force in flesh-eating dinosaurs may be estimated by ratcheting up the assumed forces applied at points along the tooth row: these studies confirm estimates that *Tyrannosaurus* bit with a point force of 13,000 Newtons at its longest teeth, and the skull, although superficially lightly connected, could readily withstand tearing forces as it yanked off great chunks of flesh from its prey (Figure 5).

Dinosaurs were large, and their secret seems to have been a combination of abundant small juveniles (dinosaur nests contain 8–50 eggs; juvenile body size was constrained by maximum egg size), rapid growth to sexual maturity in 5–15 years, and variable physiology (switching from full endothermy to inertial homeothermy). Modern reptiles cannot match the rapid growth rates seen in dinosaurs, and modern birds and mammals are committed to endothermy and so cannot enjoy the benefits of switching it off at large body size. Future biological studies of dinosaurs may focus on their population structures and energy pathways in Jurassic ecosystems as we seek to understand how these astonishing animals retained their key position on Earth for so long.

Further reading

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Filling-in afterimage colors between the lines

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It is known that when a colored surface is viewed for some time and a blank screen is presented afterwards, an afterimage can be perceived in the complementary color. Color appearances in afterimages are due to adaptation of retinal cones and they are especially vivid when contours, presented after the adapting image, coincide with the blurred edges of the afterimage [1]. We report here that one and the same colored stimulus can induce multiple, differently colored afterimages, and that colored afterimages can also be perceived at regions that were not adapted to color. The observed filling-in of afterimage colors strongly depends on contours presented after the colored stimulus, revealing color–contour interactions that resemble filling-in of ‘real’ colors.

We measured the effect of contours on the filling-in of afterimage colors by adapting to star-like shapes that comprised red and cyan colored quadrilateral spikes attached to a grey central area (Figure 1A). This adapting star alternated over time with different achromatic test outlines. These test outlines were positioned either to include the red spikes and exclude the cyan spikes of the adapting star, or *vice versa*. The afterimage-color, which appeared to be tinged with red or cyan, filled in the outlined area, even within the grey central area that was never colored (see Movie S1 in the Supplemental Data). Moreover, when both test outlines were presented in succession (as indicated in Figure 1A), the color of the afterimage switched rapidly (see Movies S2A/B in the Supplemental Data). That is, multiple colored afterimages were perceived in the central area of the test outline, following one and the same adapting stimulus.

Apparently, the shift of contours presented after the colored stimulus changes the signals that are averaged between the contours. Figure 1B shows color matching data from three observers, using the same procedure as in Figure 1A (see also Experiment 1 in the Supplemental Data). The perceived afterimage color depended on the adapting colors that lay on both sides of the subsequent test outline; the colors inside the test outline induced an afterimage in the complementary color, whereas the colors outside the test outline induced an afterimage color similar to the inducing colors, because of contrast induction [2]. Both effects were confirmed in a second experiment, using adapting stimuli with a broader range of equiluminant colors (see Experiment 2 in the Supplemental Data). In this color judgement experiment (15 observers), there were adapting stimuli with just one color that could either be included or excluded by the subsequent test outline, as well as stimuli with two different colors, balanced with regard to the position of the test outlines (as in Experiment 1). For the various color combinations, the results revealed mixed afterimage colors, but also showed that the colors inside the subsequent test outline have a dominant influence on the perceived afterimage.

Our results show that afterimage colors may spread to previously uncolored areas, triggered and constrained by contours presented after the colored image. In the past decades, similar color–contour interactions have also been reported for filling-in phenomena with ‘real’ colors like the neon-color effect or the watercolor illusion [3,4]. It is commonly believed that such color filling-in phenomena are generated by neural circuitry that also process normal color perception, where early cortical areas are thought to fill-in colors by means of a contour-based filling-in mechanism [4,5]. To date, however, a full explanatory account of filling-in effects still has to be given [4–10]. Our results with afterimages indicate that cortical color filling-in processes are also involved when incoming signals are caused by adaptation of retinal receptors. Given the similarities between ‘real-color’ filling-in and afterimage color filling-in, a common underlying mechanism for these effects seems plausible as well. For example, the same

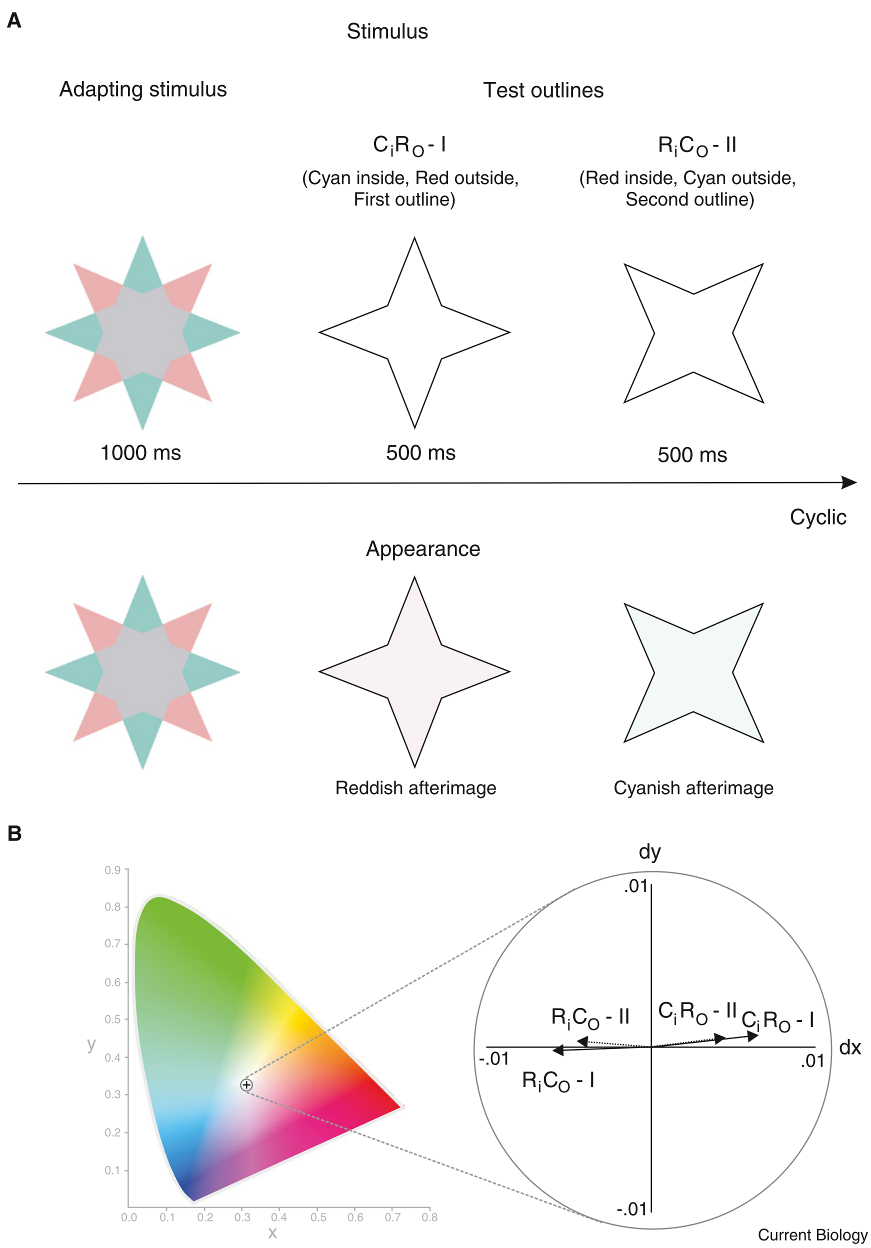

Figure 1. Matching afterimage colors.

(A) The adapting stimulus was a colored star with four red and four cyan quadrilateral spikes and a grey inner area (presented for 1000 ms), which alternated over time with two successive test outlines (presented 500 ms each). The stimulus sequence induced differently colored afterimages within the test outlines. The observers had to match the afterimage color in the center of the *first* and the *second* test outline. Four basic stimulus conditions are considered: C_iR_o-I: Cyan inside, Red outside, First outline (which refers to the condition where the cyan spikes of the previously presented adapting stimulus appeared at a position inside, and the red spikes outside the first test outline); R_iC_o-I: Red inside, Cyan outside, First outline; C_iR_o-II: Cyan inside, Red outside, Second outline; R_iC_o-II: Red inside, Cyan outside, Second outline. (B) The color matching results (mean results for 3 observers) are plotted in CIE (x,y) color space. The small cross in the diagram on the left indicates the CIE (x,y) values of the background during the matching phase; the diagram on the right zooms in on that region. The arrows represent the mean color impression with respect to the background. Generally, the R_iC_o conditions revealed cyanish afterimages, whereas the C_iR_o conditions revealed reddish afterimages. For each of the observers, the mean color impression was different from the background in each condition ($F(2,6) > 18.2$; $p < 0.005$), and the R_iC_o conditions differed from the C_iR_o conditions ($F(2,13) > 73.8$; $p < 0.0001$). See Supplemental Data (Experiment 1) for detailed results.

color-edge selective neurons that are thought to be responsible for the filling-in effect in the watercolor illusion [3,9,10] might also trigger the filling-in of afterimage colors. Various modified versions of our stimuli could be used to further explore the underlying mechanisms (see Movie S3 in the Supplemental Data for an example with illusory contours as test outlines). Altogether, our filled-in afterimages reveal color–contour interactions that resemble those of ‘real’ colors, providing additional data for understanding color filling-in.

Supplemental Data

Supplemental data are available at http://www.cell.com/current-biology/supplemental/S0960-9822(09)00811-2.

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