Neon color spreading in dynamic displays: Temporal factors

Marco Cicchini

Institute of Neuroscience, National Research Council, Pisa, Italy ✉

Lothar Spillmann

Department of Neurology, University Hospital, Freiburg, Germany 🏠 ✉

When a red star is placed in the middle of an Ehrenstein figure so as to be collinear with the surrounding black rays, a reddish veil is perceived to fill the white center. This is called neon color spreading. To better understand the processes that give rise to this phenomenon, we studied the temporal properties of the effect. Specifically, we presented a "sustained" black Ehrenstein figure (rays) for 600 ms and a "transient" red star for 48 ms, or the converse pattern, at various stimulus onset asynchronies (−100–700 ms) and asked subjects to compare the strength of the neon color in the test stimulus to that of a reference pattern in which the transient star had an onset asynchrony of 300 ms. Additional exposure durations of 24 and 96 ms were used for each transient stimulus in order to study the effect of temporal integration. Simultaneity of the on- and off-transients of the star and the Ehrenstein rays were found to optimize neon color spreading, especially when both stimuli terminated together. Longer exposure durations of the transient stimulus up to 96 ms further improved the effect. Neon color spreading was much reduced when the transient stimulus was presented soon after the beginning of the sustained stimulus, with a gradual build-up towards the end. These results emphasize the importance of stimulus onset asynchrony (SOA) and stimulus termination asynchrony (STA) for the perception of neon color spreading.

Introduction

Neon color spreading arises when a red star is inserted in the center of a black Ehrenstein figure. The color of the star assimilates onto the white interspace between the radial lines, thereby generating a reddish, semi-transparent disk that fills in the central region of the Ehrenstein figure (van Tuijl, 1975; Varin, 1971).

Redies and Spillmann (1981) studied the boundary conditions for this effect, showing that for the illusion to occur, the radial lines of the Ehrenstein figure and the star must be collinear, equally wide, and spatially contiguous. Any slight offset, misalignment, or gap between the two figures weakens and ultimately abolishes the effect. This result suggests a contribution by end-stopped neurons in the primary visual cortex (V1) (Grossberg & Mingolla, 1985; Peterhans, von der Heydt, & Baumgartner, 1986; von der Heydt, Peterhans, & Baumgartner, 1984).

Interocular presentation of the stimulus pattern points to an even earlier neural processing stage (Bressan, Mingolla, Spillmann, & Watanabe, 1997). When the colored star is presented to one eye and the black Ehrenstein figure to the other, so that they are perfectly aligned in the fused image, neon color is absent (Redies & Spillmann, 1981; Takeichi, Shimojo, & Watanabe, 1992). On the other hand, when one eye sees only the horizontal components and the other the vertical components of the combined stimulus pattern, neon color persists (Redies & Spillmann, 1981). This result suggests that neon color spreading may originate, in part, at a precortical stage before binocular convergence.

The neon color effect has typically been studied with static stimuli and long exposure durations, although it was also observed informally with presentation times as short as 50 ms, ruling out eye movements as a factor (Redies & Spillmann, 1981). Furthermore, Anstis (2006) reported that when the neon color pattern was in motion, traversing changing regions of the retina, there was good color spreading. Similarly, Cicerone, Hoffman, Gowdy, and Kim (1995) demonstrated that neon spreading can also occur in an array of moving dots that changed their color so that the hue in the region under consideration remained constant.

Here we ask a question: What are the temporal constraints for neon color to occur in an otherwise static configuration? Do the black radial lines of the Ehrenstein figure (henceforth called "rays") and the red star need to coincide in time, i.e., be shown together, or can they be shifted relative to each other? To find out we

presented either the Ehrenstein figure or the star for 600 ms ("sustained") and the complementary figure for 24, 48 or 96 ms ("transient"). The figure with the shorter exposure duration was systematically shifted relative to the onset of the figure with the longer duration and several asynchrony conditions were explored.

Methods

Apparatus

The experiment took place in a dark room. Visual stimuli were generated with a VSG 2/5 graphics board (Cambridge Research Systems, Cambridge, UK) and presented on the face of a Barco Calibrator CRT screen (refresh rate 250 Hz). Stimulus generation was controlled by Matlab running on a PC (Dell, Pentium IV, 2 GHz, 512 Mb RAM) and proprietary Cambridge Research System routines.

Stimuli

A black Ehrenstein figure and a red star with eight radii each were presented on an otherwise white background subtending $30° \times 20°$ of visual angle. The background had a luminance of 30 cd/m^2, the radial lines of both stimuli were 40 arcmin wide, and their length was 2.5° for the star and 7° for the Ehrenstein figure. Luminance of the red star was 18 cd/m^2 and the CIE coordinates were $x = 0.62$ and $y = 0.34$.

There were two main experimental conditions. In Condition 1, labeled "Sustained Rays/Transient Star" (Figure 1A, left), the rays of the Ehrenstein figure were shown for 600 ms, while the red star was presented "transiently" for 48 ms at different stimulus onset asynchronies (SOAs), ranging from −100–700 ms. In Condition 2, labeled "Sustained Star/Transient Rays" (Figure 1A, right), the temporal relationship was reversed and the red star was shown for 600 ms, while the Ehrenstein figure was presented for 48 ms at the same SOAs as before. The temporal profiles are illustrated by Figure 1B and C.

SOA was randomized within each session. Asynchrony was defined as the difference in time between the onset of the sustained and the transient stimulus. Therefore, an SOA of 0 ms indicates that the red star and the Ehrenstein figure were presented together. An SOA of 600 ms, on the other hand, indicates that the transient stimulus was presented, when the sustained stimulus ended.

Two further conditions were also tested. In one condition, the exposure duration of the transient stimulus was either 24 or 96 ms instead of 48 ms; in the other, the duration of the sustained stimulus was lengthened from 600 ms to 1600 ms.

Subjects

Three subjects participated in the experiment. Their mean age was 27 years; one of them was author GMC; the other two were naive to the purpose of the experiment. All had normal or corrected-to-normal vision and were familiarized with the neon color effect before data acquisition. Observation was binocular. The experiments were conducted in accordance with the Declaration of Helsinki.

Task and procedure

Subjects determined the strength of neon color spreading by comparing it to that of a reference, consisting of an Ehrenstein figure lasting 600 ms and a red star flashed for 48 ms at an SOA of 300 ms (see also Figure 1B). These parameters were kept constant throughout the experiments and were used both for the Sustained Rays/Transient Star condition and its converse.

Thus, there were two patterns in each trial, i.e., the test stimulus and the reference, both consisting of a combination of black rays and red star. Each trial started with a uniform white background, exhibiting a small gray fixation point (0.1° diameter) in the middle. Subjects used a chinrest to keep head position steady. After a random delay of 700 ms–2500 ms, the first stimulus pattern was presented and, after a further delay of 1500–2500 ms, it was followed by the second stimulus pattern. At the end of the sequence, subjects indicated whether the neon color effect had been stronger in the first or second configuration by pressing one of two keys on the keyboard. The order of the reference and test stimuli was randomized across trials. Each experimental session comprised 50 trials, and overall each subject participated in more than 10 sessions, yielding a minimum of 20 repetitions per data point.

Results

Sustained Rays/Transient Star

In the first experiment we studied the optimal temporal conditions (SOAs) for neon color spreading, when the black rays of the Ehrenstein figure were presented for 600 ms and the red star was shown for 48 ms at various temporal asynchronies. Figure 2 shows the percentage of trials when neon color spreading in
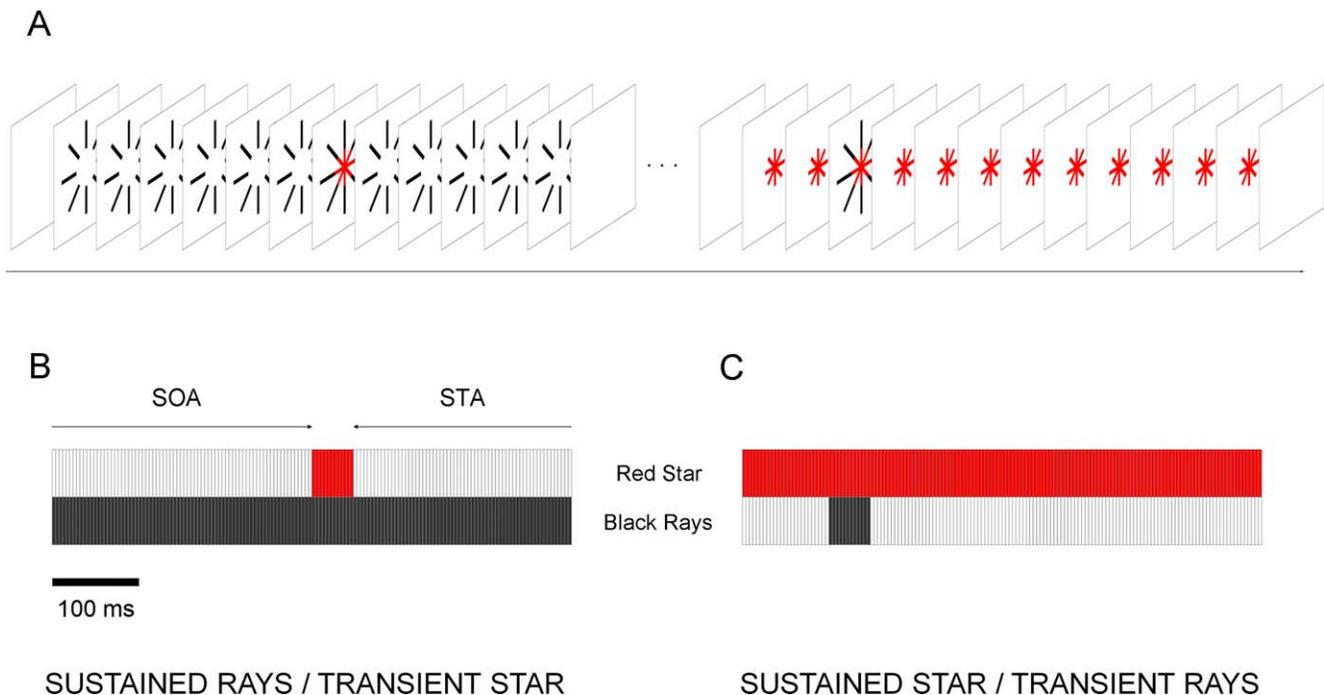
Figure 1. **(A)** Illustration of stimulus sequence in a sample trial. Left: The first stimulus is a brief, transient red star presented midway through the presentation of an Ehrenstein figure ("rays"). Right: A "transient" Ehrenstein figure is presented shortly after the onset of a red "sustained" star. SOAs are chosen arbitrarily for illustration only. (B) Temporal profile of the Sustained Rays/Transient Star condition. In this condition the two configurations are presented for 600 ms and 48 ms, respectively. Stimulus onset asynchrony (SOA) is defined as the difference in time between the onsets of the two stimuli, whereas stimulus termination asynchrony (STA) is defined by the interval between the offsets of the two stimuli. In this example SOA is 300 ms. (C) Temporal profile of the converse condition. Duration of the stimuli is comparable, whereas SOA is 100 ms. In the experimental trials, a stimulus such as that in B (Sustained Rays, Transient Star, SOA 300 ms) served as a reference and subjects compared the strength of neon color spreading induced by various SOAs to that induced by the reference stimulus.

the test stimulus was judged stronger than in the reference stimulus, plotted as a function of stimulus onset asynchrony between the Ehrenstein figure and the briefly flashed red star. The 50% value marks chance probability.

Negative values on the axis of abscissas refer to star figures flashed before the onset of the Ehrenstein figure, while positive values refer to stars flashed after the onset. Dotted vertical lines indicate SOAs at which the black rays and the red star had either the same onset (SOA = 0 ms) or the same offset (SOA = 552 ms).

Curves show that neon color spreading in the test stimulus is stronger than in the reference stimulus (>50%), when the red star is flashed close to the onset (SOA = 0–100 ms) or offset (SOA = 400–552 ms) of the Ehrenstein figure, but is substantially weaker (equal to or <50%) for SOAs in between. This difference is particularly pronounced for subject PB.

To explore the experimental conditions that produce these peaks in greater detail, we repeated this experiment with two different exposure durations of the red star, 24 ms and 96 ms in subject GMC. Figure 3 plots perceived strength of neon color spreading as a function of stimulus onset asynchrony between the

sustained and transient stimulus for all three-exposure durations of the star (the curve for 48 ms being the same as in Figure 2; subject GMC).

Figure 3A plots the data as a function of stimulus onset asynchrony (SOA), where a value of zero on the axis of abscissas implies that both the Ehrenstein figure and the red star started simultaneously. Doubling the exposure duration from 48 to 96 ms markedly increased the strength of the neon effect. It also changed the shape of the curve from U-shaped to hump-backed (with a bias for long SOAs). After an initial peak, the curve briefly decreases and thereafter rises monotonically to a second, higher maximum shortly before the end of the stimulus presentation. In contrast, reducing the exposure duration to 24 ms weakened the effect significantly, leaving only small peaks (<50%) at the onset and offset of the sustained Ehrenstein figure.

For comparison, Figure 3B plots the same data as a function of stimulus termination asynchrony (STA). Here, a value of 0 ms on the axis of abscissas implies that the Ehrenstein figure and the red star terminated together. In this representation, the late peaks of the curves for all three exposure durations become closely aligned, supporting the idea that a maximal neon color
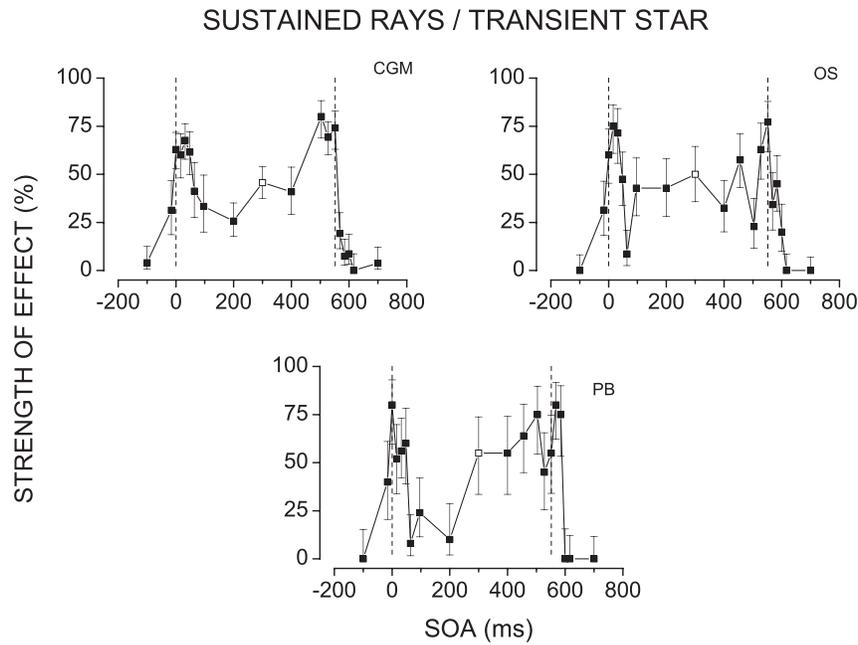
SUSTAINED RAYS / TRANSIENT STAR

Figure 2. Strength of neon color spreading for the Sustained Rays/Transient Star condition. Exposure duration of the rays was 600 ms and of the star 48 ms. Stronger-than-reference responses (in %) are plotted as a function of stimulus onset asynchrony (SOA). Data are averages at least of 20 repetitions for each of 3 subjects. Error bars represent binomial standard errors. The empty square at SOA = 300 ms gives the datum when test and reference had the same temporal characteristics. Dotted vertical lines at 0 ms and 552 ms indicate that the Ehrenstein figure and star either onset or offset together.

effect is obtained when rays and star terminate together.

To further verify that maximal neon spreading occurs when the red star is briefly presented at the onset or offset of the Ehrenstein figure, we repeated the experiment, prolonging the exposure of the sustained Ehrenstein figure from 600 ms to 1600ms, while leaving the red star (48 ms) and the reference stimulus (600 ms sustained rays, 48 ms flashed star, 300 ms SOA) unchanged. Figure 4 plots the results of this experiment. The curve peaks when the star and the Ehrenstein figure onset and offset together, just as had happened with an exposure duration of 600 ms. The curve connecting these two maxima increases slightly
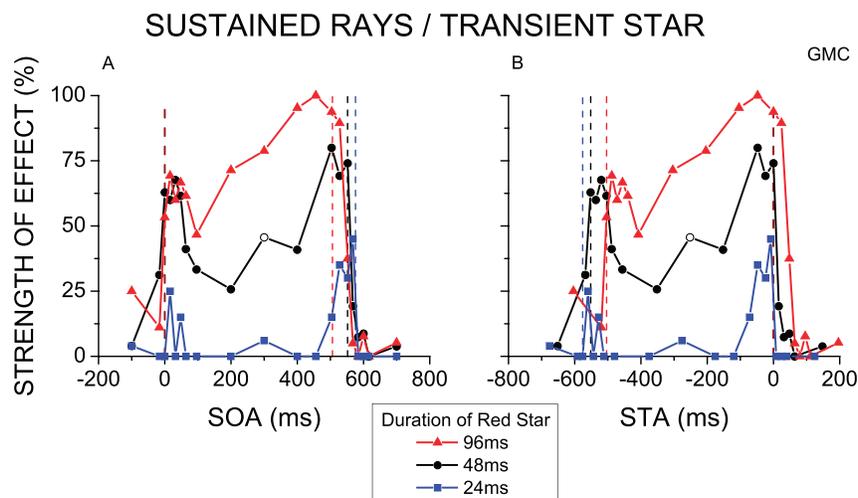
SUSTAINED RAYS / TRANSIENT STAR

Figure 3. Strength of neon color spreading for the Sustained Rays/Transient Star condition. (A) Data plotted as a function of stimulus onset asynchrony (SOA), (B)Same data replotted as a function of stimulus termination asynchrony (STA). Colored curves refer to 3 different exposure durations of the red star. The results for an exposure duration of 48 ms are taken from Figure 2. Data from subject GMC. Error bars are not shown to keep the graph uncluttered. Dashed vertical lines indicate stimuli that either onset or offset together. As in Figure 2, the datum for SOA = 300 ms has been marked with an empty symbol.
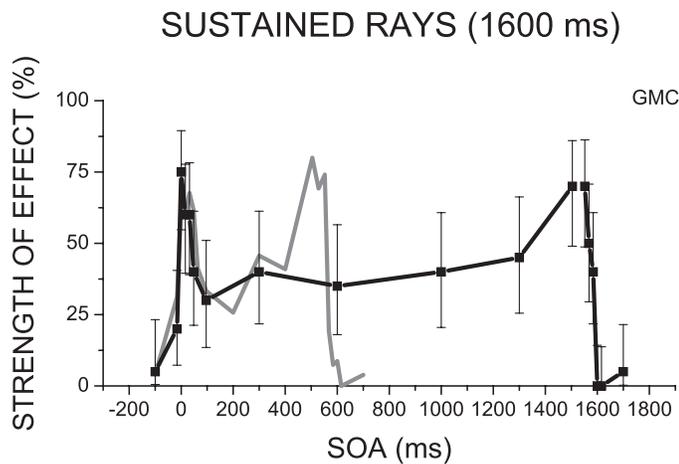
Figure 4. Same as in Figure 2, but with the black rays presented for 1600 ms (thick curve). For comparison, the data obtained with an exposure duration of 600 ms are given by the gray line (from Figure 2, subject GMC).

over more than 1s, but does not rise above 50%. The gray curve is taken from Figure 3A.

Sustained Star/Transient Rays

In a second series of experiments, we rated the strength of neon color spreading using a sustained red star presented for 600 ms and a transient black Ehrenstein figure, flashed for 48 ms at various SOAs. This experiment is complementary to the first one and permits a comparison of the effect when transient and sustained stimuli are exchanged.

Figure 5 shows the percentage of times that the neon color effect elicited by the transient presentation of the Ehrenstein rays in conjunction with a sustained red star was judged stronger than the reference stimulus (Sustained Rays/Transient Star, SOA 300 ms). The curve rises monotonically from 0 to 600 ms with only small intervening peaks after the onset. It crosses the 50% mark at SOAs of 200–300 ms. Neon color spreading is maximal when both the red star and the Ehrenstein figure offset together.

In analogy to Experiment 1, we repeated this experiment with two additional exposure durations for the Ehrenstein figure in observer GMC. Figure 6A plots the data for stimulus onset asynchrony (SOA), whereas Figure 6B shows the results for stimulus offset asynchrony. The curve for 48 ms is taken from Figure 5 (GMC). When the black rays are presented for 96 ms, the resulting curve is generally higher, but changes little in shape. Even with an exposure duration of 24 ms, the curve is clearly higher than its counterpart in Figure 3A. Note the two sharp peaks at SOAs of 0 and 48 ms, when the Ehrenstein figure and the red star onset approximately together.
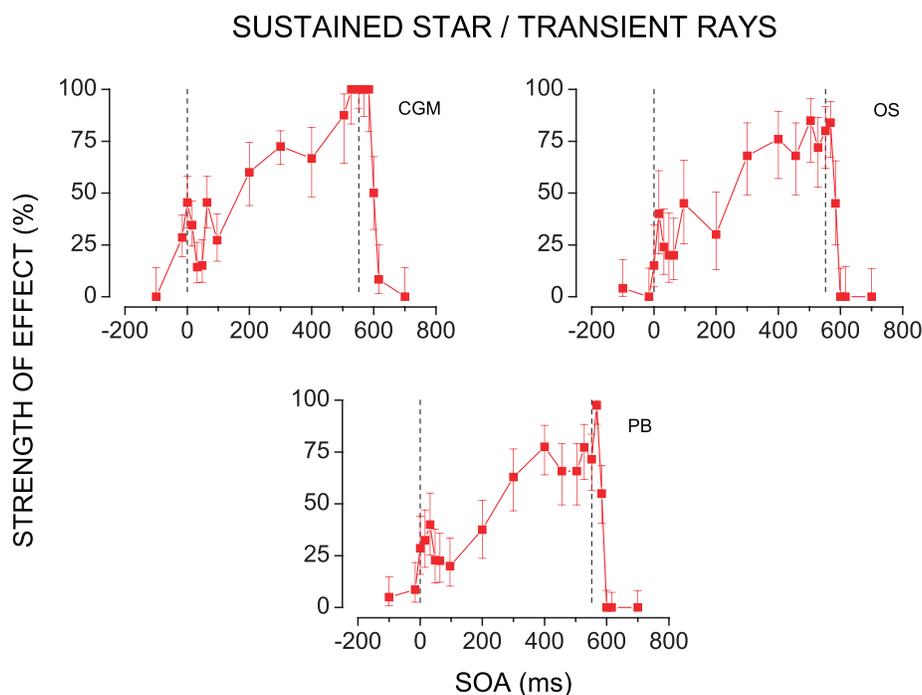

Figure 5. Strength of neon color spreading for the Sustained Star/Transient Rays condition. Exposure duration of the star was 600 ms and of the rays 48 ms. Percentage of responses "Test stronger-than-reference" is plotted as a function of stimulus onset asynchrony (SOA). Dotted vertical lines at 0 ms and 552 ms indicate that the Ehrenstein figure and star either onset or terminate together. The same three subjects from Experiment 1 served as observers. For other details see legend to Figure 2.
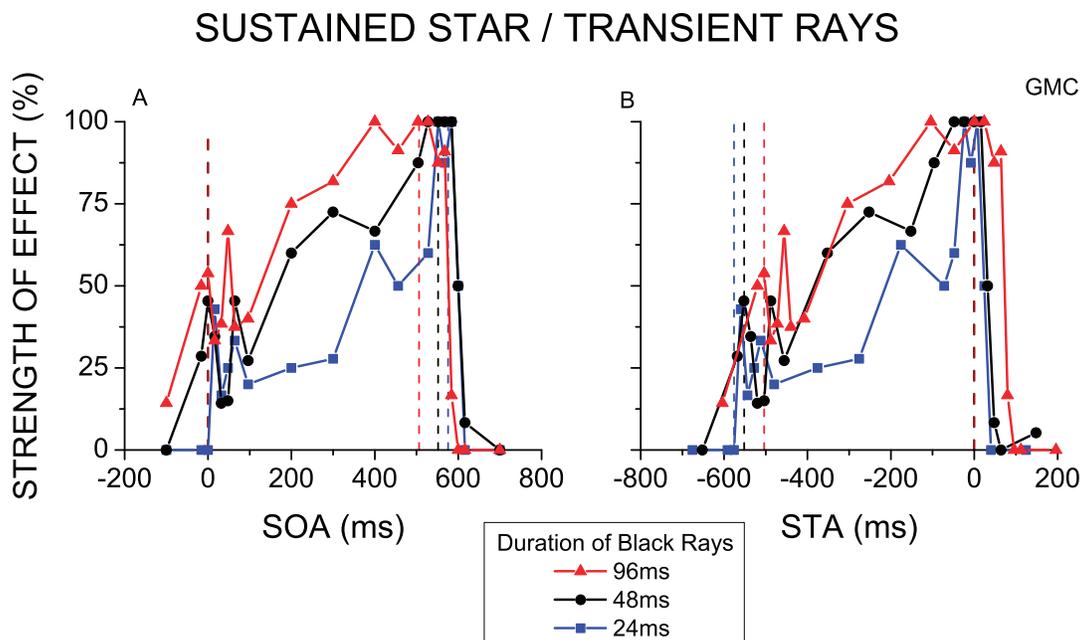
SUSTAINED STAR / TRANSIENT RAYS

Figure 6. Strength of neon color spreading for the Sustained Rays/Transient Star condition. Curves refer to three different exposure durations of the black rays; the red star was shown for 600 ms. The results for an exposure duration of 48 ms are taken from Figure 5. For details see legend to Figure 3. (A) Results are binned according to stimulus onset asynchrony (SOA). (B) Results binned according to stimulus termination asynchrony (STA).

As before, we also used an exposure duration for the star of 1600 ms. Figure 7 plots the results. After a minor peak when both the Ehrenstein figure and the red star onset together, the curve continues to rise and reaches a maximum, when the two stimuli offset together. For most SOAs the gradual incline lies over 50%. The gray curve refers to a sustained star of 600 ms and is taken from Figure 5 (GMC).

Discussion

In this study we used a red star inserted in a black Ehrenstein figure to systematically study the temporal constraints for the emergence of neon color spreading. In particular our work revealed that

1. Neon color spreading occurred consistently, when the Rays-Star pattern was presented for 48 ms and 600 ms, respectively, confirming and extending previous informal reports by Redies and Spillmann (1981).
2. The illusion was strongest when the two patterns (Black Rays and Red Star) onset or offset together, with a bias in favor of the offset. Intermediate SOAs yielded much weaker effects. This indicates that visual transients are critical for the assimilative spreading of color in the neon color effect.
3. The strength of the effect depended on the temporal properties of the channels for the red star and black rays. It increased with increasing exposure duration of the transient stimulus (from 48 ms to 96 ms), but was little affected by an increase of the sustained stimulus (from 600 to 1600 ms).
4. Neon color spreading was stronger for the Sustained Rays/Transient Star condition than for the converse condition. For example, no neon color spreading was observed with a transient star presented for 24 ms compared to a moderately strong effect for a transient Ehrenstein figure shown at the same exposure duration.

The finding that stimulus transients enhance the neon color spreading is consistent with a growing body of literature in macaque and man that shows that transients augment stimulus visibility and this increase may affect stimulus-stimulus interactions (Macknik & Livingstone, 1998; Macknik, Martinez-Conde, & Haglund, 2000; Rieiro, Martinez-Conde, Danielson, Pardo-Vazquez, & Srivastava, 2012; Saarela & Herzog, 2008). In particular, Macknik et al. (2000) using optical imaging showed that the strength of masking varies throughout mask presentation with maximal effects at mask onset and mask termination and intermediate SOAs producing weaker effects. Such effects are likely to originate at early visual processing stages and suggest an early origin also for the observations on neon color spreading reported here.

Whereas SOAs close to the beginning and end of the sustained stimulus produce a strong neon color effect, SOAs between 150 ms and 450 ms elicit relatively weak
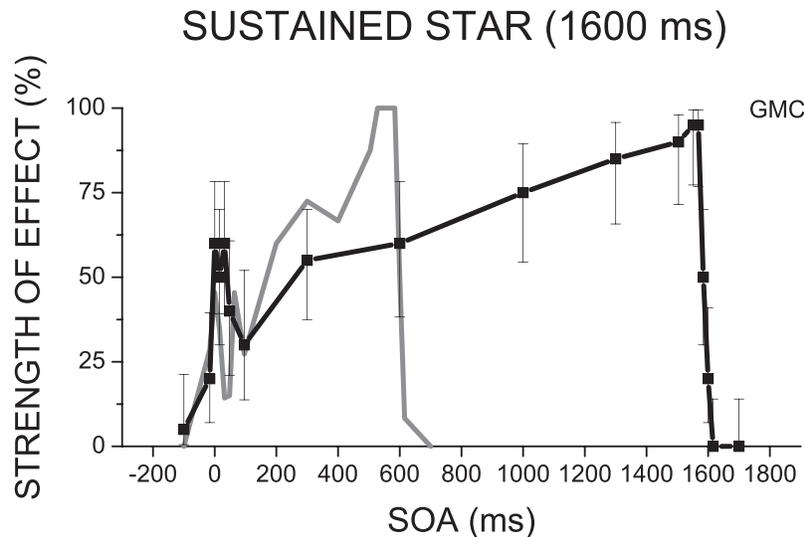
SUSTAINED STAR (1600 ms)

Figure 7. Strength of neon color spreading with a red star presented for 1600 ms (thick curve). Data for the standard condition of 600 ms are given by the gray line (from Figure 5, subject GMC).

effects. Curves for this range of SOA-values have different shapes: roughly U-shaped, when the black rays were sustained and the red star was transient, with little variation during intermediate SOAs (Figure 3A); and monotonically increasing with time, when the relationship was reversed (Figures 5 and 7). These findings suggest different mechanisms for the temporal integration of the black rays of the Ehrenstein figure and the red star.

This notion is consistent with the observation that for intermediate SOAs the sustained red star produces a stronger neon color effect than the sustained Ehrenstein figure. Figure 8 plots the strength of the effect in the Sustained Star condition as a function of the strength of the Sustained Black Rays condition in the central range of SOAs (200–400 ms). The neon color effect produced by the sustained star combined with transient rays is consistently greater than that produced by the converse stimulus pattern. This suggests that the red star is processed by a mechanism having a longer integration time.

The difference between the channels mediating the red star and black lines is also demonstrated by plotting the strength of the neon color effect for an intermediate SOA (300 ms) as a function of the duration of the transient stimulus (Figure 9). The curves show how in the case of Sustained Star/Transient Rays, an increase of the exposure duration above 48 ms has relatively little effect, suggesting that saturation is quickly reached. On the other hand, for the Sustained Rays/Transient Star condition, the neon spreading starts out more gradually, suggesting that an exposure duration of up to 96 ms is still beneficial to the illusion.

A prolonged exposure duration may be beneficial to the illusion for two reasons: (a) It enables neon color

spreading to build up. This would explain why STAs of 0 were optimal. (b) It increases the likelihood that a microsaccade occurs while both stimuli are simultaneously presented (Martinez-Conde, Macknik, & Hubel, 2002, 2004; Rucci, Iovin, Poletti, & Santini, 2007),

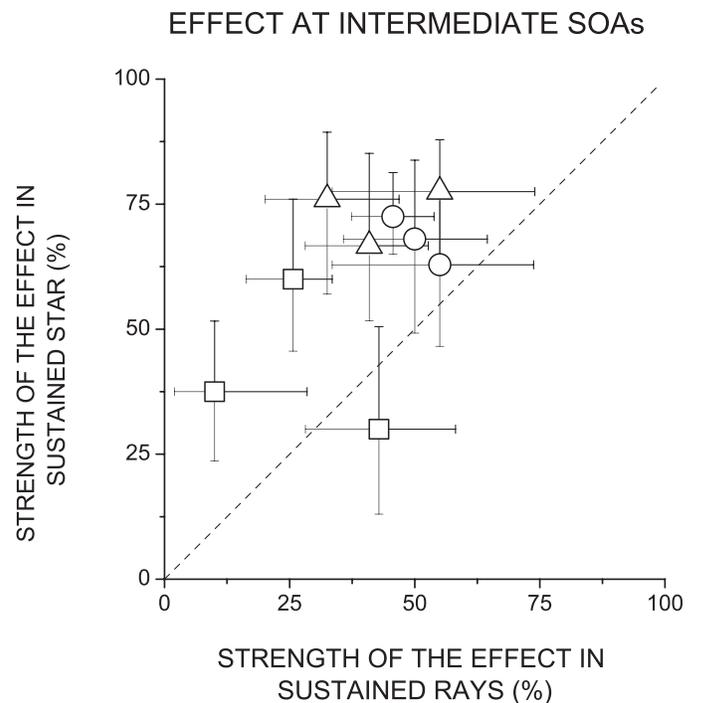## EFFECT AT INTERMEDIATE SOAs

Figure 8. Strength of the neon color effect for the Sustained Star/Transient Rays plotted against the converse stimulus, Sustained Rays/Transient Star, for intermediate SOAs. Each data point refers to one subject at one of three intermediate SOAs: 200 ms (circles), 300 ms (squares), and 400 ms (triangles). Error bars indicate binomial *SEM*.
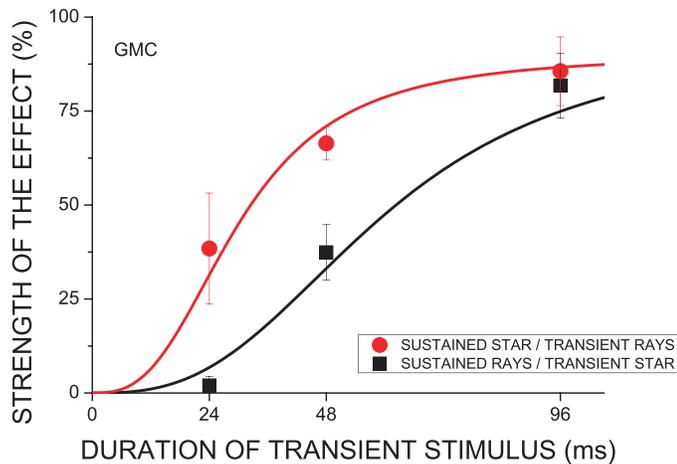
Figure 9. Strength of the neon color effect as function of the duration of the transient stimulus. Data are replotted from Figures 3 and 6 considering only conditions when the transient stimulus appeared in the middle of the sustained stimulus (i.e., SOA = 300 ms). Black indicates data from condition Sustained Rays/Transient Star, Red from condition Sustained Star/Transient Rays. Continuous curves correspond to a Naka-Rushton type monotonic saturating function. See text for more details.

causing a simultaneous transient response in both stimuli and thus enhancing the illusion. The neural responses of both stimuli at this time would be maximal (Macknik & Livingstone, 1998).

The difference between the time course for the black rays and the red star may be explained by the observation that luminance-modulated stimuli are processed faster than color-modulated stimuli (Breitmeyer, 1975; Burr & Corsale, 2001; Burr & Morrone, 1996; Cicchini, 2012; McKeefry, Parry, & Murray, 2003). An estimate of the temporal constants of the channels processing the star and the rays may be obtained by fitting the data with a standard saturating function akin to the Naka-Rushton equation

$$ y = A \frac{x^\beta}{x^\beta + C_{50}^\beta} $$

where A is an arbitrary scaling factor, β determines the steepness of the transition (and typically ranges from 2–4), and C_{50} is the semi-saturating constant (in our case the duration that yields half of the maximum effect). We fixed A and β for both curves (respectively to 90% and 2.8) and we varied C_{50}. The values of the semi-saturating constant yielding the best fit are 30 ms for the Transient Rays and 60 ms for the Transient Star, confirming that the two channels are processed by markedly different temporal properties. Further, these values are consistent with the finding that temporal integration in the channel-mediating the red star could last for a few hundred milliseconds. Indeed, the semi-

saturation values underestimate the full extent of the temporal integration with a nominal value of 60 ms, describing a process that can last up to 150–200 ms.

Our experiments demonstrate that the neon color effect has two constraints: a spatial one and a temporal one. In a static stimulus pattern, the temporal aspect does not reveal itself. However, when the two inducers, rays and star, are shifted in time relative to each other, the resulting illusory effect changes in strength. Conditions are optimal when both stimuli either offset, or less pronounced, onset together. Transients may also be critical for the formation of the crisp illusory contour delineating the reddish disk in the center of the Ehrenstein figure, although this factor was not tested.

There may be other phenomena of a similar kind where two or more stimuli need to be spatially aligned for a strong illusory effect, such as the Kanizsa triangle (Kanizsa, 1979) or Pinna's watercolor effect (Pinna, Brelstaff, & Spillmann, 2001) which may show a similar behavior when presented sequentially. The first illusion is based on end-to-end alignment, whereas the second requires side-by-side alignment (Devinck & Spillmann, 2009). Subjecting these illusions to the same kind of transient-sustained regimen as in the experiments on neon color spreading used here may be an interesting research topic for the future.

Acknowledgments

References

Anstis, S. (2006). In honour of Lothar Spillmann—filling-in, wiggly lines, adaptation, and aftereffects. *Progressive Brain Research, 155*, 93–108.

Breitmeyer, B. G. (1975). Simple reaction time as a measure of the temporal response properties of transient and sustained channels. *Vision Research, 15*(12), 1411–1412.

Bressan, P., Mingolla, E., Spillmann, L., & Watanabe, T. (1997). Neon color spreading: A review. *Perception, 26*(11), 1353–1366.

Burr, D. C., & Corsale, B. (2001). Dependency of reaction times to motion onset on luminance and chromatic contrast. *Vision Research, 41*(8), 1039–1048.

Burr, D. C., & Morrone, M. C. (1996). Temporal impulse response functions for luminance and colour during saccades. *Vision Research, 36*(14), 2069–2078.

Cicchini, G. M. (2012). Perception of duration in the parvocellular system. *Frontiers in Integrative Neuroscience, 6,* 14.

Cicerone, C. M., Hoffman, D. D., Gowdy, P. D., & Kim, J. S. (1995). The perception of color from motion. *Perception & Psychophysics, 57*(6), 761–777.

Devinck, F., & Spillmann, L. (2009). The watercolor effect: Spacing constraints. *Vision Research, 49*(24), 2911–2917.

Grossberg, S., & Mingolla, E. (1985). Neural dynamics of form perception: Boundary completion, illusory figures, and neon color spreading. *Psychological Review, 92*(2), 173–211.

Kanizsa, G. (1979). *Organization in vision. Essays on Gestalt perception.* New York: Praeger.

Macknik, S. L., & Livingstone, M. S. (1998). Neuronal correlates of visibility and invisibility in the primate visual system. *Nature Neuroscience, 1*(2), 144–149.

Macknik, S. L., Martinez-Conde, S., & Haglund, M. M. (2000). The role of spatiotemporal edges in visibility and visual masking. *Proceedings of the National Academy of Science, USA, 97*(13), 7556–7560.

Martinez-Conde, S., Macknik, S. L., & Hubel, D. H. (2002). The function of bursts of spikes during visual fixation in the awake primate lateral geniculate nucleus and primary visual cortex. *Proceedings of the National Academy of Science, USA, 99*(21), 13920–13925.

Martinez-Conde, S., Macknik, S. L., & Hubel, D. H. (2004). The role of fixational eye movements in visual perception. *Nature Reviews Neuroscience, 5*(3), 229–240.

McKeefry, D. J., Parry, N. R., & Murray, I. J. (2003). Simple reaction times in color space: The influence of chromaticity, contrast, and cone opponency. *Investigative Ophthalmology and Visual Science, 44*(5), 2267–2276, http://www.iovs.org/content/44/5/2267. [PubMed] [Article]

Peterhans, E., von der Heydt, R., & Baumgartner, G. (1986). Neuronal responses to illusory contour stimuli reveal stages of visual cortical processing. In J. D. Pettigrew, K. J. Sanderson, & W. R. Levick (Eds.), *Visual Neuroscience.* (pp. 343–351). Cambridge, UK: Cambridge University Press.

Pinna, B., Brelstaff, G., & Spillmann, L. (2001). Surface color from boundaries: A new "watercolor" illusion. *Vision Research, 41*(20), 2669–2676.

Redies, C., & Spillmann, L. (1981). The neon color effect in the Ehrenstein illusion. *Perception, 10*(6), 667–681.

Rieiro, H., Martinez-Conde, S., Danielson, A. P., Pardo-Vazquez, J. L., Srivastava, N., & Macknik, S. L. (2012). Optimizing the temporal dynamics of light to human perception. *Proceedings of the National Academy of Science, USA, 109*(48), 19828–19833.

Rucci, M., Iovin, R., Poletti, M., & Santini, F. (2007). Miniature eye movements enhance fine spatial detail. *Nature, 447*(7146), 851–854.

Saarela, T. P., & Herzog, M. H. (2008). Time-course and surround modulation of contrast masking in human vision. *Journal of Vision, 8*(3):23, 1–10, http://www.journalofvision.org/content/8/3/23, doi:10.1167/8.3.23. [PubMed] [Article]

Takeichi, H., Shimojo, S., & Watanabe, T. (1992). Neon flank and illusory contour: Interaction between the two processes leads to color filling-in. *Perception, 21*(3), 313–324.

van Tuijl, H. F. (1975). A new visual illusion: Neonlike color spreading and complementary color induction between subjective contours. *Acta Psychologica 39*(6), 441–445.

Varin, D. (1971). Fenomeni di contrasto e diffusione cromatica nell organizzazione spaziale del campo percettivo [Translation: Contrast and chromatic diffusion effects [arising] with the spatial organization of the perceptual field]. *Rivista di Psicologia, 65,* 28.

von der Heydt, R., Peterhans, E., & Baumgartner, G. (1984). Illusory contours and cortical neuron responses. *Science, 224*(4654), 1260–1262.