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## Perceptual consequence of normalization revealed by a novel brightness induction

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### ABSTRACT

The human brain is renowned for its dynamic regulation of sensory inputs, which enables our brain to operate under an enormous range of physical energy with sensory neurons whose processing range is limited. Here we present a novel and strong brightness induction that reflects neural mechanisms underlying this dynamic regulation of sensory inputs. When physically identical, stationary and moving objects are viewed simultaneously, the stationary and moving objects appear largely different. Experiments reveal that normalization at multiple stages of visual processing provides a plausible account for the large shifts in perceptual experiences, observed in both the stationary and the moving objects. This novel brightness induction suggests that brightness of an object is influenced not only by variations in surrounding light (i.e. simultaneous contrast) but also by dynamically changing neural responses associated with stimulus motion.

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### 1. Introduction

Decades of research reveals that subjective experience of brightness involves complicated neural processing that takes into account illumination (Schirillo & Shevell, 1997), surface reflectance (Gilchrist et al., 1999), spatial and temporal relation between an object and its context (Adelson, 1993; De Valois et al., 1986; Gilchrist, 1977; Schirillo, 1999; Todorovic, 1997). Theories of brightness posit that computation of brightness of an object involves both contrast between the object and its adjacent surround, and also between the object and remote surround (Hong & Shevell, 2004a; Rudd & Arrington, 2001; Shapley & Reid, 1985; Shevell, Holliday, & Whittle, 1992).

Normalization is important in processing spatial contrast by adjusting the neural response of an object depending on its surrounding context (Barkan, Spitzer, & Einav, 2008; Blakeslee & McCourt, 1999, 2004) by computing a ratio between the response of an individual neuron and the summed activity of a pool of neurons (Carandini & Heeger, 2012). For example, retinal ganglion cells respond to the same object much less in a high-contrast than in a

low-contrast environment (Shapley & Victor, 1978). Since the summed activity of the object and the surrounding environment is higher in the high-contrast than in the low-contrast environment, the neural response of the object is reduced when divided by the summed activity obtained in the high-contrast environment.

We here report a novel brightness induction in which brightness of objects is modulated by simply setting some of them in motion and propose that normalization can explain several characteristics of this brightness induction. Observers viewed one set of stationary black dots presented on a white background and another set of black dots orbiting around those stationary dots (Fig. 1a). Despite the same physical characteristics of the stationary and moving dots in their light intensity, size and physical contrast, the stationary black dots appeared gray (Fig. 1b). This induced brightness perception was robust and strong in that observers perceived a large shift in brightness immediately after the onset of the motion and the changed brightness continued as long as the motion lasted. The results from a series of experiments suggest that this large shift in brightness of the stationary dots can be understood within a framework of contrast normalization.

### 2. Materials and methods

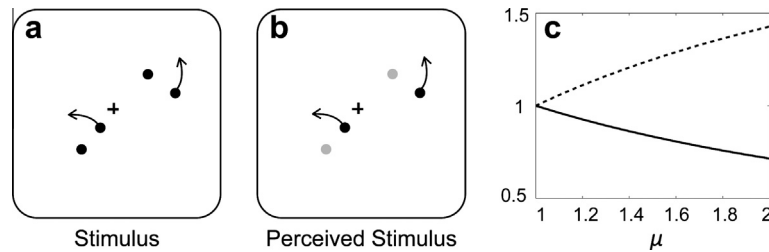
#### 2.1. Participants

From Experiment 1 to Experiment 4, seven observers (6 naïve) who had normal or corrected-to-normal vision participated in

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**Fig. 1.** Illustration of stimulus and perceptual experience of brightness induction by motion in context. (a) Schematic illustration of stimuli. Two pairs of the stationary and moving dots (diameter  $0.25^\circ$ ) were presented against the 'white' background ( $70 \text{ cd/m}^2$ ). The stationary dots were presented  $2^\circ$  away from the fixation cross ( $0.25^\circ \times 0.25^\circ$ ) and each moving dot was presented  $1.0^\circ$  away from the paired stationary dot. The positions of the stationary dots were randomized in each trial but separated equally by  $180^\circ$  in polar angle. The speed of moving dots was 2 cycle/s in the counterclockwise direction and initial positions of those four moving dots were randomized in each trial. (b) Schematic illustration of perceived stimuli. The stationary dots appear gray when paired dots are orbiting around them. (c) Response of the stationary (solid line) and the moving (dotted line) dots obtained from Eq. (1). In the equation,  $\sigma$  is set to 0.5;  $\alpha$  is set to 2.5;  $C_M$  and  $C_S$  is set to 1.

the experiments. One observer who could not make binocular fusion did not participate in the experiment with binocular stimulus presentation. Otherwise, all seven observers participated in all experiments. Seven, naïve observers were additionally recruited for Experiment 5. All participants provided the informed consent approved by Florida Atlantic University Institutional Review Board.

## 2.2. Stimulus and procedure

Stimulus presentation on a Sony CPD-G520, 21" CRT monitor (100 Hz frame rate) and the collection of behavioral responses were controlled by the Psychophysics Toolbox (Brainard, 1997; Pelli, 1997). Stimuli were presented in a dark room to observers positioned 90 cm from the CRT monitor whose luminance was linearized from 'black' ( $0.5 \text{ cd/m}^2$ ) to 'white' ( $70 \text{ cd/m}^2$ ). The whole display was  $1024 \times 768$  pixels, and 1-degree of visual angle was covered by 45 pixels. Pairs of the stationary and moving dots (diameter  $0.25^\circ$ ) were presented against the 'white' background ( $70 \text{ cd/m}^2$ ). Two pairs of dots were presented at the opposite side of fixation in most experiments to reduce subjects' gaze-shifts. In some experiments, we presented either one pair or four pairs of dots (specific reasons are described in each experiment). The stationary dots were presented  $2^\circ$  away from the fixation cross and the moving dots were presented  $1.0^\circ$  away from the paired stationary dots (except where the distance between the stationary and the moving dots was an independent variable). The positions of the stationary dots were randomized in each trial but separated equally in polar angle. The speed of the moving dots was 2 cycle/s (except where the speed of moving dots was an independent variable) in the counterclockwise direction and initial positions of moving dots were randomized in each trial.

Brightness of the stationary and the moving dots was measured by a memory based choice task. In each trial, all dots were presented at their initial locations for 1 s. Then, the moving dots started orbiting around the stationary dots, and the presentation of both stationary and moving dots lasted 2 s (except where the presentation time was an independent variable). The physical luminance of the stationary and the moving dots was identical for each trial and if not stated otherwise, we set the luminance of dots at  $7.5 \text{ cd/m}^2$  (higher than the lowest luminance level of the monitor) to measure possible changes in brightness of the moving dots. A sound cue, high or low pitch, was provided to indicate the brightness of which dot (either stationary or moving) had to be reported. To measure the brightness of the cued dots, a circular array of 20 luminance patches (dots with the same size of the stimuli) was presented  $2^\circ$  away from the fixation after the stimulus offset. The luminance of the dot array increased linearly from 'black' to 'white' in the counterclockwise direction and the position of the 'black' dot was randomized. Ten trials were given for each

condition. Observers chose one of the 20 dots, which they believed the closest to the brightness of the cued dots, by clicking the dot with a computer mouse. In the baseline condition, the same configuration of the stimulus was presented for 2 s except all dots were stationary. Observers, therefore, reported the brightness of the stationary dots.

## 3. Results

### 3.1. Experiment 1: Perceptual consequence of normalization

Since the brightness induction reported here is a novel observation, it is necessary to characterize the phenomenon. To quantify the magnitude of brightness induction, we devised a memory-based choice task, in which observers reported the brightness of either the stationary or the moving dots. When both the stationary and the moving dots were black against a white background (Fig. 1a), the stationary dots appeared gray (Fig. 1b), and the estimated change in brightness was more than one log unit greater in light intensity (physical luminance:  $0.5 \text{ cd/m}^2$ , matched luminance:  $8.6 \text{ cd/m}^2$ ).

How then can simple stimulus motion in the context alter the appearance of the stationary dots? We propose that normalization (Heeger, 1992) – a computational account controlling gain of neural responses – can explain several characteristics of this brightness induction. Specifically, the Eq. (1) below describes the neural response of the stationary ( $S$ ) and the moving ( $M$ ) dots. The neuron's contrast response  $C$  increases with the luminance difference between the dot and the background;  $\mu$  is the speed of the moving dot, which equals to 1 when stationary;  $\sigma$  is the semi-saturation constant and  $\alpha$  determines the attainable maximum response. Once the motion signal is introduced to half of the dots ( $\mu > 1$ ), the contrast responses to the moving dots are amplified by the magnitude of motion signal while the neural responses elicited by both the stationary and the moving dots are divided by the sum of their total responses.

$$R_S = \alpha \frac{C_S}{\sigma + C_S + \mu C_M} \quad \& \quad R_M = \alpha \frac{\mu C_M}{\sigma + C_S + \mu C_M} \quad (1)$$

Fig. 1c shows the  $R_S$  (solid line) and  $R_M$  (dotted line) as a function of  $\mu$ , which demonstrates the perceptual shifts of both the stationary and the moving dots compared to when both were stationary where  $\mu$  equals to 1. Consequently, the brightness of the stationary dots and the brightness of the moving dots should shift away from each other due to amplification induced by motion signal.

To characterize the brightness shifts of the stationary and the moving dots from their initial presentation, where all dots were stationary for 1 s, we set the luminance of dots at  $7.5 \text{ cd/m}^2$ , so that

any shift in brightness of stationary and moving dots could be detected. In addition, observers performed the base condition, in which all dots were stationary, to measure the brightness of those initial 1-s presentation of the stationary dots before motion signal was introduced. Results showed that the appearance of the stationary dots shifted toward the background, and the appearance of the moving dots shifted away from the background. One-way ANOVA with planned contrast analysis reveals that, the stationary dots appeared brighter than the base ( $F(1,6) = 75.51, p < .001$ ), and the moving dots appeared darker than the base ( $F(1,6) = 6.82, p < .05$ ) when they were presented on a white background (Fig. 2a). This is consistent with the prediction of normalization in that both the stationary and the moving dots change their brightness once half of the stationary dots set in motion.

More importantly, if normalization operates on the contrast, not on the brightness of dots per se, shift in brightness should be observed in an opposite direction when the luminance of the background is reversed. We tested this prediction by presenting the same dots on a black background (Fig. 2b). The result showed that the moving dots appeared brighter than the base ( $F(1,6) = 17.86, p < .01$ ), and the appearance of the stationary dots was not significantly different from the base ( $F(1,6) = 1.82, p = .22$ ). This result clearly demonstrates that the contrast normalization mediates changes in brightness of both stationary and moving dots.

### 3.2. Experiment 2: Perceptual shift increases with stimulus motion speed

This large shift in brightness can also be induced by presenting a set of dots flickering (10 Hz) at random locations over time, indicating that a smooth, orbiting motion is not essential. A planned contrast test between the random flicker condition and the base, brightness measured for a stationary dot presented in isolation, revealed significant difference ( $F(1,6) = 16.82, p < .01$ ). However, flickering dots at fixed locations were not sufficiently potent to induce a strong brightness illusion, resulting in no significant difference between the fixed flicker and the base conditions ( $F(1,6) = .78, p = .413$ ). These results mean that spatiotemporal changes are critical in inducing this novel brightness illusion, which is consistent with the explanation based on normalization because position changes increase number of neurons activated by dots in context, whose responses are then pooled together. Consistently, we found that the magnitude of brightness illusion increased monotonically and reached an asymptote quickly with increasing velocity of the moving dots (Fig. 3;  $F(3,18) = 5.77, p < .01$ ).

### 3.3. Experiment 3: Neural adaptation as an alternative explanation

One might think that bright induction reported here can be accounted for by neural adaptation. The stationary objects fatigued

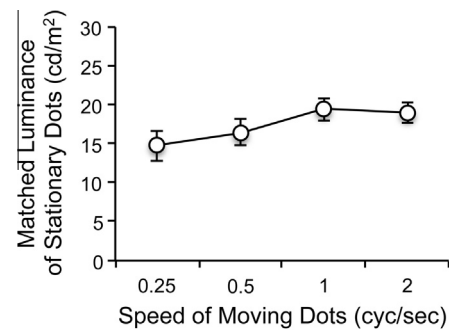


Fig. 3. Matched luminance of stationary dots as a function of the speed of moving dots. Error bars indicate  $\pm 1$  S.E. of the between subjects.

neural tissue resulting in apparent contrast reduction, whereas the moving objects stimulate unaffected neurons in different receptive fields resulting in apparent contrast increment (Blake-more, Muncey, & Ridley, 1971). We tested the neural adaptation account by varying the duration of stimulus presentation. This is because normalization of contrast response can occur within tens of milliseconds of stimulus onset (Shapley & Victor, 1981; Tsai, Wade, & Norcia, 2012; Victor, 1987; Yeh, Lee, & Kremers, 1996) whereas neural adaptation is slow, requiring a couple of seconds (Blakemore, Muncey, & Ridley, 1971). The result shows that the magnitude of brightness induction was not affected by the duration of stimulus presentation (Fig. 4). Observers clearly perceived large shifts in brightness of the stationary dots even when stimulus was presented for 500 ms. Furthermore, the magnitude of the brightness induction did not significantly change when the exposure duration increased up to 4 s, indicating that it is difficult to explain this brightness induction based on neural adaptation.

### 3.4. Experiment 4: Neural locus of brightness induction from motion

Contrast normalization occurs in multiple levels of visual processing from in retina (Shapley & Victor, 1978; Victor, 1987), in sub-cortical regions including LGN (Felisberti & Derrington, 1999) and in cortical level (Dhruv et al., 2011; Gardner et al., 2005; Ohzawa, Sclar, & Freeman, 1985; Truchard, Ohzawa, & Freeman, 2000). We first tested whether the shift in brightness of the stationary and the moving dots occurred before or after the binocular summation by measuring brightness while one stationary dot was presented to one eye and one moving dot was presented to the other eye. We reduced the number of dot pairs to avoid possible suppression of the stationary dots induced by the moving ones by interocular presentation. If retinal and sub-cortical contrast gain-control is responsible for mediating the brightness induction reported here, there should be no shift in brightness with this interocular setting.

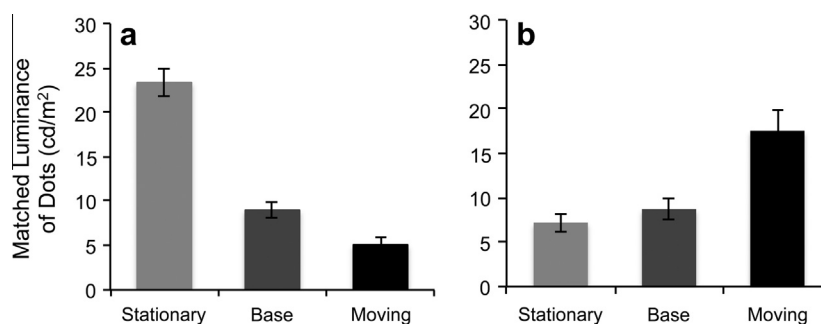
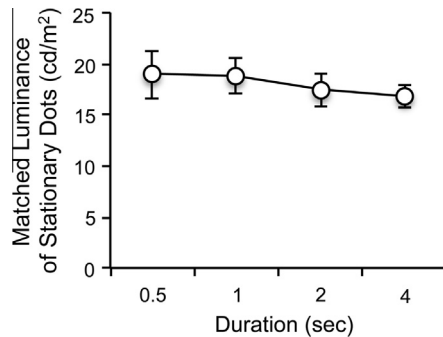


Fig. 2. Result of the memory-based brightness matching task. (a) Matched luminance of the stationary dots (light gray bar) and the moving dots (black bar) when the background luminance was  $70 \text{ cd/m}^2$ . The base (dark gray bar) represents the matched luminance when no moving dot was presented. (b) Same as (a) but when background luminance was  $0.5 \text{ cd/m}^2$ . Error bars indicate  $\pm 1$  S.E. of the between subjects.



**Fig. 4.** Matched luminance of the stationary dots as a function of duration of stimulus presentation. Error bars indicate  $\pm 1$  S.E. of the between subjects.

We, however, found a comparable size in the brightness induction when the stationary and the moving dots were presented to the two eyes separately (Fig. 5a). For comparison, only one pair of dots was used in binocular condition, in which both the stationary and the moving dots were presented to both eyes as in other experiments. A planned contrast test reveals that there was no significant difference between the interocular and the binocular viewing conditions for the stationary dots ( $F(1,5) = 1.00$ ,  $p = .36$ ) and also for the moving dots ( $F(1,5) = 0.01$ ,  $p = .97$ ). This result indicates that cortical mechanism mainly contributed to the shift in brightness induced by motion in context.

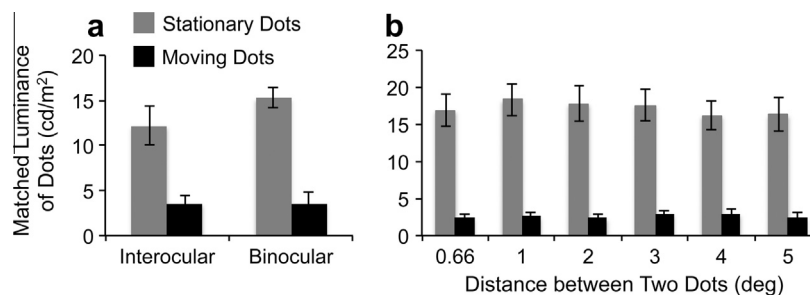
We then tested the spatial range of brightness induction from motion in context by systematically varying the distance between the stationary and the moving dots. Here we used only one pair of dots to probe spatial range as large as possible. The range of interaction has been used to probe the neural locus in visual processing based on the fact that the size of receptive field increases over the visual processing stream (Smith et al., 2001; Zeki, 1978). The magnitude of brightness induction did not change while the distance between the stationary and the moving dots was varied from  $0.66^\circ$  up to  $5^\circ$  (Fig. 5b,  $F(5,30) = 1.318$ ,  $p = .28$ ). The spatial range of brightness induction observed here is much larger than the spatial range of induction that can be explained by integration of adjacent and remote contrast (Hong & Shevell, 2004b; Rudd & Zeman, 2004). It is tempting to interpret that the brightness induction occurred in MT based on the fact that this brightness induction was accompanied with the stimulus motion. Further, the receptive field size of MT can be as small as  $4^\circ$  (Felleman & Kaas, 1984) while there was no modulation in the magnitude induction up to  $5^\circ$  in this experiment. However, we also acknowledge that the range of spatial pooling of signals in retinal circuitry can extend  $2\text{--}10^\circ$  (Demb et al., 1999; Freed et al., 1996). It has also been shown that reduction in contrast gain can be induced by long-range (over  $5^\circ$

visual angle) in the lateral geniculate nucleus of cats (Felisberti & Derrington, 1999). The long-range spatial pooling and interaction can also account for the extent of interaction shown in Fig. 5b. At least, comparable shift in the brightness induction between the interocular and the binocular viewing conditions, and across varying distance between the stationary and the moving dots suggests that cortical mechanisms play a major role in the brightness induction accompanied with stimulus motion.

### 3.5. Experiment 5: Contribution of higher cognitive processes on the brightness induction

We examined whether high-level cognitive processes are also involved in the brightness induction by stimulus motion. In particular, attention can be a possible candidate in the context of normalization. Specifically, if moving dots draw attention from stationary dots as a bottom-up manner, the perceived contrast of the moving dots should increase whereas the perceived contrast of the stationary dots should decrease (Carrasco, Ling, & Read, 2004; Herrmann et al., 2010). In turn, changes in contrast response can alter brightness of dots in the current study. To test this hypothesis, with all new seven observers, we directly measured the influence of attention using the well-established cueing paradigm. For half of the trials, the auditory cue, indicating which set of dots (stationary vs. moving) to be reported, was presented before the stimulus onset (pre-cue). For the other half of the trials, the auditory cue was provided after the stimulus offset (post-cue). These two cueing conditions were randomly intermixed and observers were notified the type of cue ahead of each trial with 'PRE-CUE' or 'POST-CUE' sign. We hypothesized that if the greater bottom-up attention contributed to the brightness induction by normalization (Reynolds & Heeger, 2009), adding top-down attention should also modulate the magnitude of brightness induction. If top-down attention is added to the stationary dots and, thus, reducing the effect of the bottom-up attention associated with the motion in context, the magnitude of brightness induction in stationary dots should be also reduced. Similarly, if top-down attention is added to the moving dots, it will facilitate the neural response of the moving dots even further that they should appear even darker against the background. In short, both the moving and the stationary dots should appear in higher contrast in the pre-cueing compared to the post-cueing condition. Note that we used four pairs of dots in this experiment with a concern that attention could be deployed to all two pairs of stationary and moving dots since observers could easily track about four moving objects (Scholl & Pylyshyn, 1999).

The results showed that the magnitude of the brightness induction is comparable between the pre-cue and the post-cue conditions (Fig. 6). Brightness of the stationary and the moving dots



**Fig. 5.** (a) In interocular condition, a stationary dot was presented to one eye and a moving dot was presented to the other eye. In binocular condition, both stationary and moving dots were presented to two eyes, but only one pair of dots was presented. (b) Brightness induction as a function of distance between stationary and moving dots. Gray bars represent the matched luminance of the stationary dots, and black bars represent the matched luminance of the moving dots in both (a) and (b). Error bars indicate  $\pm 1$  S.E. of the between subjects.

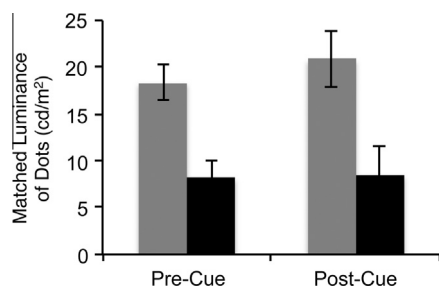
was similar between the pre-cue and post-cue conditions, yielding neither significant effect of the cue ( $F(1,6) = 0.53, p = .47$ ) nor interaction between the cue and stimulus type ( $F(1,6) = 0.34, p > .5$ ). This result suggests that attention is not a major factor of this novel brightness induction by motion in context.

#### 4. Discussion

In the current study, we introduced a novel brightness induction in which brightness of stationary objects was dramatically altered by motion in context. A series of psychophysical experiments suggest divisive normalization as a plausible neural computation explaining the interdependent nature of brightness induction. The brightness of the stationary objects shifted away from the brightness of the moving objects, even though both have the same physical light intensity. In particular, when we reversed the background from 'white' to 'black', brightness shift occurring in the stationary and the moving dots was also reversed.

Normalization is a general process that occurs at multiple stages of visual processing (Carandini & Heeger, 2012). Although the normalization was originally proposed to explain neural responses in early visual areas accompanied with cross-orientation inhibition (Carandini, Heeger, & Movshon, 1997; Heeger, 1992), a growing number of empirical findings indicate that normalization provides a framework to understand neural responses associated with sensitivity regulation in photoreceptor (Baylor & Fuortes, 1970; Boynton & Whitten, 1970), retinal contrast gain control (Brown & Masland, 2001; Passaglia, Freeman, & Troy, 2009; Shapley & Victor, 1981; Victor, 1987), and attention (Herrmann et al., 2010; Lee & Maunsell, 2009; Reynolds & Heeger, 2009). The brightness induction reported in this study indicates that normalization at multiple stages can alter the appearance of an object. However, several questions regarding the contrast normalization remain to be answered. For example, to what extent the contrast normalization is involved in brightness induction and whether the same motion in context affects the perception of apparent contrast as well as brightness? Answering to these questions will further reveal the relationship between contrast normalization and brightness in greater detail.

Although neural response based on stimulus contrast is an important factor that determines brightness of an object (Barkan, Spitzer, & Einav, 2008; Blakeslee & McCourt, 1999, 2004), the relationship between other objects in a scene also affects brightness. For example, anchoring theory of lightness perception (Gilchrist et al., 1999) proposed two distinct aspects of lightness processing, *scaling* and *anchoring*. The former is to establish the scale of relative lightness (contrast gain control mechanism may contribute to this process), and the latter is to determine lightness based on comparison of lightness among objects in a scene, following *anchoring rules* (i.e. highest luminance is perceived as 'white' and others are



**Fig. 6.** Influence of attention tested by pre-cueing paradigm. Gray bars represent the matched luminance of the stationary dots, and black bars represent the matched luminance of the moving dots. Error bars indicate  $\pm 1$  S.E. of the between subjects.

determined by comparing them with the 'white' which serves as an anchor). This type of *comparison* mechanism may provide an explanation for the large spatial range of the brightness induction reported here, since comparing the appearance of two objects in a visual scene is not limited by distance once both are visible.

One might question whether this brightness induction is a weaker version of motion-induced blindness (MIB): in MIB, stationary dots temporarily disappear from visual awareness when moving dots are presented simultaneously (Bonneh, Cooperman, & Sagi, 2001). Both MIB and our brightness induction are indeed similar in that brightness of the stationary objects becomes similar to the background when the moving objects are presented in the surround. However, this brightness induction should be distinguished from MIB. First, it is well known that adaptation plays an important role for MIB because MIB does not occur immediately after the stimulus presentation (Gorea & Caetta, 2009); but our brightness induction was evident even with a brief presentation and remained unchanged over time (Fig. 4). Second, it has been thought that disrupting attention might be responsible for the MIB (Bonneh, Cooperman, & Sagi, 2001), but the brightness induction was robust even with observers' full attention to either the moving or the stationary dots (Fig. 6). Instead, we argue that this brightness induction may make a critical contribution to MIB by reducing contrast between the stationary objects and background. Other debated mechanisms explaining MIB, such as disruption of attention and motion streak, then operate further, resulting in modulating awareness of the stationary objects (Bonneh, Cooperman, & Sagi, 2001; Wallis & Arnold, 2009).

In a related vein, perceptual fading associated with visual transient cannot explain the brightness shift induced by stimulus motion. Visual transients can induce perceptual fading of a target (Kanai & Kamitani, 2003). This fading induced by visual transients was observed in periphery (about  $10^\circ$  eccentricity) and also was perceptually time-locked to the transient. Importantly, fading effect was diminished as increasing the distance between the target and the inducer. In contrast, our brightness induction was clearly observable near foveal region ( $1^\circ$  away from the fixation) and was not affected by distance between the stationary and moving stimuli (Fig. 5b). Further, our brightness induction sustained as long as motion (or flicker) remained in context.

#### 5. Conclusion

The current study introduced a novel brightness induction whose characteristics can be explained by normalization. Studies on brightness induction mainly focused on the spatial and temporal influence of a context on shift in appearance of a central target. To our knowledge, our study for the first time demonstrated interdependence of target and context, which is one of the fundamental characteristics of normalization. Normalization is a canonical process that allows individual neurons with limited ranges of variation in responses to deal with enormous variations in energies in our environments. The current research extends our understanding of the human visual system that operates efficiently within a dynamically changing environment.

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