p = 0.38, respectively). Moreover, analyses of only high confidence states yielded similar results as when high- and low-confidence states were pooled (see Supplemental Data). Together with the numerically large and robust difference between expected and unexpected percepts in the test phase, these observations speak to a true perceptual bias rather than a mere response bias.

Our work shows that experimentally manipulated expectations not only affect the perception of pain [1,6] or emotion, but can have a more general influence on how we experience the world, as evidenced by a striking effect of expectations on the contents of visual awareness. This opens the door for studies of how perception and belief systems are biased by expectation in general and in pathological states such as delusions.

Supplemental data

Supplemental data are available at http://www.current-biology.com/cgi/content/full/18/16/R697/DC1

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Neural basis for unique hues

Cleo M. Stoughton and Bevil R. Conway

All colors can be described in terms of four non-reducible 'unique' hues: red, green, yellow, and blue [1]. These four hues are also the most common 'focal' colors — the best examples of color terms in language [2]. The significance of the unique hues has been recognized since at least the 14th century [3] and is universal [4,5], although there is some individual variation [6,7]. Psychophysical linking hypotheses predict an explicit neural representation of unique hues at some stage of the visual system, but no such representation has been described [8]. The special status of the unique hues "remains one of the central mysteries of color science" [9]. Here we report that a population of recently identified cells in posterior inferior temporal cortex of macaque monkey contains an explicit representation of unique hues.

Color in humans and macaque monkeys depends on the differential responses of the three cone types — L, M and S — an operation typified by parvocellular neurons of the lateral geniculate nucleus of the thalamus (LGN). LGN cells can be categorized according to color preference, but these categories do not correspond to unique hues [6,10,11]. Instead, multi-stage models have been developed, locating the essential color calculation to brain regions subsequent to the LGN in the visual processing hierarchy [12,13]. Such models describe a recombination of the cone signals to produce color tuning that corresponds to perception, but it is also plausible that the LGN output is simply filtered so that only that minority of LGN cells with appropriate color tuning is routed to color-processing regions of cortex. In either case, neurons downstream of the LGN at the first cortical stages of vision (V1 and V2), are, however, unlikely to encode unique colors [14–17]: like neurons in the LGN, color-opponent neurons in V1 are tuned to colors lying close to the cardinal color axes defined by cone opponency: L –M (bluish-red),; –L+M (cyan), S –(L+M) (lavender), and –S+(L+M) (lime) [15,16,18]. As in the LGN, the overwhelming majority of color-opponent neurons in V1 are tuned along the red-cyan axis [15,16].

Color-tuned neurons have recently been found in posterior inferior temporal cortex of the macaque monkey, clustered within millimeter-sized modules dubbed globs, downstream from V1 and V2 [19,20]. We determined the color tuning of the population of glob cells described in that study (Figure 1). Although neurons tuned to all directions in color space were found [20], the population distribution was not uniform, and is markedly different from that obtained in LGN or V1. The population distribution contains three prominent peaks. The largest peak aligns with red; the second largest, with green; and the third, with blue. The distribution also includes a bulge that peaks in the yellow. These peaks are roughly consistent with unique colors identified by human subjects (symbols, Figure 1). The three prominent peaks also correspond to the three most saturated colors in the stimulus set (see Figure S1 in the Supplemental data available on-line with this issue); and the size of each of the peaks corresponds to the relative saturations of the hues, suggesting that both hue and saturation are represented by relative number of glob cells. The relative size of each of the peaks also corresponds to the frequency with which these color terms is adopted by language: red is adopted first, then yellow or green, followed by blue [4]. These results extend those of Zeki [21] and Komatsu *et al.* [22] and are, to our knowledge, the closest explicit neural representation of unique colors in the primate brain.

The stimuli consisted of flashed (200 ms ON/200 ms OFF) optimally shaped bars surrounded by a neutral-adapting gray field. Color tuning was assessed by varying the color of the bar. Three sets of equiluminant colors were used: one set was equiluminant with the adapting-gray field; one set was higher luminance than the adapting field; and one set was lower luminance than it. The population tuning was consistent across stimulus sets, except for a subtle shift in the location of the

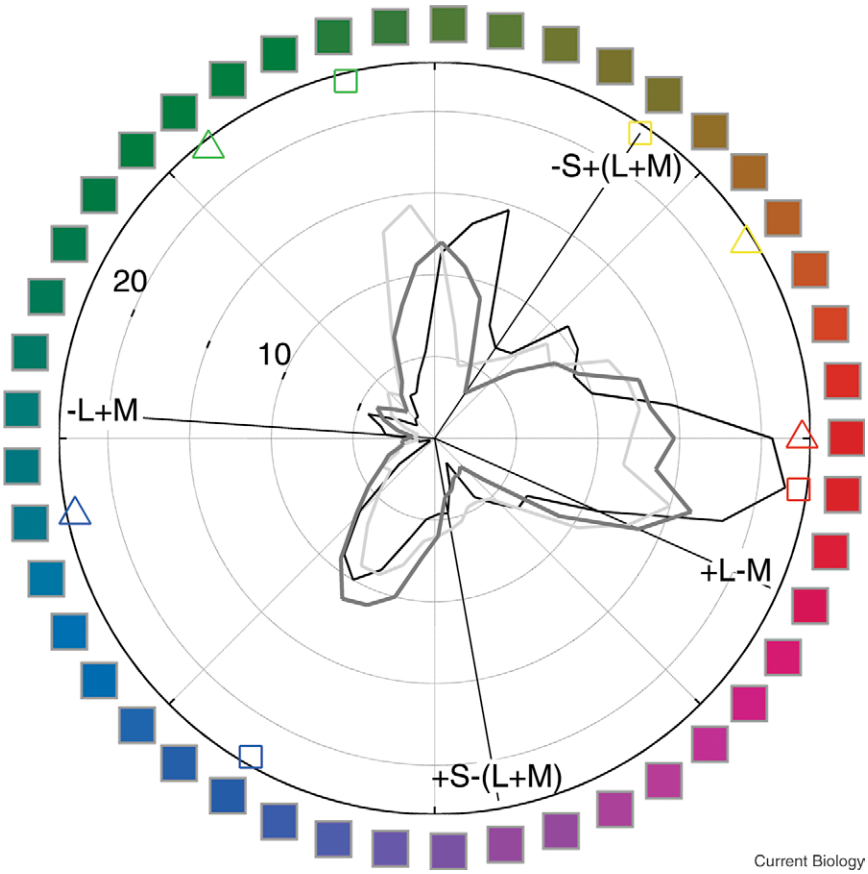

Figure 1. Histogram of optimal color tuning of glob cells recorded in alert macaque monkey shown as a polar plot.

Globs are regions of posterior inferior temporal cortex (including V4, PITd and posterior TEO) that show higher fMRI responses to equiluminant color than to black-and-white [19,20]. Single-unit responses were obtained from two monkeys using microelectrodes targeting globs (for all methods and detailed description of the stimuli see [20]). Number of cells tuned to each color is indicated by the radius (308 cells; smoothing: 1-bin-wide boxcar). Cells were tested with stimuli of optimal spatial configuration, varied only in color (Table S1 in the Supplemental data gives C.I.E. values; colors around the perimeter are approximate). Color tuning was assessed with three sets of equiluminant colors: one set was equiluminant with the adapting gray field (thick dark-gray line); one set was higher luminance than the adapting field (thick light-gray line); and one set was lower luminance than the adapting field (thin black line). The location of the cardinal color axes is shown, along with the average location of unique colors judged by human subjects from two studies (squares, [11]; triangles, [23]).

peaks, most pronounced for green (compare the three plots, Figure 1). These shifts were consistent with the Bezold-Brücke hue shift — at lower luminance, a green stimulus must contain more intensity at long wavelengths (yellow) to appear constant green — providing further evidence that this population of cells is encoding color experience.

The population of glob cells has a strong explicit representation of three of the four unique colors; yellow is weak. The stimuli were generated with a computer monitor, and were constrained to be equiluminant; thus all colors were limited by the maximum luminance of the dimmest computer phosphor gun (blue). At this luminance, stimuli in the yellow region appear ochre, lacking the brilliance one associates with focal yellow. We interpret the weak yellow peak not to a lack of neurons tuned to yellow, but rather to a lack of focal yellow in the stimulus set.

Supplemental data

Supplemental data are available at http://www.current-biology.com/cgi/content/full/18/16/R698/DC1

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