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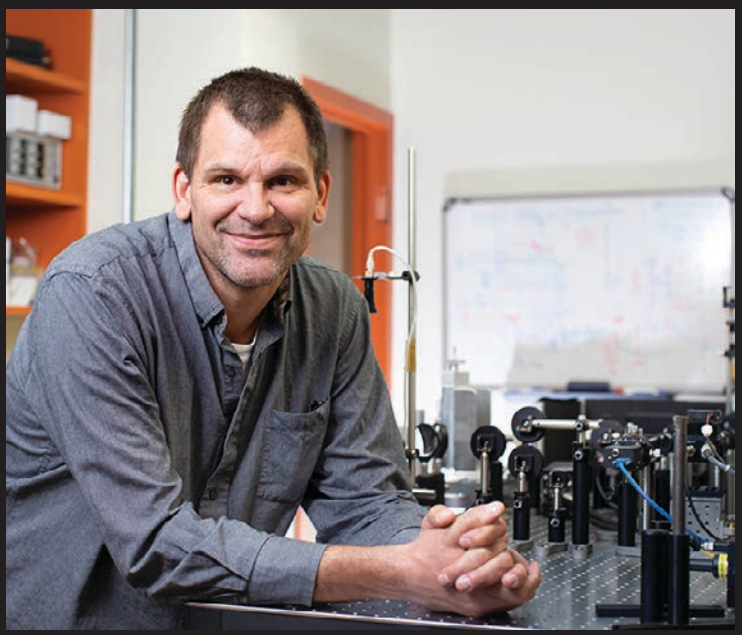
Seeing Beyond Color:

Exploring Novel Colors Through Single-Cone Stimulation

INTERVIEW WITH: DR. AUSTIN ROORDA

BY: ALMA RAZAVILLAR AND ROHIT DIVEKAR



Dr. Austin Roorda is an optometry and vision science researcher and emeritus professor of UC Berkeley, currently based at the University of Waterloo. After receiving his PhD from the University of Waterloo in 1996 in Vision Science & Physics, Dr. Roorda spent several decades in the United States, including 20 years as a professor at UC Berkeley.

At the Roorda Lab at UC Berkeley, Dr. Roorda researched and designed optical tools and instruments that aid in the development of optical medical treatments, track retinal activity, and study visual perception and visual structure. Dr. Roorda is a Fellow of the Optical Society of America and of the Association for Research in Vision and Ophthalmology. In 2009, he received the Glenn Fry Award from the American Academy of Optometry, the John Guggenheim Fellowship in 2014, and the Alcon Research Institute Award in 2016. He also became a Gold Fellow of the Association for Research in Vision and Ophthalmology in 2019.

BSJ: Your research introduces the technology, Oz, as a way to control human color perception at the level of individual photoreceptors. How did this idea originate? Was it primarily a technological possibility that invited a new perceptual question, or was it a perceptual question that drove the technology?

AR: It was a bit of both. I have been working with this technology for almost 30 years. We built a platform that was originally designed to just take pictures of the inside of the eye, which allowed us to see individual cone photoreceptors in a living eye. The next step was correcting for constant eye motion. We then coupled that with an ability to track the eye motion and deliver images to the retina. By about 2014, we were able to see individual cones in the eye, track them, and deliver light to those cones as well.

At that point, we started investigating color vision on the scale of single cones, asking, for example, what would you see if you stimulated a single cone? What we learned was that we have three cone types, L, M, and S. If you stimulate the L cone, it may elicit a sensation of redness, regardless of the laser color that you use to stimulate it. Similarly, activation of the M cone would elicit a sensation of greenness, while activation of the S cone, though not extensively examined in our study, would presumably elicit a sensation of blueness. Ren Ng, a professor in electrical engineering and computer science, emailed me in 2018 out of the blue and sent me a proposal for a joint collaborative project. We decided to collaborate on the Oz concept, which involves imaging, tracking, and delivering light to individual cones, and we expanded it to allow thousands of cones to be observed simultaneously. There was a singular effort to expand our capabilities from 2018 to 2025, and it took that many years to go from concept to paper.

BSJ: You claim Oz is creating new colors by patterning which cones are activated (spatial metamerism), rather than mixing wavelengths (spectral metamerism). Do you see this evidence that color perception is ultimately a spatial computation in the brain, not a spectral one? How does that shift how primary colors are defined?

AR: Spatial metamerism is a manifestation of the fact that a photoreceptor on its own does not distinguish color. The only way we generate percepts of color is by comparing the three cone types. A single photoreceptor can only respond to one dimension of light, making it impossible to perceive color and brightness from one receptor alone, which is called the principle of univariates. A cone does not tell you about the color it sees. It is only the relative excitation of the three cone types that informs us about the color that we see.

We still do not know, however, if color perception is purely a spatial computation in the brain. All the brain has access to is the excitation of the photoreceptors. If they are excited identically, whether through a different spectrum or through a spatial pattern, there is no reason to think the brain would see that differently.

"Some may think that there is no room for expanding or redefining percepts to new sensory inputs. With Oz, we propose that the brain may be capable of doing so, potentially creating new perceptions for those inputs. That is really the fundamental question that we are asking with this Oz platform."

BSJ: Would you be able to explain the concept of retinal leakage from photoreceptors that is discussed in your research?

AR: What we call retinal leakage, or leakage of light, came as a complete surprise to us. Our modeling and the recorded color reports indicated that approximately two-thirds of the light was absorbed by neighboring cones, despite the expectation that over 90% of the light should have been delivered to the target cone.

Our working hypothesis to explain this leakage is that light goes through the cone, scatters in the underlying retina, and gets picked up by the neighboring cones. Due to this, the Oz colors that we were hoping to elicit were not nearly as vivid or as saturated as they might have been, yet still lie beyond the natural perception range.

However, the broader implications are much more profound, and we believe we may have stumbled on a new discovery about the fundamental limits of human vision. This leakage is going to affect everything that we see in the world. The potentially overstimulating contrast of images that land on the retina from everything that we see is reduced and limited by this retinal leakage. This was an accidental discovery, but a deeply fascinating one that the Oz platform is uniquely able to measure and quantify.

BSJ: Can you speak on the ways that you might be able to eliminate or reduce this retinal leakage in cases where it might be unwanted?

AR: Leakage represents a fundamental optical limit that cannot be eliminated with prolonged exposure or differences in the structure of the projected images. Ways to mitigate this effect involve being careful about how we focus the light shining on the cones. One method is by carefully positioning micro flashes of light, not necessarily to hit the target cone, but to try to avoid as much of the neighboring cones as possible.

There are also more ambitious methods. For example, if you project a very short pulse of infrared light, it can actually be perceived as having half the wavelength. This shorter pulse of light is useful because you can isolate the light to the point of focus and reduce the amount of collateral scattered light.

There is also two-photon microscopy, which is commonly used in biology labs. Two-photon microscopy focuses short pulses of light onto a sample and causes it to fluoresce. Normally, if you image deep into tissue with targeted light, everything fluoresces in front of and behind the object you're trying to observe. If you do it with short pulses, the effect of the fluorescence increases with the square of the power of the light. This means that when the power is especially high at the focal point of highly focused short pulses, you get preferentially way more

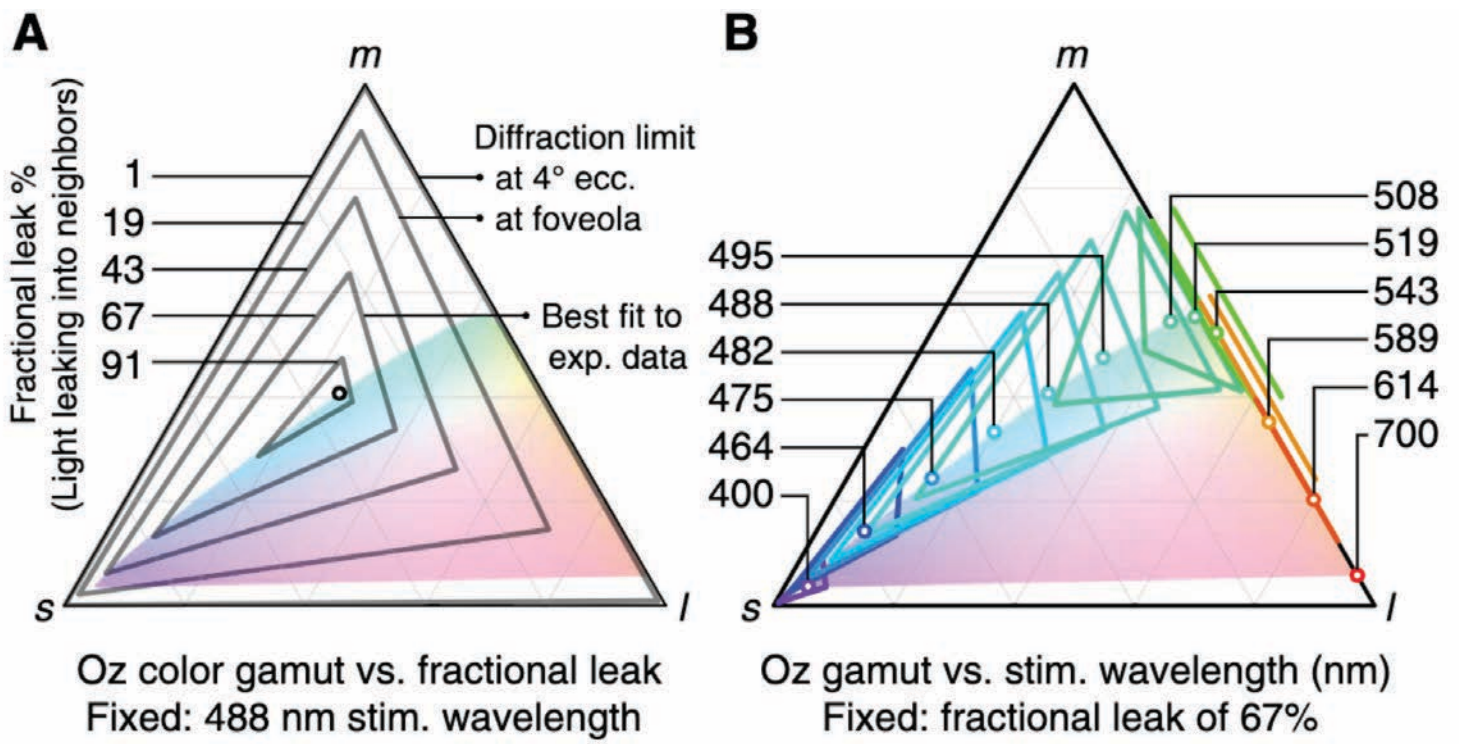


Figure 1: LMS cone chromaticity triangle diagrams that compare natural human color perception ranges versus those seen through the Oz platform. The colored portion shows natural human color perception while the full triangle shows the full bounds of color perception. (A) displays different sizes of the Oz color range at different levels of light leakage. (B) shows Oz color perception that goes beyond natural color perception.

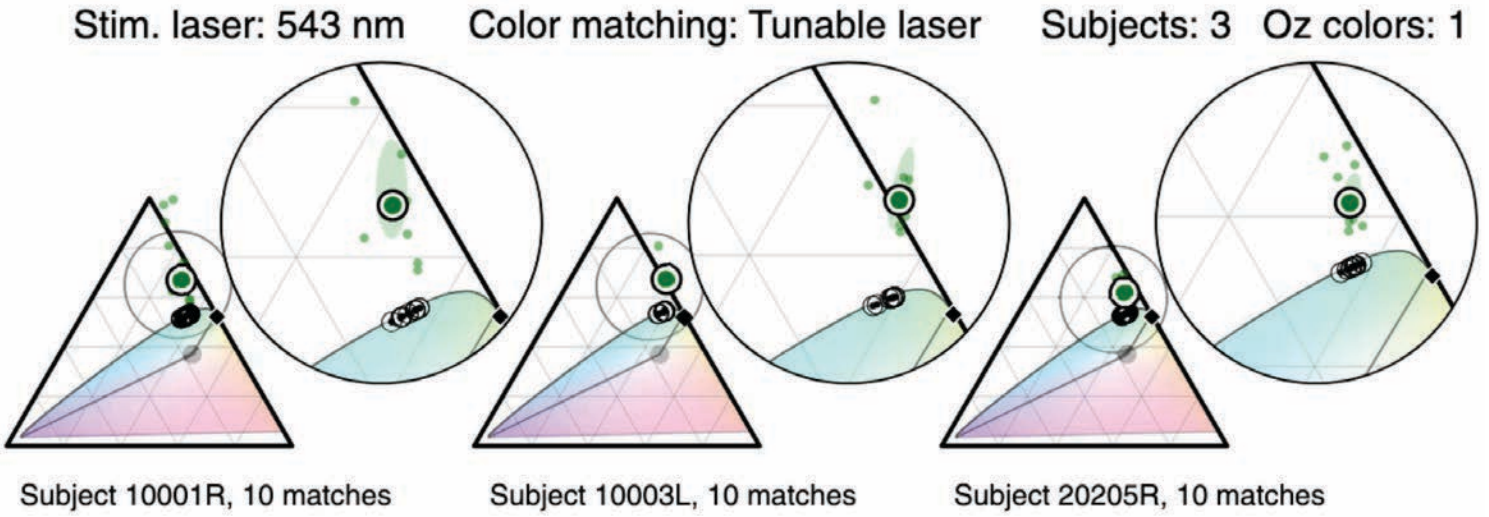


Figure 2: LMS cone chromaticity triangles, which show the saturated blue, green Olo color outside of the natural color perception range. The colored portion shows the natural color perception ranges for multiple subjects tested with Oz. They identified Olo as a color saturated beyond what humans can normally perceive, shown by the blue, green circles.

fluorescence there than anywhere else that is out of focus. This results in the image being much higher contrast. Biologists love using two-photon microscopy because they get much higher contrast images of their tissue. The same idea applies to two-photon vision. The excitation of the photoreceptor cones occurs at the focal point of the light, and any light that scatters beyond this point contributes minimally, resulting in only minimal effects from leakage.

BSJ: In the study, participants were able to observe a novel color, Olo, outside of normal human color perception. If the participants could relate the new Olo color to a super saturated blue, green, to people who have not seen the color through Oz, would they consider this a new color? What constitutes Olo to be a novel color?

AR: I described Olo as a deeply saturated blue-green color, and whether or not it is a new color can be debated. However, I stand by Olo being a novel color.

For example, everyone in the Western English-speaking world would agree that red is not pink. The only difference between those two colors is saturation, which means that pink is just a whiter version of red, and it lies between red and white in color space. Yet, pink and red have entirely different perceptual qualities, so that no one would think to say that the two colors are the same. Olo is similar. The colors that we elicited in the Oz platform are similar to this red and pink case in the sense that they are a hyper-saturated version of the blue-green we described.

The only aspect we did not agree on was the name. Somebody might say teal, somebody might say peacock, or cyan. We have different words to describe those colors, and they all have different perceptual qualities. I truly believe that with continued exposure to this sensory stimulation, beyond what natural light can produce, Olo would eventually appear and be described as different from teal, much as we use different words to describe the difference between red and pink.

I believe that our colors are learned and that you can get better at identifying colors with practice in the same way that you could get better at shooting a three-point basketball shot. For example, I am actually not particularly adept at perceiving or distinguishing colors compared to my wife or daughter. I get colors mixed up all the time, while my wife and daughter will disagree with me. They attribute distinct perceptual qualities to those colors, unlike me. It is not because they have different sensory inputs, but because they tend to recognize them more, which reinforces the notion that color percepts are learned.

BSJ: The new color, Olo, is perceived by targeting specific cones individually. However, we are still able to have this color appear despite retinal leakage (For example, the M cone is not 100% isolated and targeted). Could you elaborate more on how that works?

AR: We found Olo hypersaturated, although it did not reach the extreme corner of the LMS triangles that we show in the paper. We can still stimulate an M cone with Oz more than any natural light could ever do, right? Despite the leakage, the stimulus did not extend beyond the typical range of color perception. However, it went far enough out of the natural human perception range to achieve effects that natural light could not, eliciting these profoundly saturated sensations. It was enough to make the discovery very clear and obvious, while still leaving room for further exploration to push it further.

BSJ: You describe Oz as a potential platform for exploring neural plasticity, even simulating the addition of new cone types beyond the three dimensions of L, M, and S cones. If humans were repeatedly exposed to these novel activation patterns, what forms of adaptations or remapping might you expect in color representations? Could the brain eventually learn a fourth color dimension?

AR: That remains to be seen, but that is exactly what our investigations are aiming to do.

In the world, there are an infinite number of distributions of wavelengths of light (spectra) reflected from or emitted from an object that covers the whole extent of the electromagnetic radiation spectrum. There is a narrow sliver of that spectrum, approximately between 400 to 700 nm, that we call "light". The reason we call this "light" is that it is the electromagnetic radiation that gets through the optics of our eye and excites the photopigment in our cones. Otherwise, there is nothing special about what we call light versus other parts of that spectrum.

We are sensitive to that part of the spectrum and to small changes

"A color is a construct of the mind, and the number of colors we see is constrained by the fact that we have three types of color cone photoreceptors."

within it, and color is our way of generating percepts to attribute to those limited different spectral changes.

We only have the ability to look at three components of the spectrum and compare them. We are also constrained by the fact that these spectral sensitivities of the three cone types overlap with each other.

What if you added a fourth cone type? Wherever you add this fourth cone type, as long as it does not perfectly overlap with the others, it will add a new dimension to color. It would allow you to differentiate more spectra than you could before. If you could differentiate more spectra, it is plausible that you would have to invent new percepts to attribute to them. This is a much more profound question than the sensation of Olo, which is simply amping up the perceived differences beyond what natural light could do.

It almost becomes a philosophical question about how percepts are generated, given the sensory inputs. It is hard to imagine that if I gave you a fourth cone type, you would instantly perceive something you have never experienced before. More reasonably, this perception might emerge over time. The reason it is sensible to think that is because a newborn child faces the same problem. There is evidence that suggests that when a child is born, they do not perceive colors normally. They have three cone types, like us, and their optics are just fine, but they do not perceive or distinguish colors very well. However, over hours, days, and years of being bombarded with sensory inputs, the brain is this amazing machine that starts to make sense of these inputs and tries to look for consistencies, correlations, and changes. I believe that the child's brain is inventing new colors all the time through this development, which provides us with evidence to think that the brain might do the same for new sensory inputs, such as new cone types.

BSJ: Oz can simulate what it would look like if new cone types were added through gene therapy (e.g. for those with color blindness). How could this technology help researchers test whether the brain is capable of adapting to and processing these new color inputs?

AR: That is exactly what we are doing. We are looking at ~~tracker mats, people's~~ normal color vision, and seeing what their capabilities are in terms of leveraging a fourth cone type. We are also looking at dichromats (people who are colorblind), who only have two types of cones. Color blindness comes in different degrees. You can be an anomalous trichromat, where the L and the M cones, or the green and the red cones, are so closely overlapped that the different signals are noisy. Those people have difficulty differentiating red from green, but if the image is made bright enough, they can do it.

Then some people are profoundly dichromatic. In other words, they lack either one of the M or the L cone type entirely, leaving them with only two types of cones. From a sensory standpoint, they can only differentiate short light from long light, which they might attribute to being bluish or reddish, but everything in between goes gray. In a dichromatic individual lacking a third cone type but with an otherwise normal retina and brain, introducing a third cone would likely enable red-green discrimination, as in trichromatic vision. If the third cone type was introduced early on as a child, the individual might learn to use that information effectively, due to higher neural plasticity at a young age. We are not yet sure whether older individuals have the plasticity to leverage that third cone type. One thing we are pretty sure about, though, is that if you gave them a third cone type, they might be able to differentiate red from green to the extent where they could see an apple being a different color than the tree, where they could not before, but that differentiation may not be based on a percept of color.

BSJ: How would adding new cones affect a person's color perception? Would they actually see colors like red or green the same way we do, or would those colors appear differently to them?

AR: The classic question that people ask is: Is your red the same as my red? Of course, nobody can ever know that. When you perceive a color, what exactly makes it a color rather than, say, a texture? Color is a uniform attribution we give to a surface. For instance, I look at my yellow backpack and call it yellow. Overlaid on the perception are variations in brightness; some areas reflect more light, others are in shadow. Color is a perceptual layer we assign on top of other surface properties such as shininess, texture, or shadow. When we think about color, it is not about whether someone's red is the same as mine, but whether they attribute color in a similar way to sensory inputs. If that attribution aligns, we can reasonably say they are perceiving color.

Now imagine we give someone missing the red-sensitive, L cone, a third code type. For such individuals, a stimulus we perceive as red might initially appear as a variation in brightness conveyed by their red-sensitive cones, rather than as a distinct color. It might appear as a spatial pattern on top of red surfaces. They could differentiate it, but not as a color, more as a luminance change. Over time, though, the brain might realize that the more efficient and reliable way to interpret that signal is to assign it a color. In doing so, it effectively invents a new perceptual "red".

There are a few different theories about how we experience color. One idea is that every human is born with a fixed palette of colors, a kind of built-in "box of crayons." According to this view, there is nothing outside the range of colors we can already imagine. If someone were given new sensor inputs through additional cone types, they would not actually perceive new colors. Instead, the brain would simply remap those inputs onto the existing palette. Thus, Olo would simply take over as the new most saturated green, and it would be no different from my normal day-to-day experience. In this case, someone who is colorblind might technically have all the colors available in their mental palette but misassign them. They might call something red when others would not, simply because they lack the sensory inputs needed to assign the perception correctly. They have the concept of red in their mind, but without the right sensory signals, they cannot map it accurately.

That is one theory. The other is that you actually have to invent new colors when given new sensory inputs. Both possibilities are plausible; we just do not know which is correct.

It becomes even more complex with tetrachromacy, since adding a fourth cone type would likely require the perception of entirely new colors. You could not just remap a trichromatic space onto a tetrachromatic one: it would demand an expansion of the perceptual space itself.

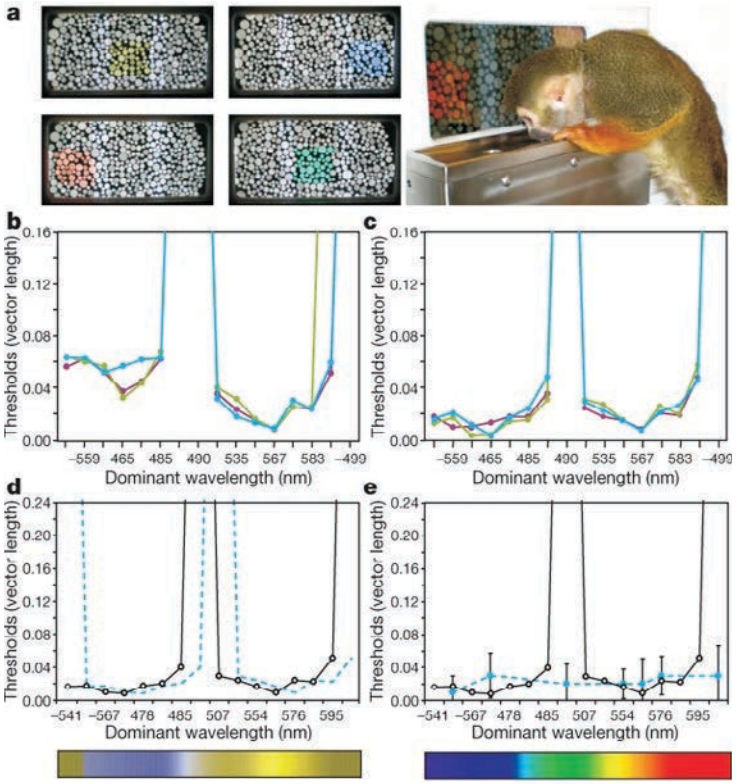


Figure 3: Acquisition of a new color-discrimination dimension following the introduction of novel cone pigment in dichromatic squirrel monkeys. ~~T (A) Adaptive optics images of each monkey's cone mosaic, where S cones are labeled in white and newly L opsin expressing cones appear in color. These images visualize how gene therapy added a new spectral class to an originally dichromatic retina.~~ (B-E) Color discrimination thresholds plotted across dominant wavelengths before and after treatment. The colored curves represent performance after the introduction of the new cone type, while the black curves denote pre-treatment thresholds. Following the therapy, the monkeys display markedly improved discrimination in wavelength regions previously indistinguishable to them, indicating the emergence of a perceptual dimension unavailable before gene addition.

BSJ: What are some of the other practical and industrial applications of this technology?

AR: We now have precise control over visual inputs at the level of photoreceptors, meaning we can selectively stimulate the L, M, or S cones to manipulate color perception in different ways by exciting those cones differently. However, there is much more we can do. One project we are currently working on, led by Hannah Doyle, a fourth-year electrical engineering and computer science graduate student, does not involve playing specific cones individually. Instead, she selectively turns off half the cones to ask a simple question: if you lost half your cones, how would that affect your vision? Specifically, how would it impact your ability to read letters on a standard eye chart?

"This work has real clinical relevance. Many eye diseases cause cone degeneration. We still do not understand the exact relationship between cone loss and visual function. That is what we are trying to uncover."

One thing we have learned is that a person experiencing cone degeneration can lose up to 50% of their cones and still almost read normally on an acuity chart. That is remarkable–human vision is incredibly robust. But from an ophthalmologist's perspective, it poses a challenge. A patient might feel that something is wrong, yet still read the chart perfectly. The doctor sends them home, unaware that half their cones are already gone and missing a critical window for intervention.

Our goal is to develop metrics that can detect this earlier. Using our setup, Oz, we can emulate cone loss in any eye: simulate it, test performance on an acuity chart, and establish clear expectations for how vision degrades as cones are lost. This is important for two reasons. First, it helps clinicians better interpret a patient's complaints and performance. Second, it can guide the creation of more sensitive diagnostic tools for early cone degeneration. Finally, this research has implications for treatments. Clinical scientists developing gene or stem cell therapies need to know what level of restoration actually matters. For instance, if restoring just 30% of a patient's cones recovers most of their visual acuity, enough to read or drive, that is a tremendous success. By emulating cone loss in controlled experiments using Oz, we can help set realistic expectations for both diagnosis and therapy in eye disease.

That is one immediate example. But there are also industrial applications to consider. Oz takes up an entire table in my lab. I sit with my head fixed into a bite bar, biting into a dental impression that locks me into place. At this point, I am practically part of the machine. Despite all this hardware, we can only generate a tiny patch of color, about the size of a fingernail held at arm's length, roughly one degree of visual angle. It is a massive setup for a very small visual display. What we would love to achieve is the opposite: a compact instrument with a wide field of view. In principle, the methods we use in Oz Vizion could be applied to that, but the technical challenge is enormous. We simply do not know how, but it would require inventing entirely new ways to deliver these visual stimulations.

BSJ: You mentioned that people who have lost about 50% of their cones can still have nearly normal vision. Is that because the brain is filling in the missing visual information, or is it that we simply do not need all our cones for the brain to get enough input to function normally?

AR: First, visual acuity, the ability to read, recognize faces, and distinguish fine detail, is robust to cone loss. That is encouraging because those are some of the most important visual tasks for humans. However, other aspects of vision do decline, such as night vision or sensitivity to low-contrast images.

It is probably not accurate to say the visual system has built-in redundancy: evolution does not usually work that way. But it is remarkably robust. The brain has an incredible ability to construct percepts over time, even from sparse information. For example, even with a patch cone mosaic, the retina still captures enough input as the eye constantly moves. One of Hannah Doyle's projects is exploring how much we rely on tiny eye movements to compensate for missing signals. She is finding that it provides a surprisingly strong advantage. If I were looking at you and missing cones in a particular part of the retina that sees one of your eyes, as long as I move my eyes around, eventually I

will capture that information.

The visual system has the remarkable ability to build a complete picture of a scene over time. Over the years, our lab and many others have shown one key principle: eye motion is not a flaw in vision; it is a feature.

BSJ: Oz opens an experimental window into both the physics of light and the biology of perception. If you could design one experiment unrestricted by technical limits, what question about human color perception would you most want to answer?

AR: So far, our work has focused on vision, specifically color. The idea of expanding to tetrachromacy raises a fascinating question: if we are given new sensory inputs, can we actually invent new percepts to interpret them?

Take polarization, for instance, something humans do not naturally perceive. Polarization is a property of light, just like wavelength. We can distinguish different wavelengths as colors, but we are completely insensitive to polarization. The only time we notice its effects is when we wear polarized sunglasses and rotate them, causing certain reflections to brighten or dim. But that is not true polarization sensitivity; it is just observing the side effects of a filter.

Meanwhile, other species, like mantis shrimp, have a dozen different spectral cone types and many that are polarization sensitive. If you have ever seen one, their eyes are constantly moving, scanning the scene. They are likely constructing a percept of the world that includes an entirely new dimension, polarization, layers on top of what we would recognize as color.

Now imagine replicating that. With Oz, we could, in principle, assign a subset of cones in the human retina to respond selectively to polarization patterns in a scene, then simulate specific cones in a way that reflects real-world signals. Theoretically, that might allow us to give humans a perceptual experience of polarization: a glimpse into sensory dimensions we never had.

Here is the big question: if we did that, if we gave someone access to polarization information, they would start to notice consistencies and patterns in their sensory input. These patterns would not correspond to color or luminance, but to something entirely new: polarization.

Would it be possible for a human to invent a percept for that? And if they could, what would it feel like? We cannot imagine it, but the mantis shrimp can. It must have some kind of percept it assigns to polarization. That is what makes this idea so exciting. Our platform could, in theory, test the limits of how new sensor inputs translate into entirely new percepts. It really pushes at the boundary between sensation and perception.

Polarization is not the only example. Some birds have magnetoreception, meaning they can sense Earth's magnetic field and orient themselves accordingly. We, on the other hand, have no awareness of magnetic orientation at all. We do not know what it feels like, what kind of sensation it is, or how it manifests to them. It is probably not visual in the same way color is, but it is still a percept, something analogous to how we feel heat, texture, or pressure. It is a dimension of experience that we simply can not imagine right now. That makes it all the more intriguing.

BSJ: Since you mentioned other species' sensory abilities, snakes, for instance, can detect infrared and essentially build heat maps of their surroundings. Would something like that be possible to simulate using this technology, or is that an entirely different kind of sensory system?

AR: It is totally related. Heat maps and heat-sensing cameras rely on much longer wavelengths of light, far beyond what humans can detect. For humans, the portion of the electromagnetic spectrum that passes through the cornea and lens to reach the retina ranges from about 400 to 1,000 nanometers. But the wavelengths that carry temperature information, infrared radiation, are around ten microns. Specialized cameras can detect those wavelengths, but our eyes cannot. There is no evolutionary reason we would have developed sensors for that range.

Snakes, though, do. They have specialized receptors, different from our cones, that can detect those long infrared wavelengths. While the mechanism is not identical to human vision, the concept is similar: they translate an unseen physical property of light into a perceptual experience.

As I mentioned earlier, all the perceptual attributes we assign to a surface exist simultaneously. You can have a red, shiny object. The shinniness is a material attribute, while the red is a color attribute, and you can perceive both at once.

In the same way, if we were to give someone polarization sensitivity or long wavelength sensitivity, it would not replace existing perception. It would simply add another layer. Rather than mask or substitute, it would provide an entirely new dimension of perception attributed to the same surface.

Like with polarization, we could imagine adding heat perception as another sensory layer through the visual stream. Using a heat-sensing camera, like those used in night vision goggles, we could map temperature data from the scene and play it back through specific cones in the retina, so that brightness or hue corresponds to heat intensity.

Right now, night vision goggles perform sensory replacement. They take infrared information and convert it into green light, so weavers can interpret heat as brightness. What we are discussing would be sensory enhancement: directly mapping that infrared input onto the visual system itself, so it becomes its own new perceptual dimension. This is still hypothetical, but potentially possible.

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