

microcircuits and specific neuronal subpopulations.

In conclusion, the study of the neuronal mechanisms of insular function promises to deepen our understanding of the neuronal underpinnings of complex aspects of brain functioning, like the impact of feelings and emotions on flexible behaviors, such as decision-making, that occur in everyday life.

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Seeing lightness in the dark

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From intense sunlight in bright snow down to a moonless night in a dark forest, we can use light to recognize objects and guide our actions. This remarkable range mainly rests on having two different types of photoreceptors, the rods and the cones. The cones are active under daylight conditions, allowing high acuity and color vision. Rods are mainly active under very dim illumination conditions and have an exquisite sensitivity to light [1]. There are obvious detriments to visual perception in near darkness, such as a central scotoma, reduced motion perception [2], and most of all a lack of color [3]. There is only one type of rod, and thus intensity and wavelength differences cannot be disentangled when only the rods are active. This is captured well by the old saying “at night all cats are gray”, meaning that different colors inevitably get mapped onto different shades of gray. Here we show that the perception of lightness is also different for night vision: our results indicate that surfaces that appear to be white under daylight conditions, at best, appear medium gray under night vision, suggesting that activation of the cones is necessary for the perception of white.

We tested whether observers report surfaces as appearing ‘white’ under dark adaptation viewing conditions. Observers were shown ten pieces of paper, either A4 sized sheets or square cut-outs with a side length of 5 cm, that were printed such that they were equally distributed along a well-established lightness scale: the L* scale of the CIELUV color space [4]. As photopic and scotopic stimulation cannot be achieved at the same time, observers were first shown our darkest and whitest papers under bright photopic conditions and were asked to memorize these as 0% white (black) and 100% white, respectively. Later on, observers were shown each paper, one at a time, and they were asked to

state their white rating for each paper, in steps of 10% along their memorized photopic white scale. We tested four illumination conditions that were all metameric to natural daylight (D65) in a counter-balanced design. The bright photopic (277 cd/m²) and dim photopic (28 cd/m²) conditions would mainly activate cone photoreceptors, the scotopic (1.2 x 10⁻⁴ cd/m²) condition would only activate rods, and the mesopic (1.8 cd/m²) condition would produce activity of rods and cones. For the smaller cut-outs, we also compared reports for foveal and peripheral viewing, since the fovea is dominated by cones.

Figure 1 contains the white ratings that observers reported for the papers. As expected, we find that observers properly recognize the brighter papers as lighter and the dimmer papers as darker across all illumination conditions. But while the most reflective paper is judged as white under photopic conditions, it is reported as gray under the mesopic and scotopic conditions, eliciting a report of 64% white under the scotopic conditions and of 79% white under the mesopic conditions (Figure 1A). For the smaller papers, the reported scotopic percept of white decreased to 47% white, with no significant difference between foveal or peripheral fixation (Figure 1B; one-sample t-test, darkest chip: $t(5) = 0.98$, $p = 0.37$, lightest chip: $t(5) = 0.70$, $p = 0.51$). For the scotopic conditions, we found that the darkest papers were consistently perceived as black. Under the brightest photopic condition, the A4 sized black paper appeared as a dark gray (11% white). Essentially, the lightness scale is compressed as either the stimulus becomes smaller or the illumination becomes darker, with the whiter end of the scale being more heavily compressed and the blacker end of the scale remaining relatively untouched.

These results present a stunning failure of lightness constancy, the ability of human observers to consistently judge surface reflectance as unchanging, despite changes in illumination. Modern lightness perception theories typically propose that the visual system separates surface reflectance (lightness) from direct and reflected illumination

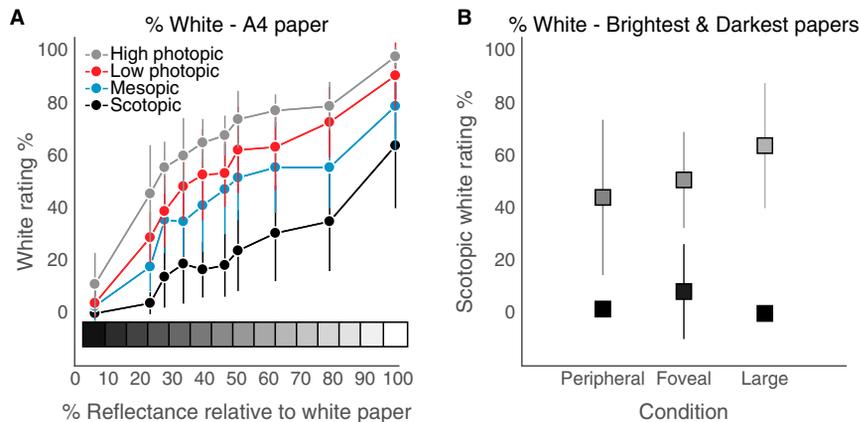


Figure 1. Reported perception of white under different adaptation conditions. (A) Percent of white perceived for A4 sized sheets of paper (population mean). The white scale at the bottom of the figure is an approximate depiction of our stimulus set. The most reflective paper in our set was rated as white under both the high photopic (gray points) and low photopic (red points) conditions. In the scotopic condition (black points), the most reflective A4 paper was rated as ~64% white and during the mesopic condition (blue points), it was rated as ~79% white. The results for the chips are shown in Supplemental Figure S1. (B) Scotopic white ratings for the brightest and darkest stimuli for each condition (population mean). The smaller cut-outs (foveal and peripheral conditions) were judged as dimmer than the larger A4 papers. During scotopic viewing, the darkest papers were consistently perceived as black. The colors of the symbols depict approximate photopic physical correlates of the reported percepts. Error bars depict the standard error of the mean (SEM).

(brightness). Once that process is complete, models that embody these theories propose mechanisms for assigning perceptual gray levels to surfaces for the purposes of object recognition, shape/material perception, and categorization. The best known of these theories is anchoring theory, which proposes that the brightest surface in a scene is assigned the percept of white and all other surfaces are placed somewhere on a perceptual gray scale, depending on their luminance relative to the chosen white surface [5]. In other words, the percept of white is ‘anchored’ or ‘attached’ to the brightest surface in a scene. If a visual scene is sufficiently variegated in terms of different reflectances, it is likely to include an object that is highly reflective. Therefore, in these conditions, anchoring promotes lightness constancy. In mesopic and scotopic viewing conditions, one would still expect lightness constancy to work, since only the photoreceptor inputs have changed, while the rest of visual processing remains presumably unaltered. Our results show the contrary: while observers do not perceive white when presented with highly reflecting surfaces in the dark, they did so

eventually when we increased the luminance of self-luminous patches on a computer display (see Supplemental Information). Observers indicated that they perceived ‘white’ after adjusting the patches to be outside of the scotopic range (see Supplemental Figure S2), indicating that a percept of white is possible once the luminance of the stimulus is high enough, presumably when cone photoreceptors are being activated.

Historically, Katz [6] had reported a change in appearance with decreasing illumination intensity, but his phenomenological account claims that he could still see “a distinct white” during scotopic viewing, although it was not “a pronounced white”. However, it does not seem that he performed a task that required observers to compare the scotopic percept to the photopic impression of white. Modern studies on lightness were mainly concerned with the photopic range. Logvinenko and Maloney [7] found that as photopic illumination becomes dimmer, the lightness scale becomes compressed, with white percepts appearing dimmer and black objects appearing brighter. One could extrapolate from their findings that in the extreme

case of scotopic vision, everything should appear as one gray value. This extrapolation seems to be invalid, because we observe dramatic changes in the appearance of gray and white, but not black, when going from cone to rod vision. Radonjic *et al.* [8] asked participants to match luminous patches from different dynamic range images (from ~30:1 to 10,000:1) to an extended Munsell neutral palette consisting of surfaces whose reflectance varied by about 30:1. They found a massive compression of the lightness scale, demonstrating that perception maps a large range of luminances onto a much smaller range of surface lightnesses. Interestingly, observers consistently matched the brightest luminance to the most reflective surface of the matching scale, suggesting that anchoring applies to scenes with different dynamic ranges. But they never went into a fully dark adapted state and their observers only made judgments about the equality of two patches of light, not about their absolute level of lightness.

More recently, Anderson *et al.* [9] presented observers with dark gray target chips (up to 30% reflectance) surrounded by darker paper chips in a black room. The targets were consistently matched to lighter samples from a matching set presented in a well-lit different room. This is different from our result, where a light patch appears darker under scotopic illumination. However, the experiments cannot be directly compared, as they did not measure the appearance of a white (highly reflective) target surface, they did not test scotopic conditions, and their observers could integrate all the reflectance changes while walking between the two rooms.

Here, we directly asked participants about the appearance of highly reflective surfaces in a state of dark adaptation — whether it is possible to experience a white percept in scotopic vision. We have shown that the lightness scale undergoes a significant, but asymmetric, compression in the scotopic range: white percepts are not present during scotopic viewing, while black objects are consistently perceived as black across illumination changes. We propose that white is

a percept that is elicited by cone activation. This indicates a failure of lightness constancy at low light levels. Even though something appears white during photopic viewing, it does not appear white at scotopic luminance levels, and even white cats at night appear gray.

SUPPLEMENTAL INFORMATION

Supplemental Information includes a description of the experimental methods and two figures, as well as further details on the experiment that used the smaller paper chips and the experiment that used a monitor to produce self-luminous patches, and can be found with this article online at <http://dx.doi.org/10.1016/j.cub.2017.05.008>.

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Chimpanzee culture extends beyond matrilineal family units

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The ‘grooming handclasp’ is one of the most well-established cultural traditions in chimpanzees. A recent study by Wrangham *et al.* [1] reduced the cultural scope of grooming-handclasp behavior by showing that grooming-handclasp style convergence is “explained by matrilineal relationship rather than conformity” [1]. Given that we previously reported cultural differences in grooming-handclasp style preferences in captive chimpanzees [2], we tested the alternative view posed by Wrangham *et al.* [1] in the chimpanzee populations that our original results were based on. Using the same outcome variable as Wrangham *et al.* [1] — the proportion of high-arm grooming featuring palm-to-palm clasping — we found that matrilineal relationships explained neither within-group homogeneity nor between-group heterogeneity, thereby corroborating our original conclusion that grooming-handclasp behavior can represent a group-level cultural tradition in chimpanzees.

Wrangham *et al.* [1] investigated how and why individuals differed in their tendency to engage in palm-to-palm clasping, and whether any variation could be explained by demographic (for example, sex or age) and/or individual (for example, motivation) factors in the chimpanzees of the Kanyawara community, looking at 35 individuals and 932 bouts of grooming handclasps. The authors concluded that “chimpanzees conform in their grooming styles only to their mothers, not to the larger group” [1]. Importantly, the authors keep open the option that other mechanisms might be guiding grooming-handclasp behavior by referring to the fact that chimpanzees at the Chimfunshi Wildlife Orphanage

Trust, Zambia, seemed to reach high frequencies of palm-to-palm clasping in the absence of long-term matrilineal relationships [1].

The Chimfunshi chimpanzees not only exhibited high palm-to-palm clasping frequencies, but their handclasp-style preferences matched within and differed between groups [2]. In contrast to the assumption made by Wrangham *et al.* [1], the handclasping groups at Chimfunshi house 16 family units (versus 5 at Kanyawara [1]), up to the third generation. Crucially, this fact allowed us to validate the claim by Wrangham *et al.* [1] that chimpanzee culture is limited to convergence within matrilineal family units or, in contrast, potentially demonstrate group-level culture in chimpanzees. To test this, we incorporated matrilineal relationships into our original models and applied these models to the largest data set on grooming-handclasp styles in chimpanzees to date. See the Supplemental Information for details on experimental procedures and statistical analyses.

Using data from two different groups across three years and including only those chimpanzees with known matrilineal relationships (42 individuals from 16 matrilineal relationships), we found that matrilineal relationship did not obviously contribute to variation in palm-to-palm clasping frequency in the Chimfunshi chimpanzees (1,033 bouts of grooming handclasps recorded; permutations of matriline within a generalized linear mixed model context, $\chi^2=3.22$, $p=0.44$, and estimated standard deviations for random intercept and random slopes of matrilineal relationships (SDs): all <0.5). Focusing on within-group tendencies, we again found no obvious effect of matrilineal relationships on chimpanzees’ tendency to engage in palm-to-palm clasping (for group 1, featuring 12 individuals, 4 matrilineal relationships and 230 bouts of grooming handclasps, $\chi^2=5.07$, $p=0.44$ and SDs <1; for group 2, featuring 30 individuals, 12 matrilineal relationships and 803 bouts of grooming handclasps, $\chi^2=2.91$, $p=0.43$ and SDs <0.7). Importantly, our originally reported group differences in palm-to-palm clasping [2] were confirmed while controlling for the effect of matrilineal relationships ($\chi^2=6.33$, $df=1$, $p=0.014$; Figure 1).

We analyzed our data with an appropriate random-effect structure