i-PERCEPTION

a Pion publication

i-Perception (2014) volume 5, pages 41–49

dx.doi.org/10.1068/i0628 ISSN 2041-6695 perceptionweb.com/i-perception

Motion influences the perception of background lightness

Hiroshi Ashida

Graduate School of Letters, Kyoto University, Kyoto 6068501, Japan; e-mail: Ashida@psy.bun.kyoto-u.ac.jp

Nicholas E. Scott-Samuel

School of Experimental Psychology, University of Bristol, 12a Priory Road, Clifton, Bristol BS8 1TU, UK;
e-mail: N.E.Scott-Samuel@bristol.ac.uk

Received 21 October 2013, in revised form 3 December 2013; published 13 January 2014.

Abstract. Uniform backgrounds appear lighter or darker when elements containing luminance gradients move across them, a phenomenon first presented by Ko Nakamura at the 2010 Illusion Contest in Japan. We measured the apparent lightness of the background with a configuration where the grey background was overlaid with moving square patches of vertically oriented luminance gradient. For black-to-grey gradients, the background appeared lighter when the black edges were leading than when they were trailing. For white-to-grey gradients, the background appeared darker when the white edges were leading than when they were trailing. For white-to-black gradients, the background appeared darker with a white edge leading and lighter with a dark edge leading, but the effects were weaker. These results demonstrate that lightness contrast can be modulated by the direction of motion of the inducing patterns. The smooth gradient is essential, because the effect disappeared when the black-to-white gradient was replaced with the binary black and white pattern. We speculate that asymmetry in the processing of a temporal gradient with increasing and decreasing contrast, as proposed to explain the "Rotating Snakes" illusion (Murakami, Kitaoka, & Ashida, 2006, *Vision Research, 46*, 2421–2431), might be the basis for this effect.

Keywords: visual illusion, lightness, motion, gradient.

1 Introduction

Perception of lightness has been extensively studied in vision science (e.g. Gilchrist, 2006; Kingdom, 2011), but the stimuli used are mostly static and the interaction between lightness and motion has been relatively neglected. In 2010 an illusion created by Ko Nakamura won the second prize in the 2010 visual illusion contest in Japan (http://visiome.neuroinf.jp/modules/xoonips/detail.php?item_id=6716). With his permission, we introduce this phenomenon to the wider vision science community. In the illusion, arrays of oval patches of horizontal luminance gradient are placed on a white background (see Figure 1). When the patches in the top and the bottom halves of the display move in opposite directions, the background lightnesses appear to be different: lighter when the black parts are leading, and darker when the black parts are trailing. This is a striking demonstration that motion can directly affect lightness perception, but the underlying cause is yet to be investigated.

Questions arise as to how this illusion occurs: is the effect polarity specific; does the effect involve lightening of an area, darkening of the other area, or both; is the crucial effect enhanced lightness contrast at the leading edges, enhanced lightness assimilation at the trailing edges, or both; and how is the lightness gradient itself crucial, apart from the asymmetry? We addressed these questions by measuring the perceived background lightness in two experiments.

Note that lightness and brightness are not obviously separable in the case of this particular illusion. We use the term lightness throughout the paper for convenience, because we tend to perceive the background as a white surface, and also because we asked the participants to judge the colour instead of the intensity of light. We do not, however, intend to restrict ideas either to phenomenology or underlying mechanisms at this stage.

2 Experiment 1

2.1 Methods

2.1.1 Participants

Six participants (including the author HA) were tested in Kyoto University, and four (including the author NSS) were tested in the University of Bristol under similar conditions. The naïve participants

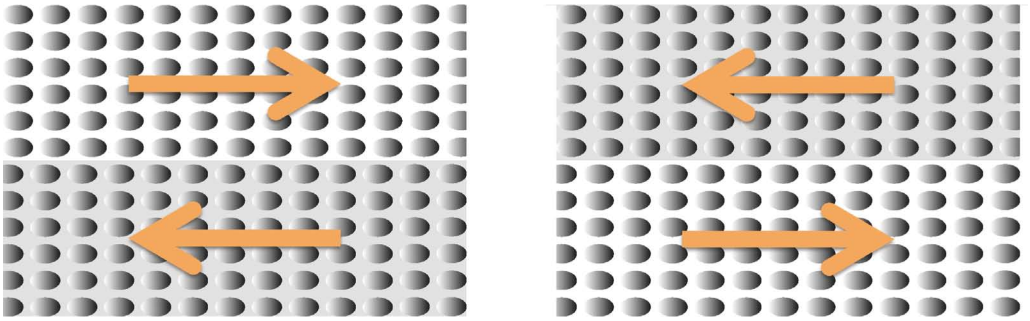


Figure 1. Illustrations of the illusion created by Ko Nakamura. The background is uniformly white, but the top and bottom parts appear lighter or darker depending on the motion direction, as illustrated by the colouring here.

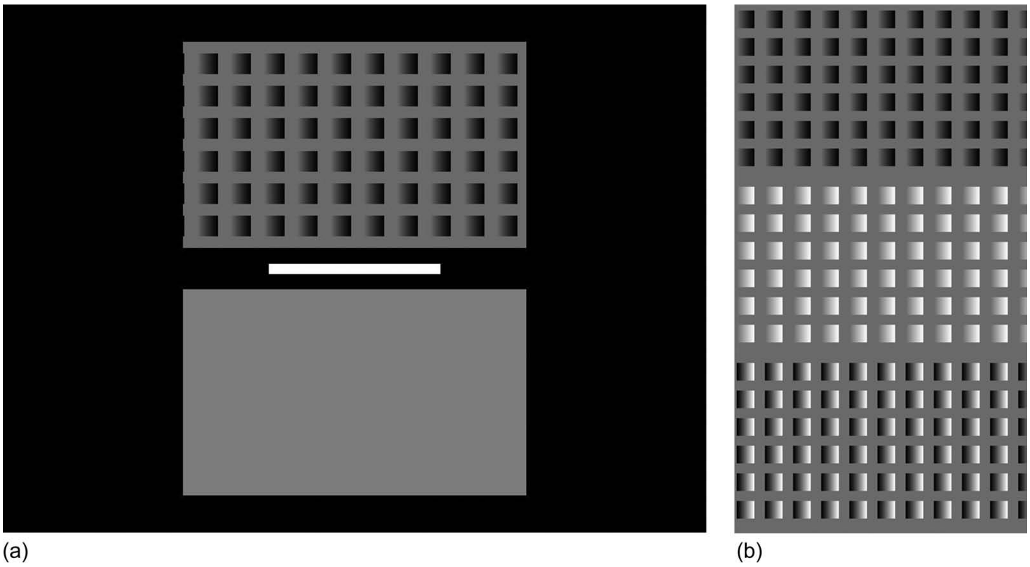
were paid for their time according to the universities' standards. One participant in Bristol was omitted from analysis due to a failure to see any illusion in the original artwork (but note that including the data from this participant did not substantially change the pattern of averaged results).

2.1.2 Stimuli

Visual stimuli were created using PsychToolbox (Brainard, 1997; Pelli, 1997) on an Apple MacBook Pro in Kyoto and a MacBook in Bristol, and presented on CRT displays (EIZO F57 in Kyoto and Sony Trinitron in Bristol) placed in dim rooms. The screen had a resolution of 1,024 × 768 pixels with a refresh rate of 100 Hz. The maximum luminance was 110 cd/m^2 in Kyoto and 130 cd/m^2 in Bristol. The viewing distance was 420 mm in Kyoto and 590 mm in Bristol.

Simplified versions of the original illusion were used (Figure 2). Grey rectangular fields (H 10 × V 6 deg) of mean luminance were presented above and below the centre of the minimum luminance display, separated by 1.2 deg. In the top rectangular area, square patches (0.6 × 0.6 deg) with vertically oriented luminance gradients were located in grids (3 rows and 10 columns), which moved horizontally at one of the four speeds (0.0, 1.48, 2.97, or 5.93 deg/s) either to the left or right. The lower rectangle was uniform and its luminance was controlled by the participants *via* the numerical keypad. We did not present the gradient patches in the comparison stimulus because changing its lightness introduces undesirable artefacts of edges at the smooth side of patches. A white fixation bar (H 7.9 × V 0.3 deg) was shown in the centre of the display.

There were three types of luminance gradient: white to grey (W-G), black to grey (B-G), and white to black (W-B), where white denotes maximum luminance and black minimum luminance.



(a) (b)

Figure 2. The stimuli in Experiment 1: (a) a screenshot and (b) the three types of gradients (B-G, W-G, W-B).

The gradient was always linear. There were two directions of gradient, and all the patches had the same gradient in each trial.

2.1.3 Procedure

Participants started each trial by pressing a key. They were instructed to adjust the lightness (grey level) of the bottom, uniform rectangle to match the apparent colour (whiteness or lightness) of the background of the upper rectangle by pressing keys. The initial grey level of the bottom rectangle was randomly set as ±32 (on a 0 to 255 scale) from the veridical value for each trial.

Participants were instructed to keep their fixation within the white bar in the centre. Control of fixation was not too strict because while direct inspection of each grey area was best avoided, restricting the comparison of lightness to the small areas around a strongly localised fixation point was also considered undesirable. There was no time limit for responding.

Each of the 48 conditions (three types of gradients, four speeds, two gradient directions, and two motion directions) was tested once in a single run in a random order. A run typically took about 5 to 10 min. Five runs were conducted for each participant, and the first run was discarded from analysis as a practice.

2.2 Results

For each trial, the difference in the matched luminance of the top and bottom panels was divided by the mean background luminance of the top panel to give the score of matching error in contrast. Positive and negative scores indicate that the top panel was perceived lighter and darker, respectively, than it actually was. Participants showed individual biases in their matching: on average, some adjusted the bottom part too light, others too dark, irrespective of the gradient elements in the upper part. Each participant's results were therefore normalised by subtracting their baseline before averaging across participants. The baseline was defined as the averaged matching luminance for the W-B stimuli at speed 0 deg/s, on the assumption that it should not have biases of either motion or overall luminance.

A four-way ANOVA (stimulus type × gradient direction × motion direction × speed) revealed significant main effects of stimulus type ($F(2, 18) = 6.78, p = 0.0074$), but the other main effects were not significant ($F < 1.38, p < 0.28$). The four-way interaction ($F(6, 48) = 5.80, p = 0.0001$), and one of the three-way interactions (stimulus type × gradient direction × motion direction: $F(2, 16) = 15.37, p = 0.0002$) were significant.

The effect of stimulus type is understood as an overall assimilation to the patch colour. In Figure 3, the data are differently organised but the overall assimilation is visible: the white patches (W-G) made the background look lighter while the black patches (B-G) made it look darker.

For the significant interactions, we then split the data by stimulus type. This allows analysis of the data in terms of specific combinations of motion and gradients, e.g. a comparison of the case of leading white edges versus trailing white edges for the W-G stimulus.

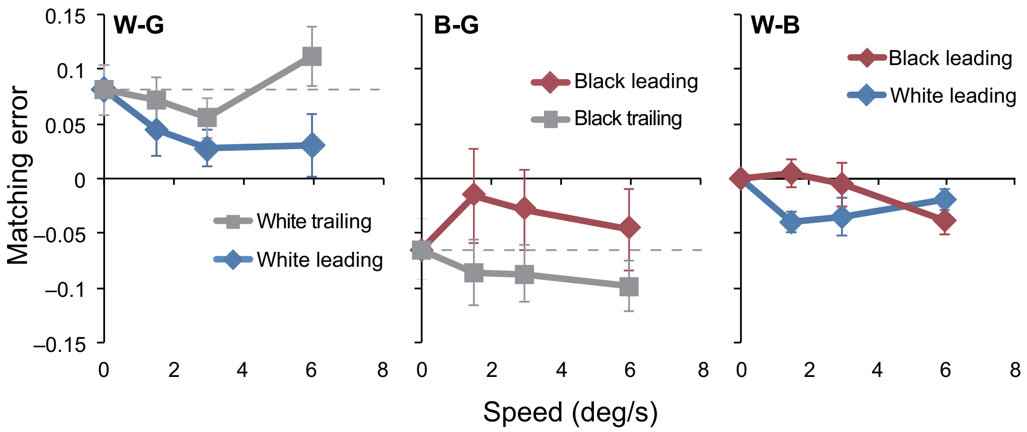


Figure 3. Results of Experiment 1. Normalised matching error, averaged across participants, is plotted as a function of speed for each gradient type and the type of leading edge. Error bars show ±1 S.E.M. Broken lines show the level of errors at speed 0 deg/s (Note that the W-B condition does not show the broken line because it served as the baseline at 0 deg/s).

For the W-G stimuli, two-way ANOVA (motion type × speed) revealed significant effects of the motion type ($F(1, 8) = 23.3$, $p = 0.0013$) and the interaction ($F(3, 24) = 3.68$, $p = 0.026$). Simple main effect analysis showed that the effect of speed was significant for "white leading" ($F(3, 24) = 3.18$, $p = 0.042$) but not for "white trailing" ($F(3, 24) = 1.99$, $p = 0.14$). For the B-G stimuli, two-way ANOVA (motion type × speed) revealed significant effects of the motion type ($F(1, 8) = 12.4$, $p = 0.0077$) and the interaction ($F(3, 24) = 5.19$, $p = 0.0066$). Simple main effect analysis showed that the effect of speed was significant for "black leading" ($F(3, 24) = 3.18$, $p = 0.42$) but it was not for "black trailing" ($F(3, 24) = 2.48$, $p = 0.085$).

To summarise these results, the overall assimilation to the white or black patches was reduced when the white or black edges were leading, and it was not significantly affected when these edges were trailing. A weak tendency of further assimilation by trailing white or black edges could contribute to enhance the illusion, but this secondary effect was not statistically supported.

For the W-B stimuli, two-way ANOVA (motion type × speed) revealed no significant main effect (motion type: $F(1, 8) = 4.98$, $p = 0.056$; speed: $F(3, 24) = 2.02$, $p = 0.13$) but the interaction was significant ($F(3, 24) = 4.21$, $p = 0.016$). A significant simple main effect of speed was found for "white leading" ($F(3, 24) = 3.195$, $p = 0.042$) but not for "black leading" ($F(3, 24) = 2.68$, $p = 0.070$). These results are somewhat weaker or mixed, but are basically consistent with the effects of leading white or black edges for W-G and B-G stimuli.

These asymmetrical effects of motion on lightness contrast and assimilation appear to be the basis of the illusion (in which the elements of the same gradient direction move in opposite directions in the two areas). To our knowledge, this is the first evidence that motion affects lightness perception directly (although see Agostini & Proffitt, 1993, for an effect of lightness contrast derived from "common fate" of element movement). The effect at the leading edges seems more important than the effect at the trailing edges. A remaining question is whether the gradient plays an essential role, or whether the lightness contrast at the leading edges is the critical factor. This question was addressed in Experiment 2.

3 Experiment 2

To determine if the gradient is crucial, the effects of patches with black-to-white smooth gradient were compared with those with black-and-white stepwise lightness changes. If the contrast of the leading edge is the crucial factor, these two types of stimuli should have similar effects on the perceived lightness of the background. If, on the other hand, the gradient is essential, the latter would have much smaller effects.

The results for W-B stimuli in Experiment 1 were less clear than the other two conditions. This could be due to the steeper gradient with double the lightness change (compared to the W-G and B-G stimuli) in the same space. We therefore doubled the width of each patch from those in Experiment 1. In addition, the effect of stimulus speed could have been obscured by relatively free eye movement along the motion axis. Fixation was therefore restricted in Experiment 2 to assess the effect of speed more stringently.

3.1 Methods

3.1.1 Participants

Seven participants (including the two authors) were tested in Kyoto University. The naïve participants were paid for their time according to the universities' standards. Two of the naïve participants only participated in this experiment, and the others participated after they completed Experiment 1.

3.1.2 Stimuli

The stimuli were similar to those in Experiment 1, with the following exceptions (see Figure 4). The width of the patches was doubled in order to keep the gradient slope the same as in the W-G and B-G stimuli in Experiment 1. The number of patch columns was therefore reduced to 5. There were only two types of patches: black-to-white gradient (gradient) and black-and-white steps (no gradient). Stationary patches were presented in the bottom rectangle to make the backgrounds look more similar to each other. The patches in Experiment 2 had clear edges on both sides and did not show the previously mentioned artefacts of undesired lightness gaps between the patches and the background when the background level was changed while the gradient remained the same. The spatial location (phase) of the stationary patches was randomised for each trial. The stimuli moved at one of five speeds

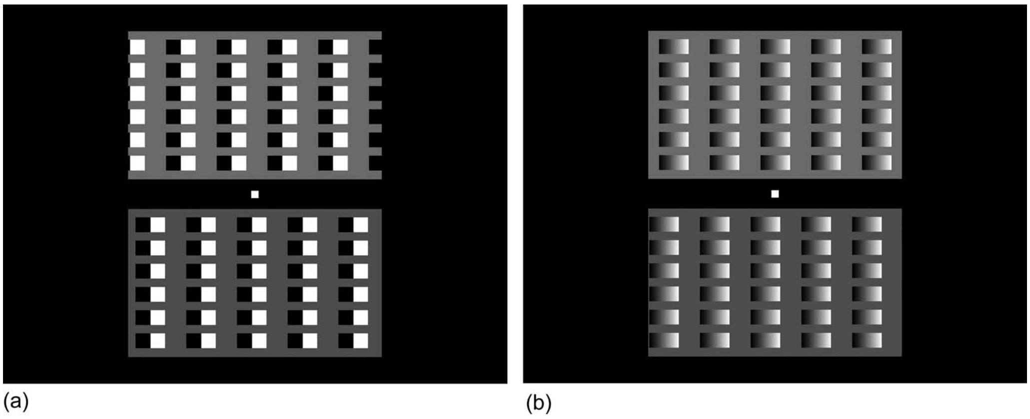


Figure 4. A screenshot of Experiment 2: (a) no gradient and (b) gradient conditions.

(0.0, 1.48, 2.97, 5.93, or 8.90 deg/s), and a smaller fixation point (a white square of 0.3 × 0.3 deg) was used to assess the effect of speed more clearly.

3.1.3 Procedure

The participants adjusted the background lightness of the bottom panel to match the perceived lightness (colour) of the top panel, as in Experiment 1. The procedure was the same as in Experiment 1 except that fixation was restricted to the centre horizontally as well as vertically.

3.2 Results

Matching errors were computed as in Experiment 1 (Figure 5). A two-way ANOVA (motion type × speed) was conducted separately for the two types of stimuli. For the no-gradient stimuli, the effect of speed ($F(4, 32) = 4.00$, $p = 0.0097$) was significant but the effect of motion type ($F(1, 8) = 0.324$, $p = 0.58$) or the interaction ($F(4, 32) = 1.10$, $p = 0.38$) was not. For the gradient stimuli, the effect of motion type ($F(1, 8) = 9.10$, $p = 0.017$) and the interaction ($F(4, 32) = 4.00$, $p = 0.0097$) was significant, but the effect of speed ($F(4, 32) = 1.63$, $p = 0.19$) was not. The simple main effect of speed was significant for “black leading” ($F(4, 32) = 4.98$, $p = 0.0031$) but not for “white leading” ($F(4, 32) = 1.25$, $p = 0.31$) stimuli. The effects of white and black edges in the gradient stimuli appear asymmetric about the x axis, but it should be noted that these results are not consistent with those in Experiment 1 where the effect of speed was significant only for “white leading”. The overall shapes of curves are similar and the effect of the gradient is evident, but it remains unclear whether the effect is asymmetric as to the gradient direction.

Most importantly, the effect of motion type, i.e. the colour of the leading edge, was found only for the gradient stimuli. A slightly reversed effect for the no-gradient stimuli at higher speed, although not supported statistically, might reflect motion blur at the trailing edges overriding the contrast effect at the weak leading edges, if any.

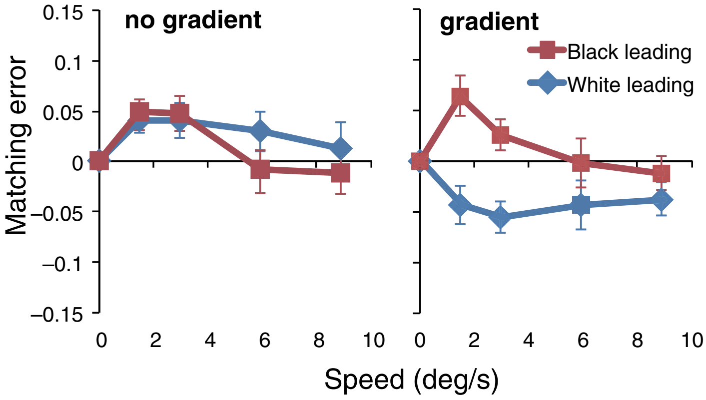


Figure 5. Results of Experiment 2. Normalised matching error, averaged across participants, is plotted as a function of speed for each type of stimulus and the type of leading edge. Error bars show ±1 S.E.M.

4 General discussion

4.1 Phenomenology

The illusion by Nakamura provides a striking and novel demonstration of the effects of motion on lightness perception. The original artwork had black patches on a white background, but here it was confirmed that the black and white patches have roughly symmetric effects on a grey background. The black or white patches have an assimilation effect on the background when they are stationary, and motion modulates this baseline assimilation. The effect of motion is characterised as lightning by leading black edges, and darkening by leading white patches.

This effect might be related to a gain control process that enhances stimulus contrast at the leading edges and suppresses it at the trailing edges of moving elements (Arnold, Thompson, & Johnston, 2007). While this could account for the original Nakamura effect, it does not explain our result that a luminance gradient is necessary for the illusion: leading edges of simple black or white patterns did not work (Experiment 2).

On the basis of these findings, we propose a possible explanation for this illusion from a computational point of view.

4.2 Gradient-based motion detection

A role for spatiotemporal gradients in motion processing has been shown empirically. Anstis (1990) reported that adapting to temporal luminance ramps (i.e. the luminance of an area changes in the form of a sawtooth function) results in motion aftereffect of a test pattern. The aftereffect direction depends on the polarity of the luminance edge between the test pattern and its background. More recently, Scarfe and Johnston (2010) demonstrated that combination of aftereffects to spatial gradient and temporal ramps produces a perception of motion. These findings are readily explained by the gradient scheme of motion detection (e.g. Marr & Ullman, 1981) as we discuss next.

Gradient schemes compute local image velocity directly from spatial and temporal gradients. Such schemes are popular in image processing (Horn & Schunck, 1981; Lucas & Kanade, 1981), as well as in biological modelling (Johnston, McOwan, & Buxton, 1992; Marr & Ullman, 1981). In addition, Harris (1980) proposed that velocity could be encoded by comparing the responses of flicker and pattern systems on the basis of psychophysical results. Finally, a Japanese patent granted in 1976 (#1323442) encapsulates a similar idea (Takahiko Fukinuki, personal communication).

In the case of one-dimensional motion, local velocity v at a location x in image I is essentially derived as $v = -(\delta I/\delta t)/(\delta I/\delta x)$. In other words, local speed is given by the temporal gradient divided by the spatial gradient. This one-dimensional model is useful for biological modelling because neurons in the primary visual cortex mostly have one-dimensional receptive fields (e.g. Daugman, 1985; Parker & Hawken, 1988), feeding to later stages of integration orientation and space. The gradient scheme is conceptually different from other major models of motion detection, such as motion energy (Adelson & Bergen, 1985) or the Reichardt detector (Reichardt, 1961; van Santen & Sperling, 1985), but the actual shapes of the implemented filters can be quite similar (Mather, 1994). Motion energy and Reichardt models do not provide estimates of invariant speed at the detector level, and a proposed scheme of computing speed by the ratio of high- and low-speed detector outputs (Adelson & Bergen, 1985) resembles the gradient scheme. Actually, the original motion energy model was constructed by using Gaussian derivatives as the spatial filters. Discussion on the basis of a simple gradient scheme, therefore, could be informative even if one does not support the gradient scheme against the others.

Murakami et al. (2006) proposed a schematic model of the “Rotating Snakes” illusion (Kitaoka & Ashida, 2003) using a modified gradient scheme. The “Rotating Snakes” figure is composed of repeated patterns of four colours (typically black-blue-white-yellow) that give rise to asymmetric spatial luminance gradients. With small involuntary eye movements (drift), the retinal image shifts and gives rise to temporal gradients at each point. Asymmetric motion responses can be derived if either the spatial or temporal gradient is slightly biased in one direction. While it is unrealistic to assume biased spatial derivative filters, the temporal derivative filters are causal and more likely have an imbalance of positive and negative lobes of their impulse response, which would introduce a bias. The assumption that decrease of contrast is overestimated compared to increase of contrast (see Figure 9 in Murakami et al., 2006), which is consistent with psychophysically derived temporal impulse responses (Burr & Morrone, 1993; Hisakata & Murakami, 2008), explains the observed illusory motion.

4.3 A schematic model of the Nakamura illusion

This assumption of overestimation of decreasing contrast and underestimation of increasing contrast (Murakami et al., 2006) can explain the Nakamura illusion. Consider the temporal changes of lightness (or luminance) at one horizontal location (shown by the dashed black line in the insets of Figure 6). The lightness physically changes as shown by the black lines in each combination of gradient and motion. The red lines show expected representation of lightness with the assumption of a biased gradient computation as described above.

The primary effect of lightness contrast was found when the white or black edge was leading (Figure 6a and b). In these cases, the lightness contrast suddenly reaches the maximum, and then gradually decreases. The temporal gradient of decreasing contrast is overestimated by the biased filters, which would yield darkening in Figure 6(a) or whitening in Figure 6(b) at the end of the gradient. This overshoot could continue into the grey area and cause the contrast effects on the background as shown by the dashed red lines. The effect was not clear when the white or black edge is trailing (Figure 6c and d). Here, the effect of biased smooth gradient may not affect the background after the final steep edge. A possible slight overshoot may be cancelled or overcome by motion blur at the edges. Prediction is even less straightforward when the gradient ranges white to black (Figure 6e and f). In Figure 6(e), the red lines were simply copied and connected from Figure 6(a) and (d). This would result in slight underestimation of the lightness at the end of the patch. Similarly, in Figure 6(f), red lines are copied from Figure 6(b) and (c). The bias in the first half is not completely nulled in the second half, but it is uncertain what happens at the final edge. Unlike in Figure 6(c) and (d), the effect of gradient bias and that of motion blur may be in the same direction.

Note that possible biases at the edges are not considered in Figure 6. While the gradient has infinite slope at the edge, retinal and neural images are blurred and should have measurable gradient slopes, which should be also biased. This possibility is ignored here in the interests of simplicity, but the scheme remains valid at least in the crucial conditions of Figure 6(a) and (b), where the effect should be enhanced if the initial contrast increase is underestimated. In Figure 6(c–f), lightness contrast could have been enhanced by overestimation of the trailing edges, which could also be true with the B-W stimuli. This did not seem to happen, however, suggesting that the steep edges have little effect in the modulation of lightness.

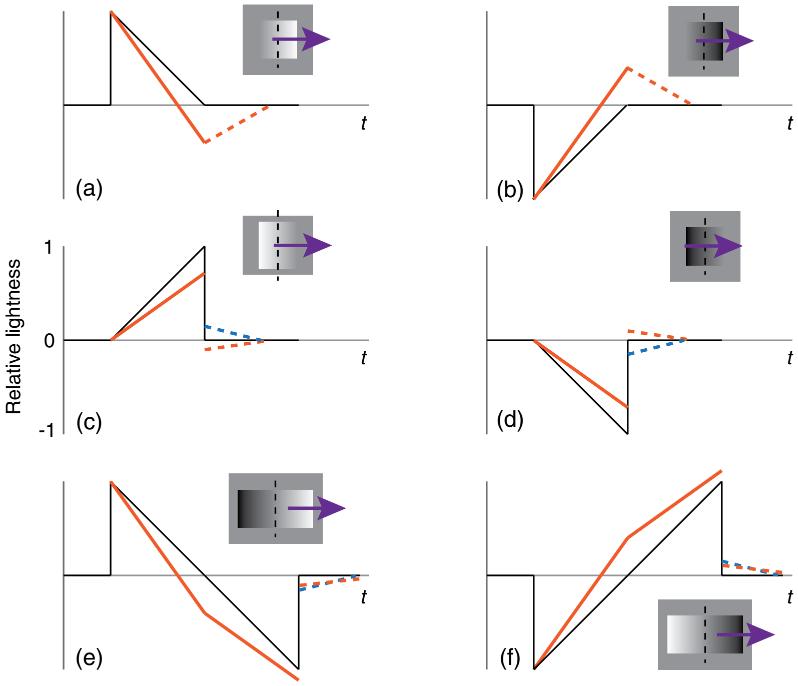


Figure 6. Gradient-based explanation of the Nakamura illusion. The time-course of the lightness change at one location (shown by the vertical black dashed line in the inset) is plotted for each type of element and each motion direction in Experiment 1. Solid black lines show the actual lightness change. Red lines show the predicted representation of lightness, assuming that increment and decrement slopes are biased by a fixed ratio of 1.4 (arbitrarily set for illustration). Dashed blue lines show possible effects of motion blur at the edges.

Lightness contrast may be modulated laterally (i.e. vertically in this case) in the top and bottom portions of the surrounding background. It is then possible that the steep edges had (apparently) little effect simply because the areas above and below the edges are small compared to the areas along the smooth gradient.

The crucial effect of enhanced lightness contrast, as shown in Figure 6(a) and (b), is well captured by this simple scheme, but only qualitatively. In order to develop a more quantitative model, more assumptions are needed about several unknown properties. Most importantly, it is not known how temporal gradient responses interact with the static representation of lightness, given the possible separate pathways for motion (mainly in the dorsal stream) and colour (mainly in the ventral stream) (Livingstone & Hubel, 1988; Vaina, 1994). Figure 6 assumes an immediate update of lightness representation by the temporal gradient, but this is not realistic, and some postdictive integration may need to be introduced. Also, static lightness contrast and assimilation are not considered in Figure 6, which should be somehow implemented in a quantitative model. Finally, motion blur may also need to be quantified.

4.4 Concluding remarks

Nakamura’s illusion of moving gradients opens the door to further inquiries into novel interactions between motion and lightness. A greater understanding of this phenomenon could enhance knowledge about the integration of visual features after relatively independent initial processing. The illusion appears to be readily explained by a scheme of motion detection based on spatiotemporal gradients.

Acknowledgments. This work was supported by JSPS grant-in-aid for scientific research (grant number 22243044) to HA and by an EPSRC Building Global Engagements in Research grant to NSS. The authors thank professor Ko Nakamura (Hokusei Gakuen University) for his permission to use his artwork and his encouragement for their work.

References

Adelson, E. H., & Bergen, J. R. (1985). Spatiotemporal energy models for the perception of motion. *Journal of the Optical Society of America A, 2*(2), 284–299. doi:10.1364/JOSAA.2.000284

Agostini, T., & Proffitt, D. R. (1993). Perceptual organization evokes simultaneous lightness contrast. *Perception, 22*(3), 263–272. doi:10.1068/p220263

Anstis, S. (1990). Motion aftereffects from a motionless stimulus. *Perception, 19*(3), 301–306. doi:10.1068/p190301

Arnold, D. H., Thompson, M., & Johnston, A. (2007). Motion and position coding. *Vision Research, 47*(18), 2403–2410. doi:10.1016/j.visres.2007.04.025

Brainard, D. H. (1997). The psychophysics toolbox. *Spatial Vision, 10*(4), 433–436.

Burr, D. C., & Morrone, M. C. (1993). Impulse-response functions for chromatic and achromatic stimuli. *Journal of the Optical Society of America A, 10*(8), 1706–1713. doi:10.1364/JOSAA.10.001706

Daugman, J. G. (1985). Uncertainty relation for resolution in space, spatial frequency, and orientation optimized by two-dimensional visual cortical filters. *Journal of the Optical Society of America A, 2*(7), 1160–1169. doi:10.1364/JOSAA.2.001160

Gilchrist, A. L. (2006). *Seeing black and white*. New York: Oxford University Press.

Harris, M. G. (1980). Velocity specificity of the flicker to pattern sensitivity ratio in human vision. *Vision Research, 20*(8), 687–691. doi:10.1016/0042-6989(80)90093-0

Hisakata, R., & Murakami, I. (2008). The effects of eccentricity and retinal illuminance on the illusory motion seen in a stationary luminance gradient. *Vision Research, 48*(19), 1940–1948. doi:10.1016/j.visres.2008.06.015

Horn, B. K. P., & Schunck, B. G. (1981). Determining optical flow. *Artificial intelligence, 17*(1), 185–203.

Johnston, A., McOwan, P. W., & Buxton, H. (1992). A computational model of the analysis of some first-order and second-order motion patterns by simple and complex cells. *Proceedings of the Royal Society of London B, 250*(1329), 297–306. doi:10.1098/rspb.1992.0162

Kingdom, F. A. (2011). Lightness, brightness and transparency: a quarter century of new ideas, captivating demonstrations and unrelenting controversy. *Vision Research, 51*(7), 652–673. doi:10.1016/j.visres.2010.09.012

Kitaoka, A., & Ashida, H. (2003). Phenomenal characteristics of the peripheral drift illusion. *Vision, 15*(4), 261–262.

Livingstone, M., & Hubel, D. (1988). Segregation of form, color, movement, and depth: Anatomy, physiology, and perception. *Science, 240*(4853), 740–749. doi:10.1126/science.3283936

Lucas, B. D., & Kanade, T. (1981). *An iterative image registration technique with an application to stereo vision.* Paper presented at the Proceedings of the 7th International Joint Conference on Artificial Intelligence, Vancouver, British Columbia, 674–679.

Marr, D., & Ullman, S. (1981). Directional selectivity and its use in early visual processing. *Proceedings of the Royal Society of London. Series B: Biological Sciences, 211*(1183), 151–180. ◀

Mather, G. (1994). Motion detector models: psychophysical evidence. In A. T. Smith & R. J. Snowden (Eds.), *Visual detection of motion* (pp. 117–143). London: Academic Press. ◀

Murakami, I., Kitaoka, A., & Ashida, H. (2006). A positive correlation between fixation instability and the strength of illusory motion in a static display. *Vision Research, 46*(15), 2421–2431. doi:10.1016/j.visres.2006.01.030 ◀

Parker, A. J., & Hawken, M. J. (1988). Two-dimensional spatial structure of receptive fields in monkey striate cortex. *Journal of the Optical Society of America A. Optics and Image Science, 5*(4), 598–605. ◀

Pelli, D. G. (1997). The VideoToolbox software for visual psychophysics: Transforming numbers into movies. *Spatial Vision, 10*(4), 437–442. doi:10.1163/156856897X00366 ◀

Reichardt, W. (1961). Autocorrelation, a principle for the evaluation of sensory information by the central nervous system. In W. A. Rosenblith (Ed.), *Sensory communication* (pp. 303–317). New York: MIT Press. ◀

Scarfe, P., & Johnston, A. (2010). Perception of motion from the combination of temporal luminance ramping and spatial luminance gradients. *Journal of Vision, 10*(7), 847. doi:10.1167/10.7.847 ◀

Vaina, L. M. (1994). Functional segregation of color and motion processing in the human visual cortex: Clinical evidence. *Cerebral Cortex, 4*(5), 555–572. ◀

van Santen, J. P. H., & Sperling, G. (1985). Elaborate Reichradt detectors. *Journal of the Optical Society of America A, 2*(2), 300–321. ◀

Hiroshi Ashida received BA, MA, and PhD at Kyoto University (psychology). After working as a postdoctoral researcher at ATR Human Information Processing Research Laboratories, research associate at Kyoto University, and associate professor at Ritsumeikan University, he is now working as an associate professor at Kyoto University. His main research interest is visual processing of motion and visual illusion in general. He also studies with fMRI after he learned the basics at Royal Holloway, UK, in 2004–2005.

Nicholas E. Scott-Samuel has a BA in Philosophy (University of Bristol) and an MSc in Cognitive Science (University of Birmingham). His PhD on human visual motion processing was supervised by Mark Georgeson (University of Birmingham), and was followed by postdocs with Andy Smith (Royal Holloway, University of London) and Robert Hess (McGill University). He is currently a senior lecturer at the University of Bristol.

a Pion publication