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Illusory colors promote interocular grouping during binocular rivalry

Chai-Youn Kim and Randolph Blake
Vanderbilt University, Nashville, Tennessee

When dissimilar monocular images are presented separately to each of a person's eyes, these images compete for visual dominance, with dominance of one image or the other alternating over time. While this phenomenon, called binocular rivalry, transpires, local image features distributed over space and between the eyes can become visually dominant at the same time; the resulting global figure implicates interocular grouping. Previous studies have suggested that color tends to influence the incidence of global dominance; in this study, we assess whether illusory color can also influence interocular grouping. To test this, we exploited the McCollough effect, an orientation-contingent color aftereffect induced by prolonged adaptation to different colors paired with different orientations. Results show that during binocular rivalry, illusory colors induced by the McCollough adaptation enhance strong interocular grouping relative to preadaptation testing, to an extent comparable in strength with the enhancement induced by real colors. Thus, illusory colors that are present only in an observer's mind are sufficiently potent to influence low-level visual processes such as binocular rivalry.

Color acts like glue: It can bind together features over space and time to promote perceptual grouping. For example, spatially distributed features identical in color tend to be grouped into larger, global forms—grouping by similarity, in Gestalt parlance (Wertheimer, 1958). In the temporal domain, features identical in color tend to be linked over space and time, thereby influencing perception of apparent motion (Gorea & Papathomas, 1989; Green, 1989; Gyulai, 2003) and global motion coherence (Krauskopf & Farell, 1990). Color's glue-like quality also plays a part in the binding of monocular features imaged in the left and right eyes in binocular vision. Color can thus influence perceived depth in complex, multifeature stereo displays (den Ouden, van Ee, & de Haan, 2005); it can promote interocular matching of otherwise uncorrelated random dot patterns (Ramachandran, Rao, Sriram, & Vidyasagar, 1973); it can support depth perception in reverse contrast stereograms (Treisman, 1962); and it can dictate feature matches in stereograms containing multiple ambiguous feature matches (Jordan, Geisler, & Bovik, 1990). Chromatic information, in other words, plays an important role when the binocular visual system attempts to establish interocular feature matches.

Given color's ubiquitous role as a visual binding agent, it is not surprising to learn that color also influences interocular grouping during binocular rivalry, a form of perceptual bistability characterized by alternating periods of dominance between dissimilar monocular images. During rivalry, component parts of a coherent pattern can be presented separately to the two eyes and yet achieve visual dominance at the same time (Kovács, Papathomas, Yang, & Fehér, 1996; Kulikowski, 1992; Papathomas, Kovács, & Conway, 2005). To experience color's effect on figural coherence during rivalry, view the two pairs of rival targets shown in Figure 1, achromatic and chromatic versions of the well-known figure designed by Diaz-Caneja in the early 20th century (see Alais, O'Shea, Mesana-Alais, & Wilson, 2000). Notice how the incidence of global coherence (i.e., complete dominance by one entire figure, the bullseye or the horizontal grating) is greater when the contours that define those figures are colored.[1] This influence of color on rivalry coherence has been confirmed in several studies (see review by Papathomas et al., 2005). In this article, we show that interocular grouping during rivalry can also be promoted by illusory colors produced by orientation-selective color adaptation, the so-called McCollough effect (McCollough, 1965). This finding reveals the perceptual potency of these illusory colors and sheds light on the nature of the interactions between rivalry and the McCollough effect.

General Method

Participants. Three naive observers (D.B., E.Y., and M.K.) and the two authors (C.K. and R.B.) participated in the experiments. All 5 observers have normal or corrected-to-normal visual acuity, normal color vision, and normal stereopsis.

Stimulus displays. Square wave gratings with a spatial frequency of 5.4 cycles/deg were used for both the adapting stimuli and the rival targets (see Figure 2). The black bars of these gratings were immeasurably low in luminance, meaning that the gratings were essentially unity Michelson contrast. During the adaptation phases of an experiment, the gratings appeared within a square aperture with 2.2º of visual angle on a side; during the rivalry phases of an experi-

C.-Y. Kim, chai-youn.kim@vanderbilt.edu

Figure 1. Achromatic (upper pair) and chromatic (lower pair) versions of Diaz-Caneja figures that produce binocular rivalry. When viewed through the stereoscope, the two dissimilar patterns on the left side compete for dominance while, at the same time, the two patterns on the right side also compete for dominance. Over time, observers experience different combinations of dominance between left and right side patterns. Specifically, the perceived image alternates among (1) bullseye on the left and horizontal grating on the right (the left monocular image); (2) horizontal grating on the left and bullseye on the right (right monocular image); (3) bullseye in its entirety; and (4) horizontal grating in its entirety. When the contours defining two patterns (bullseye and horizontal grating) that are separated between the eyes are colored, the incidence of their conjoint dominance (i.e., complete dominance of one entire figure) is greater than when the contours are in black and white. Readers who can free fuse may verify this tendency by comparing rivalry with the lower pair of targets to rivalry with the upper pair of targets.

ment, the gratings occupied a circular field smaller than the adapting patterns. We made the gratings in the rivalry phases smaller so that no parts of them were imaged outside the region of the visual field in which the McCollough effect, which is retinotopically specific (Stromeyer, 1972), was induced. In those parts of an experiment involving color adaptation, the adapting patterns comprised one of the following pairs of diagonal gratings: a red, left-tilted grating and a green, right-tilted grating or a green, left-tilted grating and a red, right-tilted grating. All gratings had contours oriented 45º clockwise from vertical. The Commission Internationale de l'Eclairage (CIE) coordinates for the red color were: $x = .623$, $y = .330$, luminance = 9.72 cd/m^2; for the green color, $x = .289$, $y = .592$, luminance = 36.7 cd/m^2.

For periods of the adaptation experiment in which rivalry was being tested, one of the two rival targets had right-tilted diagonal contours on the left and left-tilted diagonal contours on the right, and the other target had left-tilted diagonal contours on the left and right-tilted diagonal contours on the right. Thus, these rival targets were configured in such a way that the left half of one target and the right half of the other target comprised a coherent pattern when grouped together.

All stimuli were presented on a 21-in. NEC video monitor (1,024 × 768 resolution, 75-Hz frame rate) under the control of a Macintosh G4 computer. Dioptic (eyes receive the same image) adaptation patterns and dichoptic (eyes receive different images) rival targets were presented on the left and right halves of the monitor, which was viewed from a distance of 35 in. through a mirror stereoscope. High-contrast checkerboard frames (width of 0.32º of visual angle) surrounded the pattern seen by the left eye and the one seen by the right eye, with these two frames serving to promote and maintain stable binocular alignment.

EXPERIMENT 1
Binocular Rivalry and Real Color

The experiments that have shown that color enhances global coherence during rivalry have used deeply saturated, highly conspicuous colors (see, e.g., Papathomas et al., 2005). The orientation-contingent colors defining the McCollough effect, on the other hand, are faint (i.e., weakly saturated). Before proceeding to our main experiment, we felt it necessary to determine whether enhanced coherence during rivalry could be obtained with weak, desaturated colors comparable to those produced by the McCollough effect. This was the purpose of our first experiment.

Method

Stimulus conditions for these measurements are illustrated schematically in Figure 2. Observers tracked binocular rivalry while viewing achromatic rival gratings—the no-color (NC) condition—and while viewing rival gratings for which the light portions of the grating were colored faint green or faint pink—the real color (RC) condition. For the RC condition, we tried to imitate the color appearance created by the adaptation conditions used in our main experiment, but we did not use a formal procedure to obtain a precise match.

For both NC and RC conditions, observers viewed a pair of rival targets for 60 sec and pressed and held a button whenever the dominant pattern consisted of one orientation entirely (i.e., the perceptual state indicative of interocular grouping). If the observer was depressing the button at the end of the 60-sec tracking period, the rival targets remained present until the observer released the button; this procedure was followed to preclude truncation of periods of exclusive dominance at the end of a trial. Each trial was followed by at least 1 min of rest, and a total of 12 tracking periods were administered for each of the two conditions.

Results

Results from this preliminary experiment are given in Figure 3A, which shows the mean percentage of interocular grouping (i.e., the total duration of exclusive visibility of a single orientation with respect to the entire trial duration, which was set at 100%) for the NC and RC conditions. For all 5 observers, the RC condition yielded a higher incidence of interocular grouping than did the NC condition, meaning that the cumulative duration of exclusive dominance of a single orientation was longer when the two matching components of the rival target were the same color. To rule out the possibility that the result in the RC condition was attributable to the presence of color per se, we also measured interocular grouping in 2 observers using rival targets in which the faintly

Figure 2. Schematics of targets used during rivalry and patterns used during induction and maintenance of the McCollough effect. (A) For the no color (NC) condition, rival targets consisted of black and white diagonal contours oriented 45º clockwise in one half of the circular target and 45º counterclockwise in the other half. Contours on corresponding regions of the left- and right-eye rival targets were opposite in orientation, producing stimulus conditions that evoked vigorous binocular rivalry. (B) For the real color (RC) condition, the contours were colored faint green and faint pink to simulate the color sensations characteristic of the McCollough effect. (C) The McCollough effect was induced and maintained by exposing both eyes to black and green and to black and red gratings, with the orientations of those gratings differing by 90º (and always identical for both eyes). These two pairs of dioptic gratings were sequentially presented for 5 sec each during an initial 10-min adaptation period and during 60-sec refresh periods.

colored contours in both rival targets were either all pink or all green—the uniform color (UC) condition. The UC condition yielded results comparable to those from the NC condition (Figure 3A). Thus the enhanced interocular grouping in the RC condition is attributable to the pairing of unique colors with particular orientations, not to the mere presence of color.

Histograms plotting the distribution of dominance durations indicative of interocular grouping for the NC and RC conditions for all 5 observers are shown in Figure 4. Comparing the NC and RC histograms shows that for most observers, real colors increased the incidence of interocular grouping by lengthening the dominance durations for that condition—the tail of the RC histogram extends further to the right along the time axis. However, for other observers (e.g., E.Y.), real colors increased the incidence of interocular grouping by boosting the frequency of conjoint dominance—the RC histogram was more peaked at the maximum.

This result replicates earlier findings (see, e.g., Papathomas et al., 2005) and, importantly for our purposes, demonstrates that interocular grouping can be obtained with weak colors that approximate those produced by orientation-contingent color adaptation, also known as the McCollough effect. Confirming this outcome sets the stage for the main experiment, which is described next.

EXPERIMENT 2
Interocular Grouping and the McCollough Effect

In this experiment, the rivalry tracking period involved presentation of achromatic gratings only (the same rival targets as those used in the NC condition of the previous experiment). Prior to tracking rivalry, however, the test session began with an extended period of adaptation to black/green and black/red gratings differing in orientation; these conditions were designed to induce the McCollough effect.

Method

The initial 60-sec period of rivalry tracking was preceded by a 10-min period of adaptation[2] during which a pair of adapting stimuli were sequentially presented to both eyes every 5 sec. The conditions of adaptation differed among observers. Specifically, 3 observers (E.Y., M.K., and R.B.) dioptically viewed green, left-tilted gratings for 5 sec and then red, right-tilted gratings for 5 sec, and so on throughout the adapting period. The other two observers (C.K. and D.B.) adapted to red, left-tilted gratings and green, right-tilted gratings; panel C of Figure 2 shows dioptic pairs of adapting stimuli used for these two observers. After the initial 10-min adapting period, the observer dichoptically viewed the pair of black and white rival targets—the illusory color (IC) condition—for 60 sec; these rival targets were exactly the same as those used for the NC condition (see panel A of Figure 2.). During this rivalry period, the observer pressed and held a button whenever he or she perceived a single, coherent orientation over the entire circular region of the rivalry field. Each period of rivalry was followed by a 60-sec, top-up adapting period during which the red and the green gratings again appeared alternately for 5 sec each. This sequence continued until the observer had completed twelve 60-sec periods of rivalry tracking using the achromatic rival targets.

Results

Not surprisingly, none of the observers perceived any hint of color when viewing the achromatic rival gratings prior to the extended adaptation period. But as expected, all observers reported experiencing faint but conspicuous colors when they viewed the diagonal rival targets during the adaptation phase of the experiment. As an aside, the illusory colors experienced when viewing diagonal contours persisted for days after this experiment, a definitive

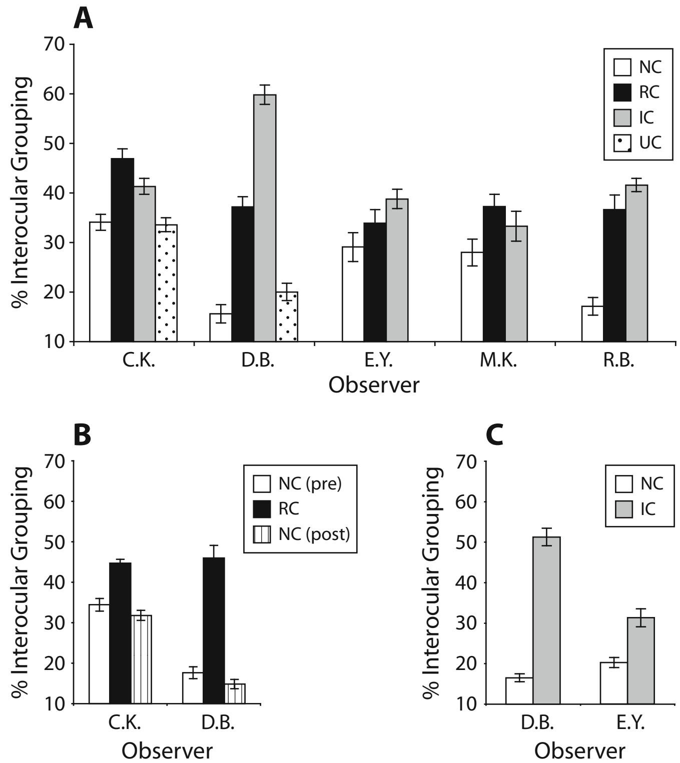

Figure 3. Results from Experiments 1 and 2 and control experiments. Histograms showing the incidence of interocular grouping (total percentage of time that a given orientation was dominant throughout the entire extent of the circular rival target). (A) Results from Experiments 1 and 2 (NC, RC, and IC conditions) and the control experiment that used uniform colors (UC) for both rival targets. (B) Results from the control experiment that tested the priming hypothesis. (C) Results from the control experiment using vertical and horizontal gratings.

characteristic of this orientation-contingent color aftereffect (Jones & Holding, 1975; Riggs, White, & Eimas, 1974).

The incidence of interocular grouping for IC targets is shown in Figure 3A. Comparing these values with the tracking results measured prior to adaptation (NC condition) shows that adaptation increased the incidence of interocular grouping for each of the 5 observers. As mentioned earlier, no attempt was made to match precisely the faint real colors to the illusory colors produced by adaptation, so we have no reason to expect the incidence of grouping to be equivalent for the RC and IC conditions. Still, just as with the faint real colors in the RC condition, the increased incidence of interocular grouping in the IC condition resulted either from a general lengthening in the average duration of dominance of contours with the same apparent color or from a more pronounced peak in the maximum of the histogram (see Figure 4, bottom row).

Is it possible that enhanced interocular grouping produced by the RC condition in Experiment 1 influenced the IC results in Experiment 2? To rule out this priming hypothesis, we performed the following control experiment. Two of the observers (C.K. and D.B.) who participated in Experiments 1 and 2 were tested in the sequence of 12 NC trials, 12 RC trials, and 12 NC trials. Results showed no significant difference between grouping during the NC trials that preceded the RC trials and those that followed the RC trials (Figure 3B). These results imply that experiencing real colors does not per se influence grouping on subsequent trials in which physical colors are not presented.

To test the generality of our results, two observers (D.B. and E.Y.) were retested on NC and IC conditions using a new set of adaptation and test patterns. Within both conditions of this follow-up experiment, 12 60-sec trials involving rival targets comprising both vertical and horizontal contours were presented to the observer. At the start of this follow-up experiment, these new rival targets appeared uncolored, as would be expected given the orientation selectivity of the McCollough effect (cf. Ellis, 1977). In the IC condition, D.B. adapted to a red vertical grating and a green horizontal grating, and E.Y. adapted to a green vertical grating and a red horizontal grating. As shown in Figure 3C, the results from Observers D.B. and E.Y., both of whom adapted to colored horizontal and vertical gratings and were tested with achromatic vertical and horizontal rival gratings, were identical to the results for these observers shown in Figure 3A. These results show that

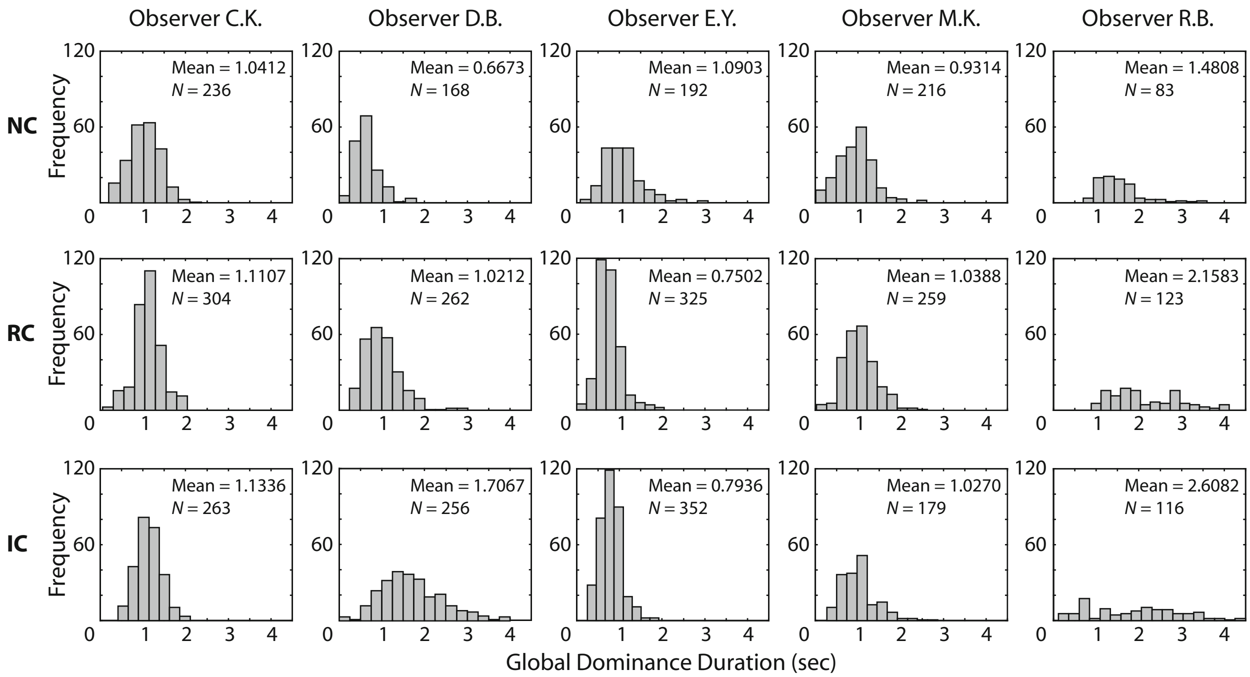

Figure 4. Frequency distributions showing individual durations of interocular grouping for NC, RC, and IC conditions for all 5 observers.

interocular grouping enhanced by the McCollough effect is not restricted to a specific stimulus configuration; we found the same pattern of results with diagonal gratings that we found with vertical and horizontal gratings.

It is natural to wonder about the consequences of introducing different colors into the two halves of a rival target consisting of identically oriented contours. Would this decrease the incidence of interocular grouping? While this condition could be tested using real colors, the conditions necessary for inducing a McCollough aftereffect make it infeasible to induce different illusory colors in different regions of a rival target consisting of identical orientations. To do so would require strict fixation throughout the lengthy period of adaptation, and this requirement would introduce complications associated with the colored afterimages that would invariably be induced (afterimages that are precluded by the freedom to move the eyes during the McCollough induction period).

DISCUSSION

Vision scientists have developed a number of tricks for producing compelling illusory colors—that is, for creating an impression of color when only achromatic stimuli are visible. One trick, for example, creates illusory colors by rapidly flickering specially configured achromatic contours (see, e.g., Benham, 1894), and another creates illusory colors within the uncolored interior of a figure defined by chromatic boundaries (see, e.g., Pinna, Brelstaff, & Spillmann, 2001). While fascinating in their own right, illusory colors also offer an effective means for dissociating physical stimulation from perceptual experience. With this idea in mind, we used a well-known form of color–contour adaptation (McCollough, 1965) to imbue achromatic gratings with illusory colors; our aim was to discover whether these colors could exert an influence on visual grouping despite their exclusive origins in the mind and not in the world.

In Experiment 1, we confirmed that weakly saturated colors can promote perceptual grouping between the eyes during binocular rivalry and thus extended the known range of conditions under which color influences interocular grouping (Papathomas et al., 2005). Note that this conclusion was reached by comparing visual grouping under two distinct conditions, NC and RC, in which physical stimulation and perceptual experience covaried, as they ordinarily do in the natural environment. The more important, novel finding in our study came from Experiment 2, in which we used the McCollough effect to dissociate physical stimulation and perceptual experience, a useful trick that can be performed in the laboratory (Kim & Blake, 2005). Thus it was possible to compare the effects of two conditions, NC and IC, wherein physically identical stimuli (black and white contours) evoked different perceptual experiences: The NC condition evoked achromatic gratings; the IC condition, colored gratings. Here we found that the IC stimuli enhanced perceptual grouping relative to the NC stimuli, even though the two sets of stimuli were physically identical. Perceptual appearance per se, in other words, determined the strength of grouping. Conversely, we also compared the effects of two conditions, IC and RC, wherein physically different stimuli (black and white contours in the IC condition; red and green contours in the RC condition) evoked essentially equivalent perceptual experiences (i.e., colored gratings). And, again, perceptual appearance, not physical stimulation, determined the strength of grouping: The IC stimuli, although devoid of actual color, enhanced grouping to a degree comparable with that found with the genuinely colored RC stimuli.

Our study provides a unique, compelling demonstration of the perceptual potency of illusory colors. Perhaps the closest analogue to our result can be found in synesthesia literature, in which several studies have shown that illusory synesthetic colors evoked by alphanumeric characters behave like real colors in a variety of perceptual tasks (Laeng, Svartdal, & Oelmann, 2004; Palmeri, Blake, Marois, Flanery, & Whetsell, 2002; Ramachandran & Hubbard, 2001; Kim, Blake, & Palmeri, 2006). Indeed, the effect of illusory colors on interocular grouping found in the present study is reminiscent of the effect of synesthetic color on binocular rivalry: synesthetic colors promote grouping among illusory colored achromatic characters comprising rival targets (Kim et al., 2006).

To reiterate, we find that illusory colors created by the McCollough effect act just like real colors in their ability to promote perceptual grouping between the eyes during binocular rivalry: Contours of a given orientation distributed between the two eyes remain dominant in awareness for longer durations, on average, when those contours appear to be the same color. Besides demonstrating the perceptual potency of illusory colors, our findings have implications for our understanding of rivalry and of the McCollough effect.

Considering rivalry first, we know that factors that influence vision under nonrivalry conditions—attention, salience, and context—also affect the predominance of a given stimulus during rivalry (Blake & Logothetis, 2002). Our results show that color, including illusory colors from the McCollough effect, can be added to this list of influences. Accordingly, our findings substantiate the view that dominance phases of rivalry are equivalent to ordinary vision. The present results also reveal that it is *perceived* color that binds spatially distributed features into a coherent form in rivalry. This aspect of our results dovetails nicely with other recent work showing that dichoptic differences in surface color appearance, not light wavelength, can instigate rivalry (Andrews & Lotto, 2004; Hong & Shevell, 2006; but also see Wallach & Adams, 1954).

Our findings also complement earlier results showing that the McCollough effect, a form of adaptation thought to arise early in visual processing (Byth, McMahon, & King, 2000; Humphrey & Goodale, 1998; McCollough, 1965; Stromeyer, 1972; Thompson & Latchford, 1986), can be induced even when the inducing patterns themselves are suppressed from awareness during binocular rivalry (White, Petry, Riggs, & Miller, 1978). If, as this finding suggests, the neural site of adaptation underlying the McCollough effect precedes the site at which rivalry suppression transpires, it stands to reason that the illusory colors produced by this adaptation should influence rivalry, as indeed they do.

AUTHOR NOTE

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NOTES

1. We recognize that black and gray contours can be said to possess color, but in this paper we use the term *color* to refer to chromatic conditions evoking a sense of hue.

2. For observer M.K., the initial adapting period lasted 20 min, a duration necessary to produce the McCollough aftereffect for this individual.

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