady binocular fusion. The two strips were given shallow luminance gradients, identical in magnitude but opposite in direction. Upon binocular fusion, these gradients were merged in the cyclopean view and the resulting strip appeared perceptually homogenous. As depicted in Fig. 4b, in each trial, two identical probe patches with luminance equal to the midpoint of the strip gradients, were displayed briefly (200 ms), on either the left or the right strip, equidistant from the strip center (both probe patches were located on the same strip). The subject's task was to report whether the two probes looked identical or different, and if the latter, then to indicate which probe had appeared brighter. The left–right ordering of the stereo-halves and which side the probe patches appeared on were independently randomized across presentations. It is worth noting that the probe discs' luminance was so close to the mean strip luminance, and the gradients were so shallow, that the disc-flash did not induce a change of overall image luminance, even locally, enabling stability and

maintenance of fusion. In other words, at the time of the probe discs presentation, the percept is not that of a change in the entire strip; the background stays stable, but the percept additionally includes the two probe discs.

Twenty two subjects (mean age: 18.5 years), naïve as to the purpose of the study and different from those of study 1, participated in this experiment. They viewed the stereo displays using LCD shutter glasses. We first verified whether subjects did indeed perceive a rectangle of uniform brightness in the cyclopean view when presented with equal but opposite gradients in the stereo halves. To this end, we compiled a set of 40 trials wherein half had equal but opposite gradients in the stereo pairs, while the other half had oppositely directed gradients of unequal magnitude. Using one of three keys, subjects were asked to report if they perceived the top or bottom of the rectangle as being darker, or the entire rectangle as being of uniform brightness. Results showed that when fusing equal, but opposite gradients, subjects perceived a rectangle with homogenous brightness in the cyclopean view, while when presented with unequal and oppositely directed gradients, subjects' cyclopean percepts were consistent with the stronger of the two gradients ($\chi^2 = 128.94$; $p < 0.001$).

Next, we presented trials with transient superimposition of a pair of equi-luminant discs on one of the stereo-halves when the two oppositely directed gradients were equal in magnitude. For each trial, subjects were asked to report if they perceived the top or bottom disc as

darker, or whether the two appeared equally bright. Each subject saw 60 such displays, with the side on which the probe pairs were presented as well as the left–right position of the stereo-halves randomized across the trials.

Results showed that the physically equi-luminant probe discs, superimposed on a seemingly homogenous background, were perceived by the subjects as having different brightness (Fig. 4c). There was a highly significant concordance between the subjects' choice of the seemingly darker disc and its physical background in the monocular image on which the probe-pair had been transiently superimposed ($\chi^2 = 544.157$; $p \ll 0.001$). The disc placed on the darker section of the gradient was consistently reported to be the brighter of the pair, even though participants were perceptually unaware of there being gradients in the stereo halves.

The finding that luminance structure in monocular images, despite not being evident in the cyclopean view, determines the eventual brightness percept of the probe discs, suggests that brightness in these displays is estimated prior to binocular information fusion. This conclusion also derives support from an additional study we conducted with stereo-halves that had oppositely directed gradients of *unequal* magnitudes. In the condition of unequal gradients on the two strips, binocular fusion occurs with contributions from both eyes, not rivalry. Such fusion in the presence of differences in monocular image contrast has been studied previously by, among others, Legge (1984), Legge and Gu (1989), Wilson (2017) and Riesen, Norcia, and Gardner (2019). From baseline tests with this condition, described above, we know that a gradient in the direction of the steeper monocular one is evident in the cyclopean view.

This sets up a clear test of whether the brightness of superimposed probes is governed by monocular luminance information or the fused cyclopean view. Since the cyclopean gradient is in opposite direction relative to the shallower monocular gradient, the two make converse predictions regarding which of the two probe-discs should appear darker when superimposed on the shallower monocular gradient. All subjects were presented 60 trials of this 'opposite and unequal' gradients condition (Fig. 4d). Results showed a significant association between the subjects' response and the disc predicted to be darker based on the gradient on which the disc-pair was placed ($\chi^2 = 590.087$; $p \ll 0.001$). Thus, subjects' brightness percepts were consistent not with the gradient evident in the cyclopean view, but the monocular gradient on which the disc-pair actually appeared.

An alternative explanation to consider is that rather than brightness being computed on monocular information, it may arise from an averaging of the two monocular signals (Fig. 4c). To test this possibility, we conducted an additional study. Instead of using oppositely directed gradients, the displays in this test comprised gradients in the same direction. In this condition, as illustrated in Fig. 4e, the averaging based hypothesis makes a prediction regarding the brightness ordinality of the probe discs opposite of that based on monocular computation. Six subjects participated in this test and were shown 60 trials each. Their responses regarding which of the two probe discs was darker were consistent with the monocular computation hypothesis rather than binocular averaging ($\chi^2 = 305.422$; $p \ll 0.001$). (It is worth noting that although the subjects in our study were asked to make relative brightness assessments of the two probe disks, Gilchrist (2014) has argued that such appraisals may be better thought of as lightness rather than brightness judgments).

These results strongly support the hypothesis that the simultaneous brightness contrast phenomenon may be based on 'low-level' mechanisms that are situated prior to the stage of binocular information fusion. These results make a prediction. Given how early in the visual pathway these processes appear to be located, we would expect that they will be instantiated innately without needing to be learned over the course of an individual's visual experience. Testing this prediction requires determining whether susceptibility to the brightness induction illusion is evident early in the visual developmental timeline, before

commencement of visual experience. This is the goal of study 3.

2.3. Study 3: Investigating the role of visual experience

The youngest infants in whom simultaneous brightness contrast has been studied were 4 months old (Pereverzeva & Teller, 2009; Yang, Kanazawa, Yamaguchi, & Kuriki, 2013). Although these infants were found to be susceptible to the simultaneous contrast phenomenon, the data do not permit any definitive conclusions to be drawn regarding the validity of the empiricist or nativist accounts. While the youth of the participants might appear to argue in favor of a nativist account, four months of experience constitutes a substantial amount of visual information that can subserve an empirically driven mechanism.

Our studies with a group of participants who have unique visual profiles have provided a way to address the empiricism-nativism debate. As part of Project Prakash (Sinha & Held, 2012; Sinha, 2013), we tested nine children ranging in age from 8 to 17 years (mean: 12.1 years), who had been treated for blindness due to dense bilateral congenital cataracts (participant details in supplementary information section). Determination of congenitality was based on multiple factors, as described in (Ganesh et al., 2014). Each child underwent cataract removal surgery and an intraocular lens implant. All were tested within 48 h after first eye surgery. 9 normally-sighted children (age range: 6–18 years; mean: 11.9 years) participated as controls. The stimuli comprised seven displays; all had a vertical or horizontal luminance gradient, superimposed on each of which were two small discs. In two displays, the disc-pair had an actual luminance difference (and was placed transverse to the gradient orientation, so that both discs in the pair were on the same background luminance), while in the remaining five, the discs were equi-luminant. In each display, the subjects' task was to point to the disc that appeared darker. No feedback was provided to the subjects.

As expected, control subjects were susceptible to the illusion, and all nine of them responded identically. In each of the five displays with equi-luminant discs, they reported the disc on the more luminous side of the background gradient to be darker. In the remaining two, they reported the disc with the lower luminance as darker. These control data formed the baseline against which to consider the responses of the newly sighted children. On the two displays with discs of physically different luminosities, all Prakash children pointed to the actually dimmer disc as the darker one, demonstrating that they understood the task and could make brightness judgments. Of critical interest to us were their brightness judgments in the five displays with equi-luminant disc pairs.

If these judgments in control children were driven by a learned understanding of scene structure, or of how illumination interacts with surface albedo to generate the observed image intensities, we would expect responses of the newly-sighted children, who have not had the benefit of extended visual experience, to be physically veridical and thus inconsistent with the control subjects' choices. However, the data reveal that newly-sighted children behave akin to the control group in their choices (Fig. 5). Eight of the children in the experimental group had exactly the same choices across the five displays as the control group; one child had the same choices for four of the five displays. The concordance of the eight children is statistically significant at an individual level (likelihood of chance-driven concordance of a set of five responses to control derived set: $p < 0.05$), as is the pooled data across all nine children ($p \ll 0.001$).

Thus, even at the very outset of their post-operative experience, Prakash children already exhibit susceptibility to the simultaneous brightness contrast illusion, indicating that this susceptibility is based not on an individual's learned contingencies about the visual world (Helmholtz, 1867; Lotto & Purves, 2000), but rather on processing mechanisms with which the brain comes innately prepared. We recently reported that some geometric illusions that have been believed to arise as a consequence of learning about associations between 2D image

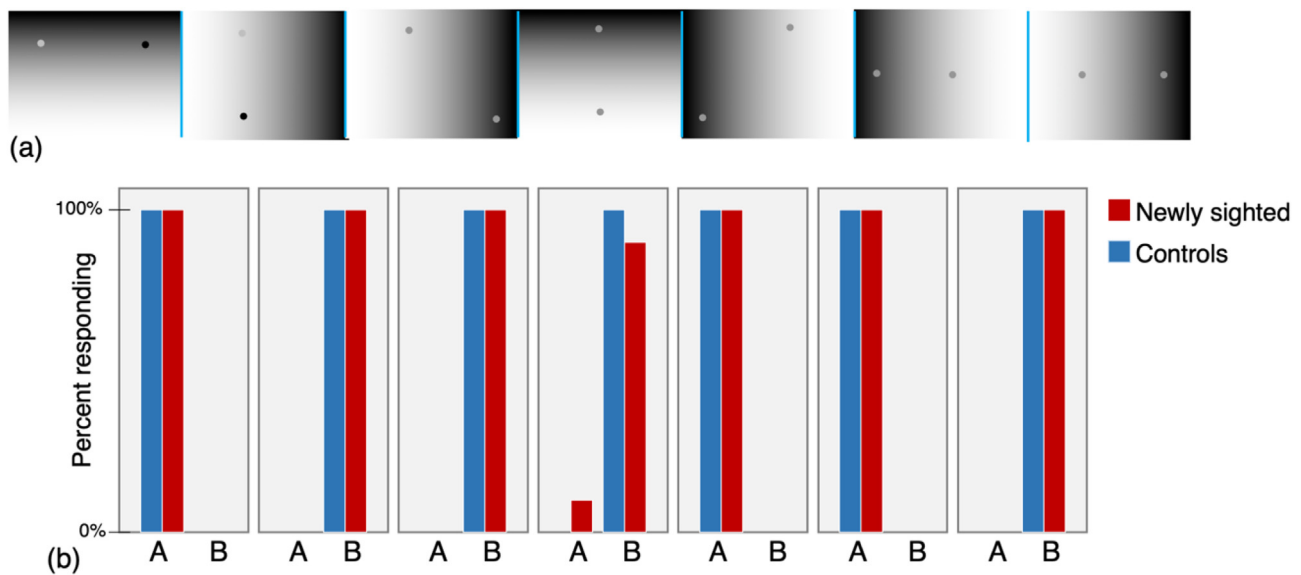


Fig. 5. (a) Displays used in our studies with newly-sighted children. For each display, children had to indicate which of the two small discs appeared darker. Discs in two displays (here the two leftmost ones) had a physical luminance difference. Disc pairs in the remaining displays were equiluminant. (b) Results from newly sighted and controls on seven displays. In each display, the two probes were arbitrarily labeled 'A' and 'B' for result recording (subjects were unaware of this labeling). The plots show percent of controls and newly sighted who chose one or the other probe as being brighter. Notably, the choices are almost entirely concordant across the two groups.

cues and 3D environmental structures, may also be driven by innate mechanisms (Gandhi, Kalia, Ganesh, & Sinha, 2015). These findings are especially interesting in the context of past studies of late sight onset which have shown that the newly-sighted have difficulty with interpreting scene images in terms of their three-dimensional layout (Fine et al., 2003; Ostrovsky, Meyers, Ganesh, Mathur, & Sinha, 2009). This reinforces the inference from the first two studies that susceptibility to the simultaneous contrast illusion likely does not depend upon a sophisticated spatial analysis of the scene.

3. Discussion

Results from the three studies above provide strong converging evidence that the simultaneous brightness contrast phenomenon is based on innately-specified 'low-level' mechanisms that are situated prior to the stage of binocular information fusion. Specifically, data from the first study show that luminance differences, even though perceptually unseen, contribute to brightness estimation. By allowing independent manipulation of the image cues relevant for 'low-level' and 'high-level' mechanisms, our displays have enabled us to investigate the trade-offs between these different kinds of explanations. The results suggest that brightness percepts in our experiments are engendered by mechanisms that are seemingly impervious to high-level percepts. Results from the second study using binocular displays with mismatched monocular components demonstrate that information from the two eyes independently influences subjects' brightness percepts. Notably, observers' brightness reports are best accounted for by the individual monocular components that may not themselves be perceptually evident, rather than by the fused cyclopean percept. We are led to conclude that the mechanisms underlying simultaneous brightness contrast are located at a stage of visual processing that precedes binocular information fusion. Finally, findings from the third study showing susceptibility of congenitally blind children to the simultaneous brightness contrast illusion immediately post-treatment suggest that this phenomenon is engendered by innately specified neural mechanisms, without requiring an individual to accumulate natural statistics through perceptual experience. Taken together, these results place significant constraints on admissible accounts of brightness perception. They rule out explanations that rely on purely high-level

mechanisms and are most compatible with low-level accounts of simultaneous brightness contrast.

How might one reconcile our findings with past work emphasizing higher-level influences (Koffka, 1935; Knil & Kersten, 1991; Adelson, 1993; Gilchrist et al., 1999; Lotto & Purves, 2000; Paradiso, 2000) in brightness perception? One possibility is that the operation of low-level factors may be evident in 'simple' displays such as the classical simultaneous contrast illusion, but in more complicated stimuli, such as those designed by Adelson (1993, 2000) or Agostini and Proffitt (1993), higher-level factors take precedence. However, in the absence of a clear definition of stimulus complexity, there is a degree of arbitrariness in this account, which makes it hard to falsify. For the sake of parsimony, we consider an alternative possibility. This is motivated by the observation that for almost all displays developed so far, the 'sign' of the illusion (which of two equiluminant regions in a display is perceived to be the brighter one) is consistent with predictions from low-level mechanisms. However, the magnitude of brightness illusion can potentially be modulated by the inclusion of cues that facilitate high-level interpretations of transparency, illumination and grouping. According to this hypothesis, then, low-level factors take precedence in determining the basic sign of brightness percepts with higher-level factors exerting a modulatory influence on the magnitude. The extent of the modulation is limited so as not to invert the sign specified by low-level factors. While this working hypothesis appears consistent with percepts associated with many experimental stimuli, it proves inadequate for some notable exceptions. Specifically, 'reverse contrast' displays, as their name suggests, invert the sign of brightness percepts relative to what low-level accounts would predict. Prominent examples include White's illusion (White, 1981) and Bressan's 'Dungeon illusion' (Bressan, 2001). While low-level accounts have been proposed for such displays (Blakeslee & McCourt, 1999), their explanatory power has been questioned (Agostini & Galmonte, 2002; Economou, Zdravkovic, & Gilchrist, 2015), in favor of mid-level accounts that are based on gestalt grouping cues. It is fair to say that we now have compelling evidence for the operation of both low and high-level factors as determinants of brightness percepts, but a unified account is still elusive. What we hope the present work has demonstrated is that such an account will likely need to incorporate mechanisms that can be instantiated early in the visual pathway and are innate in their genesis.

CRedit authorship contribution statement

PS: Conceptualization, Formal analysis, Funding acquisition, Investigation, Writing - original draft, Writing - review & editing. **SC:** Formal analysis, Investigation, Writing - original draft, Writing - review & editing. **TG:** Investigation, Writing - review & editing. **DR:** Investigation, Writing - review & editing. **AS:** Investigation, Writing - review & editing. **SG:** Investigation, Writing - review & editing. **UM:** Investigation, Writing - review & editing. **PB:** Formal analysis, Writing - review & editing.

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