# Color-detection thresholds in rhesus macaque monkeys and humans

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**Macaque monkeys are a model of human color vision. To facilitate linking physiology in monkeys with psychophysics in humans, we directly compared color-detection thresholds in humans and rhesus monkeys. Colors were defined by an equiluminant plane of cone-opponent color space. All subjects were tested on an identical apparatus with a four-alternative forced-choice task. Targets were 2° square, centered 2° from fixation, embedded in luminance noise. Across all subjects, the change in detection thresholds from initial testing to plateau performance ("learning") was similar for +L − M (red) colors and +M − L (bluish-green) colors. But the extent of learning was higher for +S (lavender) than for −S (yellow-lime); moreover, at plateau performance, the**

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**cone contrast at the detection threshold was higher for +S than for −S. These asymmetries may reflect differences in retinal circuitry for S-ON and S-OFF. At plateau performance, the two species also had similar detection thresholds for all colors, although monkeys had shorter reaction times than humans and slightly lower thresholds for colors that modulated L/M cones. We discuss whether these observations, together with previous work showing that monkeys have lower spatial acuity than humans, could be accounted for by selective pressures driving higher chromatic sensitivity at the cost of spatial acuity amongst monkeys, specifically for the more recently evolved L − M mechanism.**

## Introduction

The macaque monkey has become a premier model for physiological studies of human visual perception, including color (Conway et al., 2010). The spectral sensitivities of human and monkey cones are virtually identical (Jacobs, 2008; Schnapf, Kraft, & Baylor, 1987; Sidley, Sperling, Bedarf, & Hiss, 1965), but it is not clear whether the two species process the cone signals to achieve a similar perception of color. Early investigators documented the excellent trichromatic abilities of monkeys (Trendelenburg & Schmidt, 1930) but concluded that the color vision of rhesus monkeys was probably "at an evolutionary position just short of human vision" (Grether, 1940). The most widely cited comparative work, conducted over 35 years ago, concluded that macaque monkeys have excellent color vision that is probably on par with that of humans (De Valois, Morgan, Polson, Mead, & Hull, 1974; Sidley et al., 1965). Consistent with this conclusion, monkeys have similar higher order psychophysical chromatic mechanisms to those documented in humans (Stoughton, Lafer-Sousa, Gagin, & Conway, 2012). But direct comparisons of absolute chromatic detection have not been performed with controlled viewing and equiluminant stimuli; most previous comparative work has focused instead on the shape of spectral sensitivity functions (Harwerth & Smith, 1985). We performed a color-detection task in both humans and rhesus macaque monkeys, under identical viewing conditions and task demands similar to those that would be used in physiological studies. Tests of absolute detection threshold were performed on initially naïve subjects and then on the same subjects following extensive training, to control for differences in perceptual learning. In addition, colored targets were embedded in luminance noise to mask any luminance artifacts that may, for example, be associated with differences in macular pigmentation (Mullen, Yoshizawa, & Baker, 2003; Smithson & Mollon, 2004). Color-detection thresholds were broadly similar across species, but surprisingly, monkey thresholds for colors that modulated L or M cones were on average slightly lower than the thresholds in humans, suggesting that monkeys see some colors better than humans.

## Methods

All experiments were approved by the institutional animal care and use committees at Harvard Medical School and the institutional review board of Wellesley College and adhere to guidelines of the United States National Institutes of Health. This work followed the guidelines in the Declaration of Helsinki and the ARVO Statement for the Use of Animals in Ophthalmic and Vision Research. Informed consent was obtained from human participants. Three adult male rhesus macaque monkeys (*Macaca mulatta*) and four female human subjects with normal trichromatic vision (tested with Ishihara plates) were trained to perform a color-detection task (Figure 1A) using standard behavioral training techniques (Stoughton et al., 2012). Detection thresholds were measured using stimuli defined by the cone-opponent coordinates with which the retina encodes color (Derrington, Krauskopf, & Lennie, 1984; Hansen & Gegenfurtner, 2006; MacLeod & Boynton, 1979). The tests were conducted under dark ambient light conditions on a color-calibrated CRT monitor (Barco Display Systems; refresh rate 60 Hz) 27 in. away from the subject. Within the equiluminant plane of the color space, colors progressively further away from the origin along a vector have higher cone contrast (and appear more saturated). Colors that selectively modulate the L and M cones are depicted along the x-axis, while colors that modulate the S cones (pitted against the sum of L + M) are depicted along the y-axis. Colors that are intermediate to these cardinal axes modulate the activity of all three cone types. Weber cone contrasts shown in Figure 1 were obtained by taking the dot product of the spectral power distribution for stimuli and the cone fundamentals (Smith & Pokorny, 1972, 1975). The task design was similar to that described by Stoughton et al. (2012), with the exception that stimuli used presently were embedded in luminance noise, and all trials were performed under constant neutral adaptation.

The monkey and human subjects were trained on the same apparatus to fixate on a small spot at the center of a monitor displaying full-field neutral gray. The trial was initiated after the subject started fixating on the center spot. After 500 ms, the fixation spot disappeared and a 2° square target spot appeared at one of four locations, centered 2° from the center of gaze (Figure 1A, right panel). Trials were aborted if subjects broke fixation (deviations of >0.5° from the fixation spot). Of

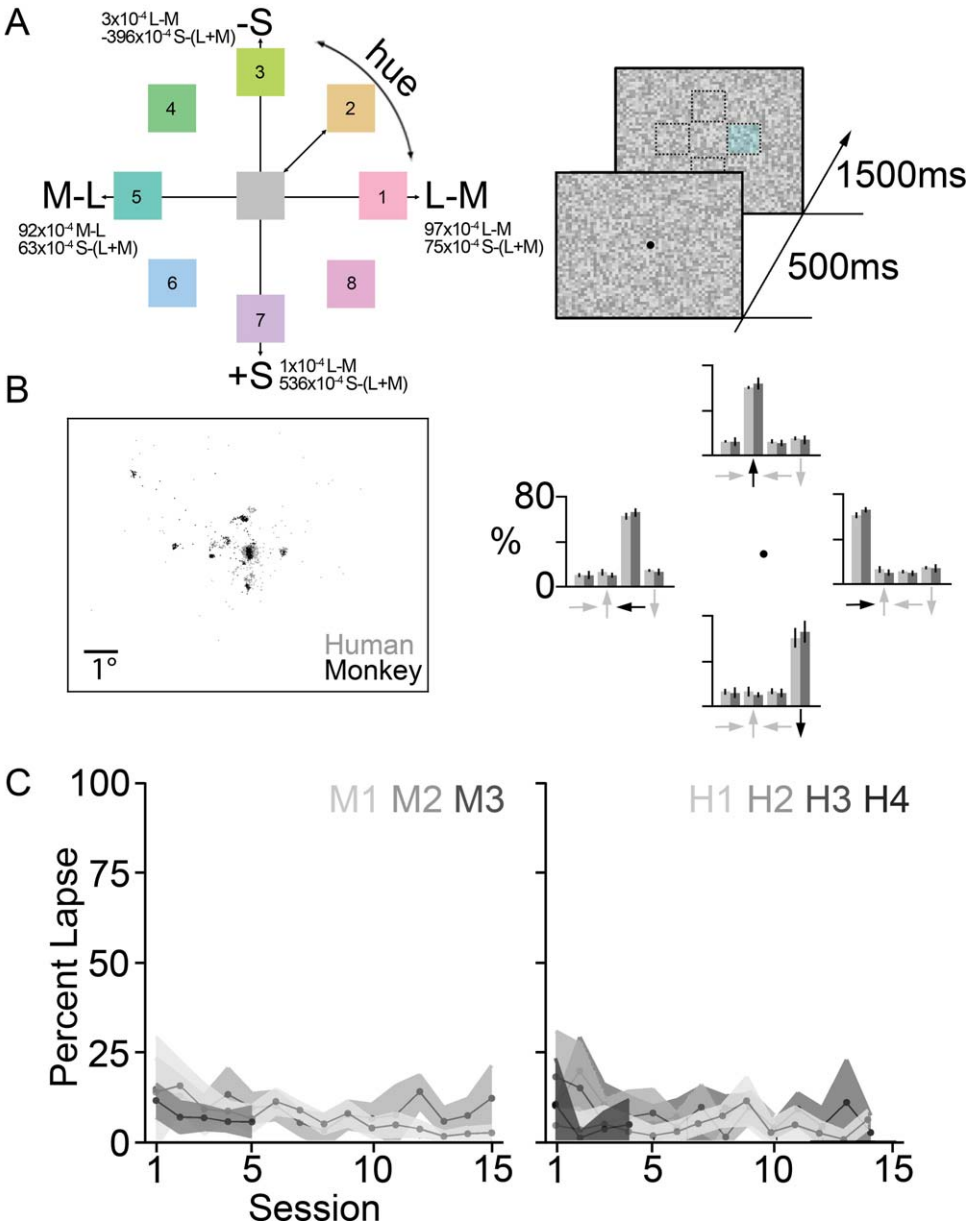


Figure 1. Chromatic-detection task paradigm. (A) Left: Stimuli colors defined by the cardinal axes of cone-opponent color space (Derrington et al., 1984; MacLeod & Boynton, 1979). Numbers show the L − M and S − (L+M) Weber cone contrast elicited by the most saturated colors along the cardinal axes; for example, the cone contrast associated with Color 1 was $(L_1 - L_g)/L_g - (M_1 - M_g)/M_g$, where $L_1$ was the L-cone activation elicited by the stimulus, $L_g$ was the L-cone activation elicited by the neutral gray adapting field, $M_1$ was the M-cone activation by the stimulus, and $M_g$ was the M-cone activation by the adapting field. Right: Four-alternative forced-choice test paradigm**.** Subjects were rewarded for making an eye movement to a colored target in one of four locations (dashed lines) after fixation. (B) Left: Example eye-position trace for a human (gray) and a monkey (black) subject performing the task. The central cluster corresponds to fixation, the four clusters around the central cluster represent eye movements to the edge of the target, and the spurious traces show eye movements between trials. Right: Proportion of saccades made by monkeys (dark gray) and by humans (light gray) during an example session, separated by the location of the target (correct choice shown by black arrow). Error bars show ±1 standard deviation across subjects. (C) Mean lapse rate for monkey (left) and human (right) subjects shown over testing sessions. Shaded region shows standard deviation over colors.

those trials conducted after perceptual learning was exhausted, humans aborted 0.8% of trials and monkeys aborted 0.3% of trials. Monkey subjects were rewarded with a juice drop and a beep, and human subjects with a beep alone, for directing their gaze to the target location. In 1/7 of the trials, no target would appear, and the subjects were rewarded randomly in approximately 25% of the trials. Eye movements were

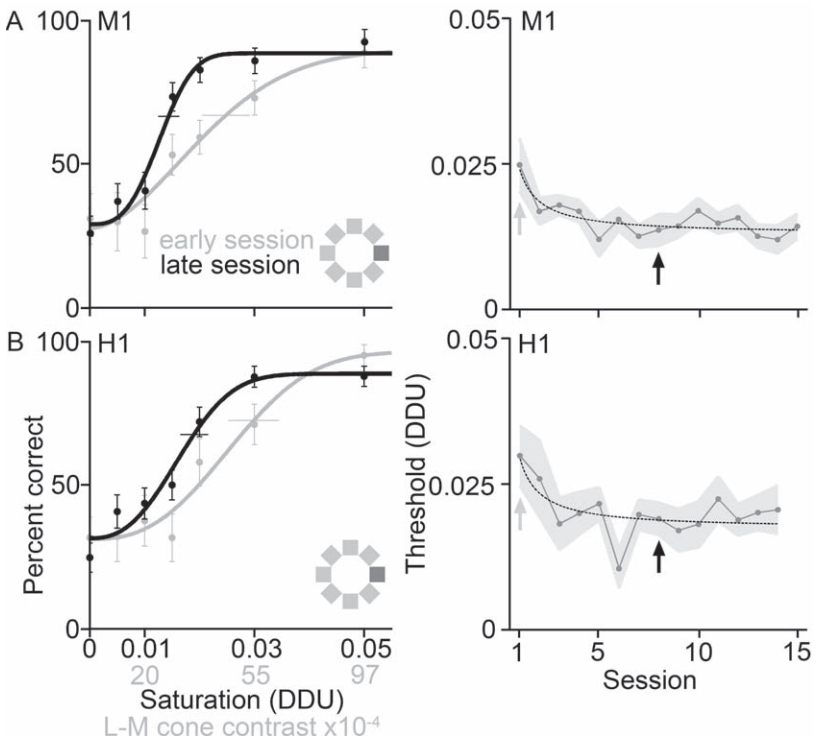


Figure 2. Performance on color-detection task improves with training, monkey data (A) and human data (B). Left: Psychometric detection curves from a single session for color 1 (blackened square in the icon inset identifies the color shown in Figure 1A), for an early session (curve fit $R^2_{human} = 0.96$, $R^2_{monkey} = 0.95$) and a session following plateau performance ($R^2_{human} = 0.98$, $R^2_{monkey} = 0.97$). Vertical error bars show $\pm 1$ standard deviation and horizontal error bars show the 95% confidence interval of the threshold value. Contrast of the target is given in device-dependent units (D.D.U.) and in (L − M)-cone contrast units calculated as described in Figure 1A. Right: Detection threshold over time for color 1; shaded region shows 95% confidence interval. Dashed black line indicates reciprocal function fit ($R^2_{human} = 0.49$, $R^2_{monkey} = 0.74$). Arrows show which session was used to generate the psychometric curves (gray, early session; black, late session).

monitored using an infrared camera tracking system (ISCAN). A trace from a sample session is shown in Figure 1B (left). Subjects showed no obvious bias in target location (Figure 1B, right). Headposts were secured to the animals' skulls (Stoughton et al., 2012) to enable head fixation, which allowed for accurate eye-movement monitoring. Human subjects used a chin rest.

Stimuli were presented with software written in MATLAB using Psychophysics Toolbox Extensions (Brainard, 1997; Kleiner, Brainard, & Pelli, 2007; Pelli, 1997). A 14-bit digital to analog converter (Bits++, Cambridge Research Systems, Rochester, England) drove the stimuli, which were generated using MATLAB code generously provided by Hansen and Gegenfurtner (2006) and calibrated with a PR 655 spectroradiometer (Photo Research Inc.). During testing, the target could vary in color and contrast (azimuth and radial length in the cone-opponent space, Figure 1A) but maintained photometric equiluminance (46.6 cd/m$^2$) with the gray background. The smaller eyes of monkeys compared to humans may have caused a slight difference in the retinal light flux; consequently, the mean retinal luminance might be slightly different for the two species. This is unlikely to have introduced any systematic difference in detection thresholds because the stimuli were embedded in luminance noise.

Trials with targets of different color and saturation were pseudorandomly interleaved, maintaining roughly the same total number of trials of each target within a given session and ensuring that no performance biases could accumulate for a given color. A trial was included in the analysis if the subject did not break fixation during the fixation period and transferred gaze to one of the four possible target locations. The psychometric curves were fit with a Weibull function (http://www.palamedestoolbox.org):

$$y = 1 - e^{-(x/\alpha)^{\beta}},$$

using the maximum-likelihood criterion, where $\alpha$ is the threshold value and $\beta$ is the slope of the fit. The threshold ($\alpha$) corresponds to 63% between guess rate and lapse rate. Thresholds for individual colors were calculated at the end of each session and a reciprocal curve fit was used to describe performance over time. Plateau performance was defined by the crossing of the

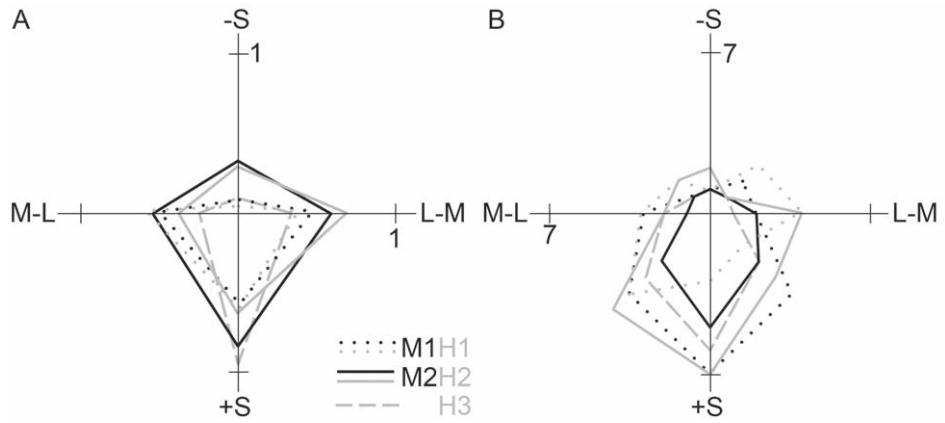


Figure 3. Change in chromatic-detection thresholds with task training. (A) The distance from the origin shows the log difference between the detection threshold obtained on the first two testing sessions and that of the last two testing sessions, for the colors plotted at different angles, for all naïve subjects. The change in detection thresholds with learning was similar for L − M and M − L colors (paired *t* test, $p = 0.3$) but differed for +S and −S colors (paired *t* test, $p = 0.01$). (B) The distance from the origin shows the number of testing sessions required to reach plateau performance for colors plotted at the different angles. Subjects required more sessions to reach plateau along the +S direction compared to the −S direction (paired *t* test, $p = 0.003$), but equal numbers of sessions along the +L − M and −L + M directions (paired *t* test, $p = 0.54$).

standard deviation of the threshold value and the asymptote value of the curve fit (Supplementary Figure S1). There were no striking differences in the lapse rates (Figure 1C) between the two species, suggesting that the motivational states of the subjects were comparable; moreover, performance on maximum-saturation targets was no different across different colors (see Figures 4 and 6), confirming that motivational state did not vary systematically by color (an unlikely possibility in any event, since trials of different color were randomly interleaved).

In pilot experiments, we tested the subjects using 2°-diameter circular targets on uniform gray backgrounds. The spots had 0.1° blurred edges to mitigate chromatic aberration and came on with a Gaussian time course (1500 ms, 250 ms standard deviation). The conclusions from these experiments are similar to those described here, with the exception that the monkeys had peculiarly low thresholds for some colors (notably color 5, Figure 1A; see Figure 11 for a summary of the results from the pilot experiments). We attribute these anomalous results to luminance artifacts, which are controlled by embedding the stimuli in luminance noise (Mullen et al., 2003; Smithson & Mollon, 2004), as was done presently. To generate the luminance noise in the experiments described presently, the screen was divided into checks that were 0.2° across (Experiment 1) or 2° across (Experiment 2). The luminance of each check was randomly assigned to be matched to the mean luminance of the display or 10% or 20% higher or lower, and this assignment changed dynamically several times a second. The cone contrast between the +20%

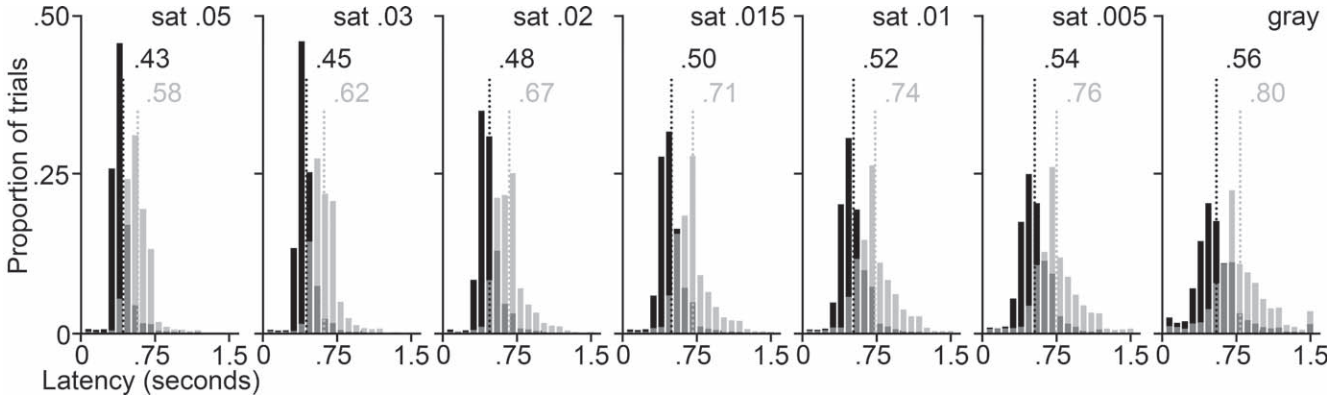


Figure 4. Reaction times for detecting chromatic targets. Average monkey (black) and human (gray) response-time histograms averaged over all colors for a given saturation level. Reaction times were calculated for correct trials except in the gray condition, when all trials were included in the analysis. Dashed lines show mean values of histograms. Stimulus saturation decreases from left to right.

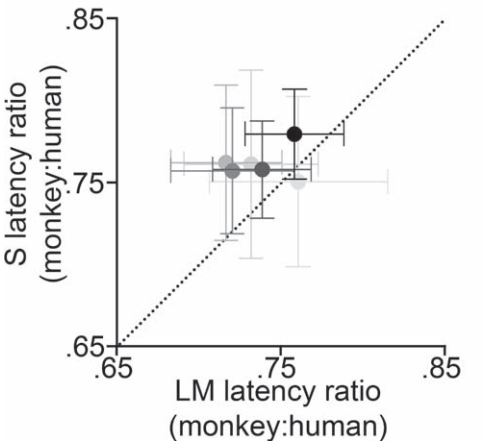


Figure 5. Monkeys detect colored targets of all saturations faster than humans, and faster still for colors along the LM axis. The ratio of the reaction time to S stimuli obtained in monkeys to the reaction time obtained in humans ($S_{\text{reaction time monkeys}}/S_{\text{reaction time humans}}$) is shown as a function of the ratio of the reaction times to L/M stimuli ($LM_{\text{reaction time monkeys}}/LM_{\text{reaction time humans}}$). Darker colors correspond to data originating from trials with higher saturation targets. Error bars show standard error over seven subjects.

and the −20% luminance checks was $24 \times 10^{-4}$ for L, $29 \times 10^{-4}$ for M, and $30 \times 10^{-4}$ for S.

## Results

We tested psychophysical performance on a chromatic-detection task in three monkeys and four humans. Two of the monkeys (M1, M2) and three of the humans (H1, H2, H3) were naïve to the task at the beginning of the present experiments; one experienced psychophysical observer (H4) participated in an extensive series of pilot experiments and was the best subject among eight humans tested; and one monkey (M3) also participated in the pilot experiments. H1 and H2 were Caucasian, H3 was Asian-American, and H4 was of African origin; we report these details because race may affect L − M ratios (McMahon, Carroll, Awua, Neitz, & Neitz, 2008). M1 and M2 performed an average of 2,576 detection trials per session, in 15 sessions over 2 months. M3 showed stable thresholds over a yearlong

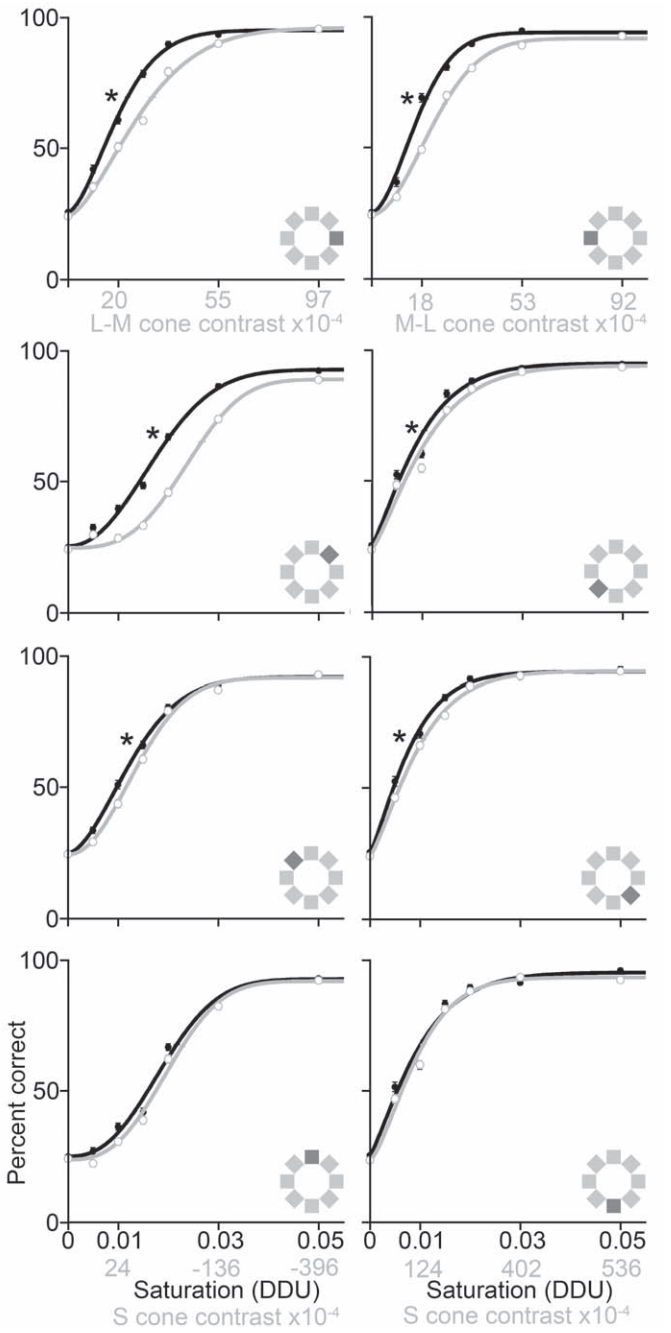


Figure 6. Psychometric curves for the detection of eight colors evenly sampling the equiluminant color plane, for monkeys and humans, using stimuli embedded in 0.2° luminance noise. Average monkey (black) and average human (gray) performance is shown for all colors (icons refer to Figure 1A). Contrast of the target is given in device-dependent units and in cone-contrast units (curve fits: color 1, $R^2_{\text{human}} = 0.99$, $R^2_{\text{monkey}} = 1.0$; color 2, ← $R^2_{\text{human}} = 0.99$, $R^2_{\text{monkey}} = 0.99$; color 3, $R^2_{\text{human}} = 0.99$, $R^2_{\text{monkey}} = 0.99$; color 4, $R^2_{\text{human}} = 1.0$, $R^2_{\text{monkey}} = 1.0$; color 5, $R^2_{\text{human}} = 1.0$, $R^2_{\text{monkey}} = 0.99$; color 6, $R^2_{\text{human}} = 0.98$, $R^2_{\text{monkey}} = 0.98$; color 7, $R^2_{\text{human}} = 0.99$, $R^2_{\text{monkey}} = 0.98$; color 8, $R^2_{\text{human}} = 1.0$, $R^2_{\text{monkey}} = 1.0$). Curves obtained for monkeys were considered significantly different from those obtained in humans if the 95% confidence intervals of the threshold values did not cross (asterisks).

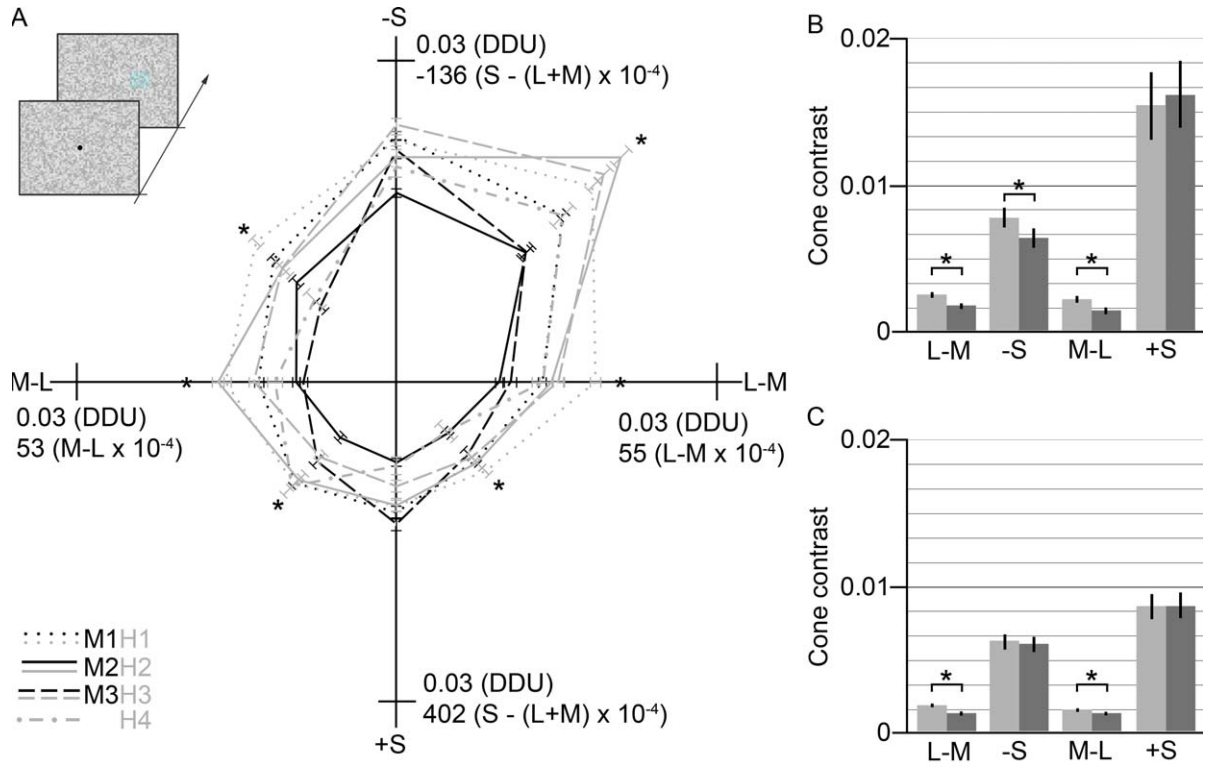


Figure 7. Detection thresholds for chromatic targets embedded in 0.2° luminance noise. (A) Average threshold value in device-dependent units and cone-contrast units (see Figure 1A for formula), shown as the distance from the origin for each color direction tested. Error bars on curves for individual subjects show 95% confidence intervals. Asterisks mark colors that showed a significant difference between average monkey performance and average human performance (see Figures 6 and 7C). Monkeys showed lower detection thresholds in general (ANOVA, $\alpha = 0.05$, $p = 7 \times 10^{-4}$). Inset shows an icon of the stimulus (see Figure 1A, right panel). (B) Average threshold for monkeys (dark gray) and humans (light gray) for the cardinal colors in cone-contrast units during initial testing, prior to exhausting perceptual learning, and (C) at plateau performance after exhausting perceptual learning. Error bars show 95% confidence intervals, asterisks indicate significant differences (see Figure 6). Values were considered significantly different if their 95% confidence intervals did not cross.

gap in training between the pilot experiments and the present experiments (Supplementary Figure S2); M3 was tested for an average of 3,136 detection trials per session for five sessions in the present experiments. H1, H2, and H3 performed an average of 1,960 trials per session, and an average of 13 sessions over 3 months; H4 performed an average of 759 trials per session and four sessions on the present experiments (but was overtrained on a very similar task in the pilot study). The naïve humans reached plateau performance at a similar time compared to the naïve monkeys (one-way ANOVA, $p = 0.2$).

During the course of the experiments, all subjects became overtrained on the task, exhausting perceptual learning. The time point at which perceptual learning was exhausted and plateau performance was obtained was defined as the crossing of the standard deviation of the threshold value and the asymptote value of the curve fit to the data (Supplementary Figure S1; Stoughton et al., 2012). Figure 2 shows an example set of psychometric curves for a monkey (Figure 2A) and a human (Figure 2B) obtained before plateau performance (gray lines) and after plateau performance (black lines); these results were obtained for color 1 (+L − M; inset Figure 2, left plots, shows an icon of the color space highlighting the L − M color). Contrast of the target is given in cone-contrast units as well as device-dependent units (D.D.U.), where, for example, 0.05 refers to 5% of the monitor's maximum contrast. As expected, target-detection performance increased with increasing target saturation for monkeys and humans. The black lines are shifted to the left, showing that training reduced the detection thresholds. Figure 3A shows a polar plot of the log change in detection thresholds between the first two testing sessions and the last two testing sessions, as a function of the color of the target, for the initially naïve subjects. Distances further from the origin show a greater learning effect. The change in detection thresholds with learning was similar for +L − M (red) colors and +M − L (bluish-green) colors (paired $t$ test, $p = 0.3$). But the learning effect for +S (lavender) was higher than for −S (yellow-

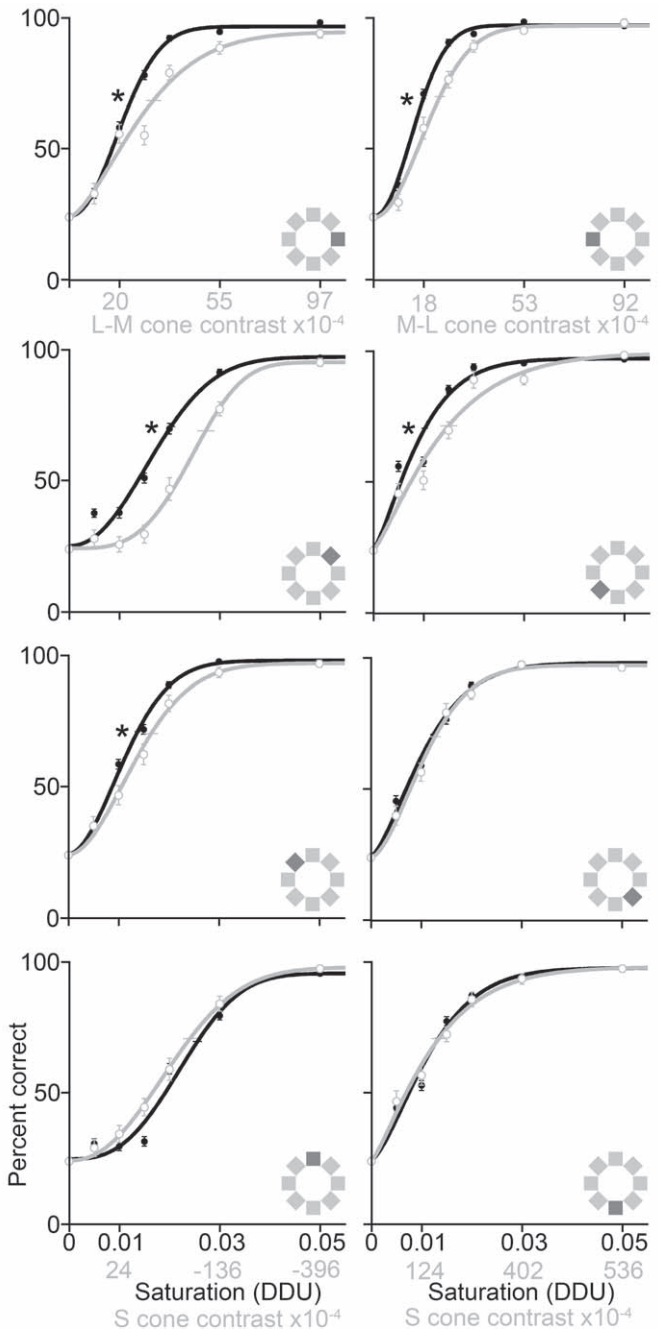


Figure 8. Psychometric curves for the detection of eight colors evenly sampling the equiluminant color plane, for monkeys and humans, using stimuli embedded in 2° luminance noise. Conventions as for Figure 6 (curve fits: color 1, $R^2_{human} = 0.97$, $R^2_{monkey} = 1.0$; color 2, $R^2_{human} = 0.99$, $R^2_{monkey} = 0.98$; color 3, $R^2_{human} = 1.0$, $R^2_{monkey} = 0.97$; color 4, $R^2_{human} = 1.0$, $R^2_{monkey} = 1.0$; color 5, $R^2_{human} = 1.0$, $R^2_{monkey} = 1.0$; color 6, $R^2_{human} = 0.97$, $R^2_{monkey} = 0.95$; color 7, $R^2_{human} = 0.99$, $R^2_{monkey} = 0.99$; color 8, $R^2_{human} = 1.0$, $R^2_{monkey} = 0.99$).

lime; paired $t$ test, $p = 0.01$). Moreover, the number of sessions necessary to reach plateau performance for the +S (lavender) compared to the −S (yellow-lime) colors was higher (paired $t$ test, $p = 0.003$; number of sessions to reach plateau for +L − M compared to +M − L colors, $p = 0.5$; Figure 3B).

Figure 4 compares the reaction times on the task for the monkeys (black bars) and humans (gray bars), for the different stimuli conditions. As expected, trials with the most saturated stimuli were associated with shorter reaction times (Figure 4, left panel) than trials with less saturated stimuli (Figure 4, right panel). Monkeys showed shorter reaction times than humans for all stimuli (compare black bars and gray bars, Figure 4). Monkeys also showed relatively shorter reaction times to L/M colors than to S colors: Figure 5 shows the ratio of the average reaction time to S stimuli obtained in monkeys to the average reaction time obtained in humans ($S_{reaction\ time\ monkeys}/S_{reaction\ time\ humans}$) as a function of the ratio of the reaction times to L/M stimuli ($LM_{reaction\ time\ monkeys}/LM_{reaction\ time\ humans}$) for targets of different saturation (data associated with more saturated targets shown in darker data points). All the data points are less than 1, reflecting the observation that monkey reaction times were shorter than human reaction times to all stimuli; the data point corresponding to the most saturated stimuli approaches 1, showing that the differences in reaction times between monkeys and humans are reduced for the most visible targets; and the data points typically lie above the unity diagonal, showing that monkey reaction times to LM targets were relatively shorter than reaction times to S targets.

Figure 6 shows average psychometric curves of the detection task obtained after plateau performance for all monkeys ($N = 3$; black lines) and all humans ($N = 4$; gray lines), for colors that modulate selectively the L and M cones (top row), intermediate colors (middle two rows), and colors that modulate the S cones (bottom row). In the top row, the black curves are shifted slightly but significantly to the left compared to the gray curves, showing that for L/M colors monkeys had, on average, lower detection thresholds than humans. The black and gray curves are overlapping in the bottom panels, showing that monkeys and humans had similar detection thresholds for S colors. Psychometric curves for individual subjects are in Supplementary Figure S3.

Figure 7A shows the detection thresholds for all colors obtained in Experiment 1, for individual subjects, as a polar plot. Data points that are further from the origin correspond to larger detection thresholds (i.e., lower sensitivity). For all colors, with the exception of red (L − M) and orange (L − M − S) colors, there was at least one human that had a lower detection threshold than one monkey, and one monkey that had a lower detection threshold than one human. But the monkey with the best performance (M2) had lower detection thresholds than the human with the best performance (H4), except for green (M − L − S),

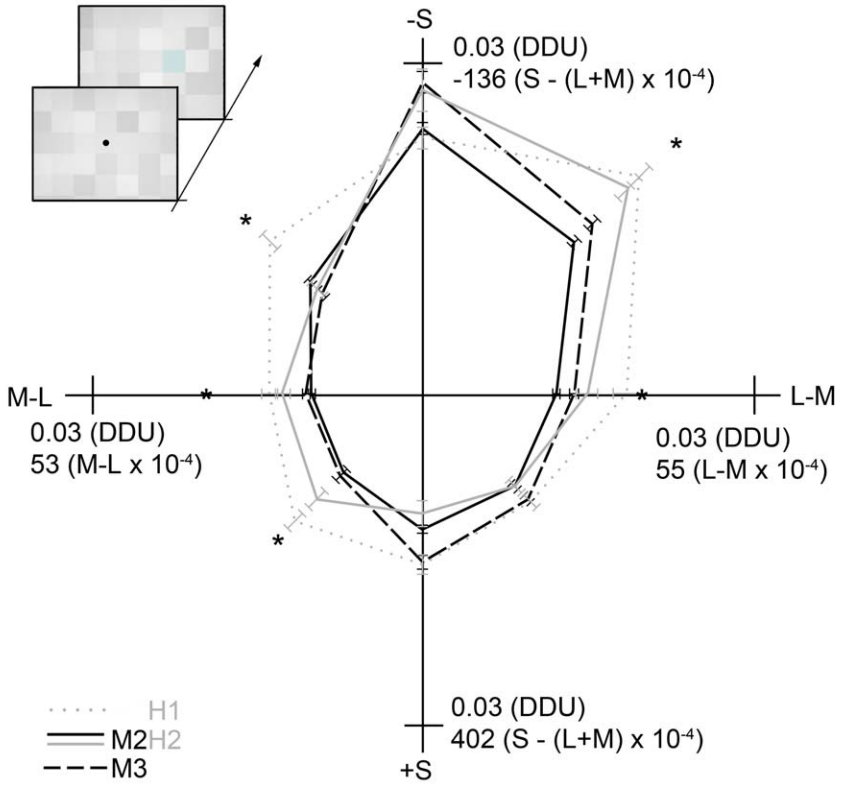


Figure 9. Detection thresholds for chromatic targets embedded in 2° luminance noise. Conventions as for Figure 7A. Monkeys showed lower detection thresholds (*n*-way ANOVA, $\alpha = 0.05$, $p = 6 \times 10^{-3}$). Inset shows an icon of the stimulus.

even though the monkey subject had less experience than the human subject on psychophysical tasks (including the present tests). On average, the black lines (monkey subjects) tend to sit inside the gray lines (human subjects) for all colors except those that selectively modulate the S cones (asterisks show significant differences between the species; significance was achieved if the 95% confidence interval of the threshold values between the two species did not cross). Across colors, monkeys had lower detection thresholds than humans (ANOVA, $\alpha = 0.05$, $p = 7 \times 10^{-4}$). These results show that chromatic stimuli that were often invisible to humans were visible to monkeys. The S axis in Figure 7A has been scaled so that any given excursion in the −S or +S direction corresponds to the same value in device-dependent units, but the equivalent device-dependent unit corresponds to a different value of absolute cone contrast depending on the

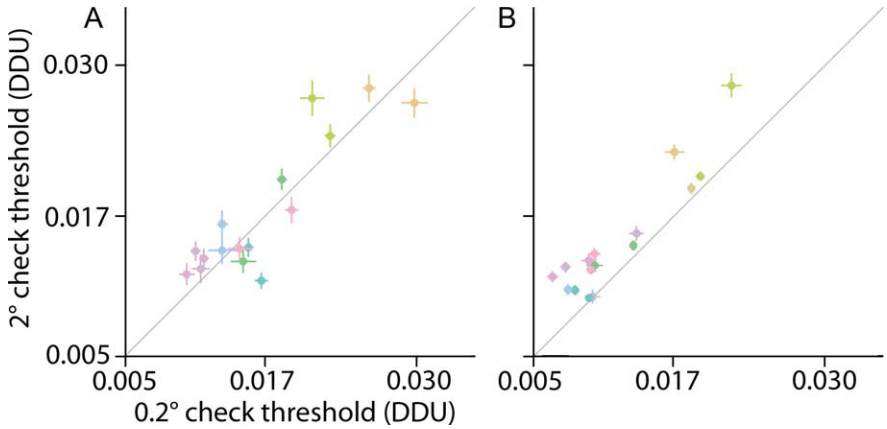


Figure 10. Detection thresholds increase when targets are embedded in 2° versus 0.2° luminance noise for humans (A) and for monkeys (B). Error bars show standard deviation of the calculated threshold value. Color of marker corresponds to the hue direction. Multiple markers of the same color correspond to performance of different subjects.

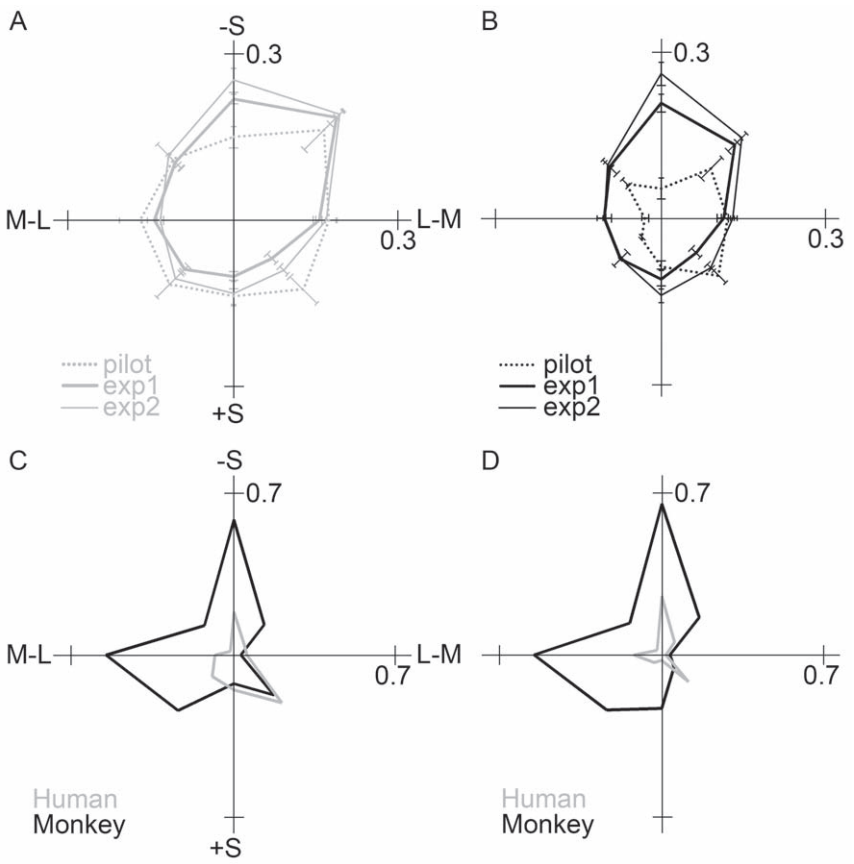


Figure 11. Impact of luminance noise on chromatic-target detection threshold. Average human threshold values are shown as the distance from the origin for each color direction obtained in Experiment 1 (thick solid line; 0.2° luminance noise), Experiment 2 (thin solid line; 2° luminance noise), and the pilot experiment (dashed line; no luminance noise) for humans (A) and monkeys (B). Normalized difference in threshold value between the pilot study and Experiment 1 (C) and between the pilot study and Experiment 2 (D) are shown as distance from the origin for each color direction for humans (gray) and monkeys (black) as given by the following equation: luminance effect $= \frac{|\text{threshold}_{\text{luminance noise}} - \text{threshold}_{\text{pilot}}|}{\text{threshold}_{\text{luminance noise}} + \text{threshold}_{\text{pilot}}}$.

direction (−S or +S), reflecting the fact that the stimulus monitor could generate more +S than −S contrast. The absolute value of the cone contrast of the stimuli required to reach threshold is shown in Figure 7B and C. The average human subject required $86 \times 10^{-4}$ S-cone contrast in the +S direction and $62 \times 10^{-4}$ S-cone contrast in the −S direction to reach detection threshold; the corresponding values for the average monkey were not significantly different ($72 \times 10^{-4}$; $59 \times 10^{-4}$). By comparison, the average human subject required $17 \times 10^{-4}$ (L− M)-cone contrast to reach detection threshold; the corresponding value for the average monkey was slightly lower ($12 \times 10^{-4}$). Note that to reach detection threshold, the amount of S-cone contrast is considerably higher than the amount of (L − M)-cone contrast regardless of the species, showing that all subjects are less sensitive to S stimuli (Figure 7B, C).

The results shown in Figures 6 and 7 were obtained using 2° targets embedded in 0.2° luminance noise. Monkeys and humans differ in their preretinal filters (Snodderly, Auran, & Delori, 1984), which may cause the targets to be perceived as a color superimposed on a luminance pedestal. To control for this possibility, we performed an additional experiment with two of the monkeys and two of the humans. The targets were the same size as in Experiment 1 but were embedded in 2° luminance noise. The targets were spatially registered to the luminance noise checks; any uniform luminance pedestal would therefore be masked. Figure 8 shows average psychometric curves for humans (gray curves) and monkeys (black curves). The results are consistent with those shown in Figure 6: Monkeys had slightly lower detection thresholds than humans for L/M colors (Figure 8, top row) and similar detection thresholds compared to humans for S colors (Figure 8, bottom row). Figure 9 shows the results of Experiment 2 as a polar plot (compare with Figure 7). Again, the results are consistent with those obtained with tests conducted using smaller grain luminance noise: Compared to humans, monkeys were more sensitive to L/M colors and showed no difference in sensitivity to S colors. The

human subjects reported that the task in Experiment 2 seemed a little more difficult than the task in Experiment 1. Consistent with this report, human detection thresholds were slightly higher on average for the experiment using 2° noise (more data points sit above the unity diagonal in Figure 10A). Monkey thresholds were also higher for this experiment (Figure 10B), and higher than the differences observed in humans, reflecting the increased task difficulty.

In Figure 11 we compare the results obtained presently with those obtained during the preliminary pilot experiment, to gain some sense of the impact of the luminance noise on chromatic sensitivity. In the pilot experiment, targets were 2° discs with 0.1° blurred edges, centered at 2° peripheral to fixation, presented on a uniform gray background. Other aspects of the psychophysical paradigm, including eye monitoring, were similar to those for the experiments described previously. All subjects were overtrained, and detection thresholds were assessed after plateau performance. Figure 11A shows a polar plot of the detection thresholds averaged across humans obtained in Experiment 1 (thick solid line; 0.2° luminance noise), Experiment 2 (thin solid line; 2° luminance noise), and the pilot experiment (dashed line; no noise). Figure 11B shows the corresponding results in monkeys. Figure 11C shows the absolute difference of the detection thresholds measured in the pilot experiment and Experiment 1, and Figure 11D shows the absolute difference of the detection thresholds measured in the pilot experiment and Experiment 2. Luminance noise was associated with a change in detection threshold for colors along the S axis (more prominently −S colors); these colors would be the most likely colors affected by luminance artifacts associated with chromatic aberration. The luminance noise also raised the detection thresholds in monkeys for M − L colors; the cause for this result is unclear.

## Discussion and conclusion

The similarity in cone sensitivities found in monkeys and humans supports the use of monkeys as a model of human color vision (Conway et al., 2010). But color perception depends on many computations implemented downstream of the cones (Conway, 2009). In order to use monkeys to test hypotheses of how this circuitry functions to bring about color perception and cognition, it is important to directly compare psychophysical behavior in the two species (Stoughton et al., 2012). Here we performed tests of one of the simplest color tasks: detection of chromatic targets. For the most part, monkeys and humans had very similar color-detection thresholds. Monkey and human thresholds were indistinguishable for colors that selectively modulate S cones, but monkey thresholds were slightly lower than human thresholds for colors that modulated L/M cones. This subtle species difference may arise because of differences in the cone fundamentals between the two species; alternatively, the difference may reflect the evolutionary trade-off between color acuity and spatial acuity, as discussed later. The data also showed, for both species, a systematic difference in the magnitude of task improvement over time between S increments (more improvement over time) and S decrements (less improvement over time). We conclude that while monkeys may not be an identical model of human color vision, they are nonetheless an excellent system for investigating physiological mechanisms of human trichromatic color vision.

Prior measurements of absolute color detection in monkeys and humans have suggested that monkeys have similar or possibly worse color abilities than humans (see Introduction). To our knowledge, the present report is the first to use equiluminant stimuli presented under careful computer control to directly compare the abilities in the two species on the same task and apparatus. The slightly better performance of the monkeys on colors that modulate L/M cones is unlikely to be attributed to luminance artifacts or higher motivation on the part of the monkeys. We assume that the subtle species difference would remain if the task were altered such that the targets were presented at the fovea, but we have not tested this. The stimuli were embedded in luminance noise, which masks luminance artifacts; and trials of different colors were randomly interleaved, so it would be impossible for the animals to show selectively higher motivation or attention on trials with some colors. The stimuli used on both species were identical, generated using human cone fundamentals that are widely used in both human psychophysics and monkey physiology. It remains unknown to what extent these fundamentals are appropriate for use in experiments with monkeys. That we obtain very similar detection-threshold measurements in monkeys using stimuli that assume human cone fundamentals suggests that the use of human fundamentals for physiological and psychophysical experiments in monkeys will not introduce grave errors. Nonetheless, the subtle species differences along the L − M axis may arise because the human cone fundamentals provide an inaccurate estimate of the sensitivity of the macaque S-cone system. Colors defined by the L − M axis are assumed not to modulate the S cone; an error in the estimated activation of the S system could cause activation of S cones to L − M colors. If so, what would be an (L/M)-isolating stimulus for humans would activate all three cone types in monkeys, potentially lowering the detection thresh-

old. We suspect this does not account for the lower L − M thresholds in monkeys, because the absolute detection thresholds for S stimuli in both species are relatively high: The L/M stimuli would need to be driving the S cone rather substantially to have any measureable effect on detection threshold. The pattern of results would seem more consistent with an alternative explanation: that monkeys have lower detection thresholds for L/M colors.

Despite the previous literature concluding that humans have similar or better color vision than monkeys, the converse is predicted by subtle differences in the spatial arrangement and relative numbers of the cones: Specifically, the ratio of L cones to M cones appears to be smaller in monkeys than in humans (Deeb, Diller, Williams, & Dacey, 2000; Hofer, Carroll, Neitz, Neitz, & Williams, 2005; Roorda, Metha, Lennie, & Williams, 2001). A balanced L:M cone ratio may make it less likely that adjacent cones have the same spectral sensitivity, and would predict better color acuity but possibly worse spatial acuity (Williams, Sekiguchi, Haake, Brainard, & Packer, 1991). It remains to be tested whether humans showing more balanced L:M cone ratios show lower color-detection thresholds, as this theory predicts (McMahon et al., 2008). But consistent with the theory, humans appear to have on average slightly higher spatial acuity than monkeys (Cavonius & Robbins, 1973; Weinstein & Grether, 1940). Taken together, the present results raise the possibility that evolutionary selective pressures have resulted in slightly higher chromatic sensitivity among macaque monkeys compared to humans, at the cost of spatial acuity. A review of previously published data is consistent with this theory (Harwerth & Smith, 1985). Such selective pressures are consistent with the importance of color to monkeys in the wild (Dominy & Lucas, 2001; Regan et al., 2001), as reflected in the dramatically lower rates of color deficiency among monkeys compared to humans (Onishi et al., 1999). The S-cone mosaic may also be subtly different in monkeys and humans. Monkeys may have a higher fraction of S cones than do humans; the S cones in monkeys may form a more regular mosaic; and monkey retinas might not show the characteristic S-cone hole found at the center of the human fovea (Bumsted & Hendrickson, 1999; Curcio et al., 1991; Curcio, Sloan, Packer, Hendrickson, & Kalina, 1987; Hofer et al., 2005; Roorda et al., 2001; Williams, MacLeod, & Hayhoe, 1981a, 1981b; but see Martin & Grunert, 1999). Despite the species differences in S-cone mosaics, we found no difference in S-cone detection thresholds between monkeys and humans.

The polar plots (Figures 7 and 9) reveal a striking asymmetry in the detection thresholds for colors that modulate all three cone types (i.e., those colors defined by the axes intermediate to the cardinal axes). Specifically, detectability for the (L − M) − S color (orange) was no better than that of the projection onto the best cardinal, particularly for humans. This observation is consistent with lack of probability summation (i.e., independent early noise), which is also consistent with neurophysiological measurements showing the prevalence of cone-opponent neurons preferring the L versus (M + S) chromatic direction in macaque V1 (Conway, 2001; Lafer-Sousa, Liu, Lafer-Sousa, Wiest, & Conway, 2012; Conway, 2014). More generally, the observation supports the importance of independent higher order chromatic mechanisms for mediating detection (Hansen & Gegenfurtner, 2006; Stoughton et al., 2012).

The present experiments provide some insight into the time course of perceptual learning for chromatic targets. Access to this information is difficult to obtain from previous comparative experiments, which often used aversive conditioning that over time engenders a long-term avoidance response to the testing situation. The present results show that subjects needed a variable number of sessions to reach plateau performance for different colors, but that the range was the same between monkey and human subjects (one to seven sessions). Monkeys and humans also showed similar variability in the number of sessions necessary to reach plateau performance ($SD = 1.9$ for monkeys, 1.8 for humans). Once plateau performance was achieved, optimal performance was maintained across long time gaps in task activity (Supplementary Figure S2). The results show a striking asymmetry in the improvement in performance over training for the +S versus −S targets for both humans and monkeys: the learning effect for +S (lavender) was higher than for −S (yellow-lime). At plateau detection, thresholds for S increments were somewhat higher than thresholds for S decrements ($p < 0.05$; 95% confidence intervals are non-overlapping; Figure 7C); but the initial detection thresholds for S increments were considerably higher than for S decrements (Figure 7B). These observations provide a psychophysical correlate of the physiological and anatomical differences in S-ON and S-OFF circuitry. The retina has a dedicated bipolar for S-ON signals but does not have one for S-OFF signals (Dacey, Crook, & Packer, 2013). S-OFF signals are communicated through the retina by way of a midget OFF bipolar cell connected to a midget OFF retinal ganglion cell (Klug, Herr, Ngo, Sterling, & Schein, 2003). Asymmetries in S-ON and S-OFF signals are propagated through the lateral geniculate nucleus (Tailby, Solomon, & Lennie, 2008) and V1 (Conway & Livingstone, 2006). Although previously reported values for detection thresholds for S increments and S decrements are similar (Bosten et al., 2014; DeMarco, Smith, & Pokorny, 1994; Figure 7), other psycho-

physical tests have revealed asymmetries likely attributed to the differences in circuitry for S-ON and S-OFF (Hughes & DeMarco, 2003; Shinomori, Spillmann, & Werner, 1999). Moreover, the spatial summation for S-cone decrements appears to be greater than for S-cone increments, providing another clue that these pathways are subserved by different circuitry (Vassilev, Ivanov, Zlatkova, & Anderson, 2005). If the better performance of the monkeys on the L − M targets is mediated by neurons early in the visual-processing hierarchy (such as midget cells in the retina), one might predict that the monkeys would also show slightly better performance on the −S targets (since retinal encoding of these targets is likely performed by the same cells). Consistent with this prediction, the results show that monkeys had significantly lower detection thresholds than humans for −S targets during initial testing (Figure 7B). But this trend was not significant after extensive training (Figure 7C), suggesting that the differential impact of learning on targets of different colors depends, to some extent, on computations in the cortex.

The results described presently were obtained by testing detection thresholds at one visual-field eccentricity (2°) using relatively large targets (2° square). This eccentricity corresponds to a region with dense macular pigmentation (Snodderly et al., 1984). Macular pigmentation functions as a preretinal chromatic filter and impacts the color-matching functions used to define the equiluminant stimuli. The extent and makeup of macular pigmentation is different in monkeys versus humans, which may introduce luminance artifacts especially with stimuli that modulate S cones. The similarity of detection thresholds in the two species, particularly to S-cone-modulating stimuli, suggests that differences in macular pigmentation are unlikely to be problematic. But in order to adequately address this issue, detection-threshold tests must be done across the visual field (G. Horwitz, University of Washington, personal communication, April 25, 2014).

*Keywords: macaque monkey, human, color vision*

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## References

Bosten, J. M., Bargary, G., Goodbourn, P. T., Hogg, R. E., Lawrance-Owen, A. J., & Mollon, J. D. (2014). Individual differences provide psychophysical evidence for separate on- and off-pathways deriving from short-wave cones. *Journal of the Optical Society of America A, 31*(4), A47–A54.

Brainard, D. H. (1997). The Psychophysics Toolbox. *Spatial Vision, 10*(4), 433–436.

Bumsted, K., & Hendrickson, A. (1999). Distribution and development of short-wavelength cones differ between *Macaca* monkey and human fovea. *Journal of Comparative Neurology, 403*(4), 502–516.

Cavonius, C. R., & Robbins, D. O. (1973). Relationships between luminance and visual acuity in the rhesus monkey. *Journal of Physiology, 232*(2), 239–246.

Conway, B. R. (2001). Spatial structure of cone inputs to color cells in alert macaque primary visual cortex (V-1). *Journal of Neuroscience, 21*(8), 2768–2783.

Conway, B. R. (2009). Color vision, cones, and color-coding in the cortex. *Neuroscientist, 15*(3), 274–290.

Conway, B. R. (2014). Color signals through dorsal and ventral visual pathways. *Visual Neuroscience, 31*(2), 197–209.

Conway, B. R., Chatterjee, S., Field, G. D., Horwitz, G. D., Johnson, E. N., Koida, K., & Mancuso, K. (2010). Advances in color science: From retina to behavior. *Journal of Neuroscience, 30*(45), 14955–14963.

Conway, B. R., & Livingstone, M. S. (2006). Spatial and temporal properties of cone signals in alert macaque primary visual cortex. *Journal of Neuroscience, 26*(42), 10826–10846.

Curcio, C. A., Allen, K. A., Sloan, K. R., Lerea, C. L., Hurley, J. B., Klock, I. B., & Milam, A. H. (1991). Distribution and morphology of human cone photoreceptors stained with anti-blue opsin. *Journal of Comparative Neurology, 312*(4), 610–624.

Curcio, C. A., Sloan, K. R., Jr., Packer, O., Hen-

drickson, A. E., & Kalina, R. E. (1987). Distribution of cones in human and monkey retina: Individual variability and radial asymmetry. *Science, 236*(4801), 579–582.

Dacey, D. M., Crook, J. D., & Packer, O. S. (2014). Distinct synaptic mechanisms create parallel S-ON and S-OFF color opponent pathways in the primate retina. *Visual Neuroscience, 31*(2), 139–151.

De Valois, R. L., Morgan, H. C., Polson, M. C., Mead, W. R., & Hull, E. M. (1974). Psychophysical studies of monkey vision. I. Macaque luminosity and color vision tests. *Vision Research, 14*(1), 53–67.

Deeb, S. S., Diller, L. C., Williams, D. R., & Dacey, D. M. (2000). Interindividual and topographical variation of L:M cone ratios in monkey retinas. *Journal of the Optical Society of America A, 17*(3), 538–544.

DeMarco, P. J., Jr., Smith, V. C., & Pokorny, J. (1994). Effect of sawtooth polarity on chromatic and luminance detection. *Visual Neuroscience, 11*(3), 491–499.

Derrington, A. M., Krauskopf, J., & Lennie, P. (1984). Chromatic mechanisms in lateral geniculate nucleus of macaque. *Journal of Physiology, 357,* 241–265.

Dominy, N. J., & Lucas, P. W. (2001). Ecological importance of trichromatic vision to primates. *Nature, 410*(6826), 363–366.

Grether, W. F. (1940). Chimpanzee color vision. I. Hue discrimination at three spectral points. *Journal of Comparative Psychology, 29*(2), 167–177.

Hansen, T., & Gegenfurtner, K. R. (2006). Higher level chromatic mechanisms for image segmentation. *Journal of Vision, 6*(3):5, 239–259, http://www.journalofvision.org/content/6/3/5, doi:10.1167/6.3.5. [PubMed] [Article]

Harwerth, R. S., & Smith, E. L., 3rd. (1985). Rhesus monkey as a model for normal vision of humans. *American Journal of Optometry and Physiological Optics, 62*(9), 633–641.

Hofer, H., Carroll, J., Neitz, J., Neitz, M., & Williams, D. R. (2005). Organization of the human trichromatic cone mosaic. *Journal of Neuroscience, 25*(42), 9669–9679.

Hughes, A., & DeMarco, P. J., Jr. (2003). Time course of adaptation to stimuli presented along cardinal lines in color space. *Journal of the Optical Society of America A, 20*(12), 2216–2227.

Jacobs, G. H. (2008). Primate color vision: A comparative perspective. *Visual Neuroscience, 25*(5–6), 619–633.

Kleiner, M., Brainard, D. H., & Pelli, D. (2007). What's new in Psychtoolbox-3? *Perception, 36*(ECVP Abstract Supplement).

Klug, K., Herr, S., Ngo, I. T., Sterling, P., & Schein, S. (2003). Macaque retina contains an S-cone OFF midget pathway. *Journal of Neuroscience, 23*(30), 9881–9887.

Lafer-Sousa, R., Liu, Y. O., Lafer-Sousa, L., Wiest, M. C., & Conway, B. R. (2012). Color tuning in alert macaque V1 assessed with fMRI and single-unit recording shows a bias toward daylight colors. *Journal of the Optical Society of America A, 29*(5), 657–670.

MacLeod, D. I., & Boynton, R. M. (1979). Chromaticity diagram showing cone excitation by stimuli of equal luminance. *Journal of the Optical Society of America, 69*(8), 1183–1186.

Martin, P. R., & Grunert, U. (1999). Analysis of the short wavelength-sensitive ("blue") cone mosaic in the primate retina: Comparison of New World and Old World monkeys. *Journal of Comparative Neurology, 406*(1), 1–14.

McMahon, C., Carroll, J., Awua, S., Neitz, J., & Neitz, M. (2008). The L:M cone ratio in males of African descent with normal color vision. *Journal of Vision, 8*(2):5, 1–9, http://www.journalofvision.org/content/8/2/5, doi:10.1167/8.2.5. [PubMed] [Article]

Mullen, K. T., Yoshizawa, T., & Baker, C. L., Jr. (2003). Luminance mechanisms mediate the motion of red–green isoluminant gratings: The role of "temporal chromatic aberration." *Vision Research, 43*(11), 1235–1247.

Onishi, A., Koike, S., Ida, M., Imai, H., Shichida, Y., Takenaka, O., ... Yamamori, T. (1999). Vision: Dichromatism in macaque monkeys. *Nature, 402*(6758), 139–140.

Pelli, D. G. (1997). The VideoToolbox software for visual psychophysics: Transforming numbers into movies. *Spatial Vision, 10*(4), 437–442.

Regan, B. C., Julliot, C., Simmen, B., Vienot, F., Charles-Dominique, P., & Mollon, J. D. (2001). Fruits, foliage and the evolution of primate colour vision. *Philosophical Transactions of the Royal Society of London, Series B: Biological Sciences, 356*(1407), 229–283.

Roorda, A., Metha, A. B., Lennie, P., & Williams, D. R. (2001). Packing arrangement of the three cone classes in primate retina. *Vision Research, 41*(10–11), 1291–1306.

Schnapf, J. L., Kraft, T. W., & Baylor, D. A. (1987). Spectral sensitivity of human cone photoreceptors. *Nature, 325*(6103), 439–441.

Shinomori, K., Spillmann, L., & Werner, J. S. (1999).

S-cone signals to temporal OFF-channels: Asymmetrical connections to postreceptoral chromatic mechanisms. *Vision Research, 39*(1), 39–49.

Sidley, N. A., Sperling, H. G., Bedarf, E. W., & Hiss, R. H. (1965). Photopic spectral sensitivity in the monkey: Methods for determining, and initial results. *Science, 150*(705), 1837–1839.

Smith, V. C., & Pokorny, J. (1972). Spectral sensitivity of color-blind observers and the cone photopigments. *Vision Research, 12*(12), 2059–2071.

Smith, V. C., & Pokorny, J. (1975). Spectral sensitivity of the foveal cone photopigments between 400 and 500 nm. *Vision Research, 15*(2), 161–171.

Smithson, H. E., & Mollon, J. D. (2004). Is the S-opponent chromatic sub-system sluggish? *Vision Research, 44*(25), 2919–2929.

Snodderly, D. M., Auran, J. D., & Delori, F. C. (1984). The macular pigment. II. Spatial distribution in primate retinas. *Investigative Ophthalmology & Visual Science, 25*(6), 674–685, http://www.iovs.org/content/25/6/674. [PubMed] [Article]

Stoughton, C. M., Lafer-Sousa, R., Gagin, G., & Conway, B. R. (2012). Psychophysical chromatic mechanisms in macaque monkey. *Journal of Neuroscience, 32*(43), 15216–15226.

Tailby, C., Solomon, S. G., & Lennie, P. (2008). Functional asymmetries in visual pathways carrying S-cone signals in macaque. *Journal of Neuroscience, 28*(15), 4078–4087.

Trendelenburg, W., & Schmidt, I. (1930). Untersuchungen über das Farbensystem der Affen. *Zeitschrift für vergleichende Physiologie, 12,* 249–278.

Vassilev, A., Ivanov, I., Zlatkova, M. B., & Anderson, R. S. (2005). Human S-cone vision: Relationship between perceptive field and ganglion cell dendritic field. *Journal of Vision, 5*(10):6, 823–833, http://www.journalofvision.org/content/5/10/6, doi:10.1167/5.10.6. [PubMed] [Article]

Weinstein, B., & Grether, W. F. (1940). A comparison of visual acuity in rhesus monkey and man. *Journal of Comparative Psychology, 30*(2), 187–195.

Williams, D. R., MacLeod, D. I., & Hayhoe, M. M. (1981a). Foveal tritanopia. *Vision Research, 21*(9), 1341–1356.

Williams, D. R., MacLeod, D. I., & Hayhoe, M. M. (1981b). Punctate sensitivity of the blue-sensitive mechanism. *Vision Research, 21*(9), 1357–1375.

Williams, D. R., Sekiguchi, N., Haake, W., Brainard, D. H., & Packer, O. (1991). The cost of trichromacy for spatial vision. In A. Valberg & B. B. Lee (Eds.), *From pigments to perception* (pp. 11–21). New York: Plenum Press.