targets of CDC42 that may largely play a role in these responses include a group of protein kinases with homology to the yeast Ste20 protein (PAK kinases), the Wiskett-Aldrich syndrome protein (WASP), and phosphatidylinositol-3-kinase (PI3-kinase) (*20*). PI3- kinase is unlikely to play a role in *S. typhimurium*–induced signaling, however, as wortmannin, a potent inhibitor of PI3-kinase, has no effect on the *S. typhimurium*–induced cell responses (*11*).

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10. Bacterial invasion was measured as in J. P. van Putten, J. F. L. Weel, and H. U. C. Grassmé [*Methods Enzymol.* **236**, 420 (1994)] with minor modifications. Each cell invaded by *Salmonella* had an average of 31 ± 14 internalized bacteria.
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TECHNICAL COMMENTS

Consequences of Retinal Color Coding for Cortical Color Decoding

Dennis M. Dacey *et al.* in their report (*1*) and Richard H. Masland in his Perspective (*2*) draw attention to important details in the encoding of color in the retina of macaque monkeys and humans. The centers of red-green opponent retinal ganglion cells can be driven by a single cone, but the cone specificity of the surrounds is in question. Dacey *et al.* state that horizontal cells that subserve red-green opponent cells are contacted by both L- and M-cones, a finding with implications for receptive field formation (*1*), retinal coding (*1, 2*), and cortical decoding (*2*). While Dacey *et al.* may well be correct that surrounds are shaped by post-horizontal cell processes, I question whether mixed cone surrounds pose insurmountable problems for retinal color coding or cortical color decoding. The color signals of units with mixed cone surrounds are less complicated if the spatial properties of the units are taken into account using the Ingling-Martinez identity (*3*)—a rigorous statement of the co-coding hypothesis discussed by Masland. Let x be the weight of a P cell–L-cone center and y and z be the weights of M- and L-cones driving the surround. The Ingling-Martinez identity that describes this P cell is

$$xLC - (yM + zL)S = 0.5[(x + z)L + yM][C - S] + 0.5[(x - z)L - yM][C + S] \quad (1)$$

where C and S are center and surround spatial weighting or modulation transfer functions. In this equation, the first term represents the bandpass spatial response to achromatic stimuli and the second term, the lowpass spatial response to chromatic stimuli. If $z = 0$, then the surround is pure, and the cone weighting of the achromatic and chromatic responses differ only in polarity. The effect of mixed cone surrounds is to give the achromatic and chromatic responses different cone weightings (*4*). This is the case psychophysically—for the CIE standard observer, the achromatic response is approximately 5L:3M, while the red-green color response is 2L:3M. Reconciling these different weights using pure surrounds has motivated several models (*5*). Mixed surrounds can yield this result directly [that is, if $(x, y, z) = (3.5, 3.0, \text{and } 1.5)$] and is roughly what would be expected (*6*) for random surrounds constructed on an L-cone rich–retina (such as that posited to underlie the standard observer's luminosity function).

Do mixed cone surrounds pose difficulties for cortical color/luminance decoding? Recent models of achromatic/chromatic demultiplexing rely on spatial filtering operations that are based on the spatial properties of the center/surround combinations in Eq. 1, but are robust with respect to surround cone ratios (*4, 7–9*). Filtering models have no problem accounting for the major red-green cell classes in cytochrome oxidase blobs; type II cells, $\frac{3}{4}$ double-opponent cells, and double-opponent cells can be created from filtering operations on parvo cells (*8*). Similar models account for extraction of achromatic information (*4, 7, 9*). These filtering operations do not always create a

perfect separation of color and luminance [a problem exacerbated by mixed surrounds (*4*, *7*)], in agreement with the behavior of a major class of cortical cells (*10*), as well as with psychophysical evidence for color/luminance interactions (*11*). All of this bears on Masland's dichotomy between the multiplexing (co-coding) and parallel channel approaches. Models that do not filter parvo cells do not account for the properties of cortical cells. Moreover, the use of parvo cells for achromatic form perception without filtering to separate color is inappropriate. As Marr pointed out, the zero crossings of the P cell signal are ambiguous if the color signal is not removed (*12*). If the color signal is extractable, it makes little sense not to use it.

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Response: As Masland [in his Perspective (*1*)] pointed out, our finding in the report (*2*) that both H1 and H2 horizontal cells in macaques receive additive input from L- and M-cones has implications for understanding the retinal circuitry that underlies spectral opponency. If it is assumed that H1 cells contribute strongly to the formation of the receptive field surrounds of red-green spectral opponent cells, such opponency cannot arise from cone type–specific connections as originally proposed by Wiesel and Hubel (*3*), and recently supported by the results of Reid and Shapley (*4*). An alternative is that H1 cells do not contribute, or contribute only weakly, to the surrounds of red-green cells and that cone type–specific opponency comes about by selective connections between bipolar cells, amacrine cells, and midget ganglion cells. However, as Masland also noted (*1*), there is growing evidence against such an alternative circuitry (*5*). Billock points out that in theory, mixed cone surrounds do not pose a serious problem for quantitative models of color opponency and coritical color and luminance coding. We agree with this conclusion, and the formalism offered by Billock is a reasonable one. However, it remains to be shown experimentally that red-green spectral opponent cells do actually have mixed receptive field surrounds. Although, a successful computational model is necessary and important, we would emphasize that the key retinal interneurons subserving red-green opponency, their physiological properties, and precise circuitry are yet to be discovered and described.

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Response: Neither Dacey [in his report (*1*)] nor I [in my Perspective (*2*)] suggested that mixed cone surrounds pose insurmountable problems for cortical color coding. A number of plausible decoding schemes may be proposed, among them the one suggested by Billock.

If the red-green system is multiplexed, though, how about the blue-yellow system, where there is evidence for a dedicated channel (*3*, *4*)? Would the red-green and blue-yellow axes be handled centrally in different ways? From the point of view of the retina, such a dichotomy seems quite possible—the blue-yellow system appears to have evolved independently (*5*). But it would require somewhat different cortical mechanisms for the two color systems, because the spatial organization of the peripheral receptive fields and the anatomical path to the cortex are different.

Given the power of current techniques (*1*, *3*, *6*), the remaining issues about the cellular basis of retinal color coding may be resolved fairly soon. Perhaps the results will raise new questions for experimentation on the striate cortex.

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Evaluating the Evidence for Past Life on Mars

David S. McKay *et al.* (*1*) deserve praise for discovering possible evidence of past Martian life. The identification of indigenous organic compounds in a martian meteorite alone is a breakthrough, reopening the possibility of life after the chill cast by Viking. The characterization of the carbonate globules sets a new standard for study of extraterrestrial materials. However, McKay *et al.* overstate their case by contending that although "[n]one of these [five] observations is in itself conclusive for the existence of past life . . . when . . . considered collectively . . . they are evidence for primitive life on early Mars." An inorganic explanation is at least equally plausible for four of their five observations.

With regard to polycyclic aromatic hydrocarbons (PAHs), McKay *et al.* (*1*) note that "in situ chemical aromatization of naturally occurring biological cyclic compounds in early diagenesis can produce a restricted number of PAHs" and suggest that "diagenesis of microorganisms on ALH84001 could produce what we observed—a few specific PAHs—rather than a complex mixture involving alkylated homologs." But aromatization works equally well for *abiotic* organic matter, which does not even need to be cyclic. Berthelot discovered such aromatization in 1862, producing naphthalene from methane in one