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Experience in Early Infancy Is Indispensable for Color Perception

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Summary

Early visual experience is indispensable to shape the maturation of cortical circuits during development [1]. Monocular deprivation in infancy, for instance, leads to an irreversible reduction of visually driven activity in the visual cortex through the deprived eye and a loss of binocular depth perception [2–4]. It was tested whether or not early experience is also necessary for color perception. Infant monkeys were reared for nearly a year in a separate room where the illumination came from only monochromatic lights. After extensive training, they were able to perform color matching. But, their judgment of color similarity was quite different from that of normal animals. Furthermore, they had severe deficits in color constancy; their color vision was very much wavelength dominated, so they could not compensate for the changes in wavelength composition. These results indicate that early visual experience is also indispensable for normal color perception.

Results and Discussion

Four female Japanese monkeys (*Macaca fuscata*) were reared in a room from 1 month after birth. The room was illuminated so that the monkeys could not see a normal spectrum of colors; the room was illuminated only by monochromatic light for 12 hr a day, the peak wavelength of which was 465, 517, 592, or 641 nm. The wavelength was changed randomly every minute so that all three different retinal cones would be activated. One year after birth, they were moved to a normal-animal room that was illuminated by sunlight (through uncovered windows) and fluorescent lamps. Their color perception was investigated and compared to those of normally reared animals.

They were first trained on a brightness-matching task. Sample luminance was 0.2, 3.5, or 23.0 cd/m^2. Two secondary stimuli were presented at the upper right or upper left of the sample, respectively (Figure 1A). The luminance of one of the two secondary stimuli was identical to the sample. Their task was to touch the secondary stimulus with the same luminosity as the sample. All four monkeys learned the task as fast as normal monkeys. After correct responses exceeded 95% for three consecutive days (criterion), they were tested on whether they could transfer the learned rules to a color-matching task. In the color-matching task, the stimuli were filled red, yellow, green, and blue rectangles, the luminance of which were approximately 15.0 cd/m^2. The normal animals could transfer the learned rules to the color domain very easily, but the color-deprived animals had difficulty (Figure 1B). They were only able to perform color matching to the same level as normal animals after extensive training (31.5 days and 55,506 trials on average).

The animals were next trained on a similarity judgment task on brightness (Table 1) and then on color (Table 2). Their task was to touch the one of the secondary stimuli more similar to the sample than the other. After learning the color-matching task, they could learn similarity judgment on brightness and transfer the learned rules to the color domain as well as normal animals. However, their color categorization was quite different from that of normal animals. They were tested how they judged color similarity for every combination of 15 different colors (Figure 2A). When they judged the secondary stimulus B as more similar to sample A than stimulus C, one point was added to the dissimilarity score for the pair of A and C. A tree cluster analysis was applied to the dissimilarity matrix [5]. The dendrograms for normal animals were quite similar to those for humans (Figures 2B–2H). Bluish, greenish, and reddish colors were clustered in three separate branches. However, the dendrograms for color-deprived animals were quite different (Figures 2I–2L). Correspondingly, human subjects and normal animals seldom judged any pair of red, green, and blue (denoted as “1,” “5,” and “9,” respectively, in Figure 2A) as similar. But, the color-deprived animals judged quite often. The difference between the normal animals and the color-deprived animals was statistically significant (Wilcoxon Rank Test, $p = 0.014$). These results suggest that humans and normal monkeys employed similar strategies for the similarity judgment but that color-deprived monkeys employed quite different ones. Their clustering patterns did not change even 9 months after being moved to the normal-animal room.

The animals were finally trained on a color identification task. The performance of the color-deprived animals was strongly influenced by the wavelength composition of the light reflected from the stimulus surface, whereas the performance of normally reared monkeys and the perception of human observers were not. The stimuli were red, yellow, green, blue, and purple Munsell chips. They were presented together with a black chip against a background of Mondrian patterns (Figure 3A). The stimuli were illuminated by long- (636 nm), middle- (525 nm), and short-wave (470 nm) light. The light intensities were adjusted so that a white chip (N9.5 in Munsell color space) would appear white for human observers. The x, y, and Y values of the chip were 0.331, 0.331, and 103 cd/m^2 in the CIE coordinates. Under the illumination, the red chip (5R6/8) appeared reddish pink for human observers because of low chroma, and the x, y, and Y values of which were 0.438, 0.328, and 35.1 cd/m^2,

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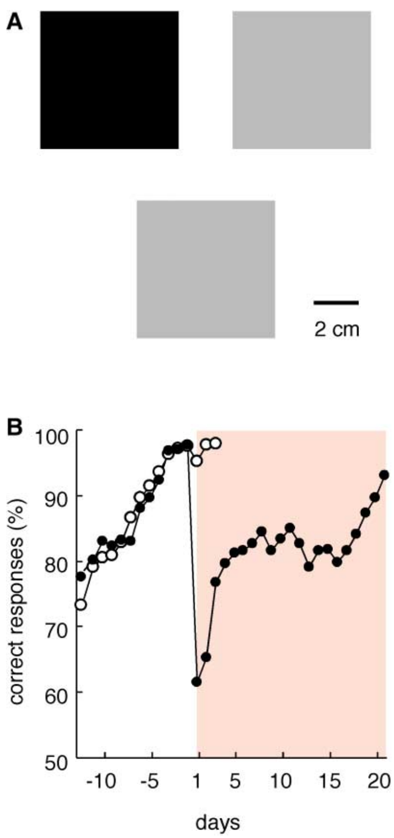

Figure 1. Matching to Sample Task

(A) Schematic illustration of stimuli.

(B) Average correct responses were plotted against training days. Open circles represent the performance of normally reared monkeys while closed circles represent that of color-deprived monkeys. Day 1 denotes the day when monkeys began the color-matching task.

respectively. They were rewarded if they touched the red chip when it was presented or the black chip otherwise. After their performance reached criterion, they were tested with 20 Munsell chips, including five chips used in the training (Figure 3B) to see how they would generalize "redness." Their generalization of redness was quite similar to that of normally reared monkeys (Figures 3C–3J), indicating that the color-deprived monkeys could identify the hue of the stimuli as well as normal monkeys. However, performance differed when wavelength composition was changed. The intensity of long-, middle-, and short-wave light was changed so that the x and y values of a yellow chip (5Y6/8) would be very similar to those of the red chip in the previous condition. Under the illumination, the x, y, and Y values of the red chip were 0.260, 0.122, and 41.6 cd/m^2, respectively, in the CIE coordinates. The red chip still appeared reddish pink for human observers as long as it was presented against the Mondrian patterns. The x, y, and Y values of the yellow chip (5Y6/8) were 0.438, 0.326, and 32.7 cd/m^2, respectively. Although the x and y values were equivalent to those of the red chip in the previous condition, the yellow chip still appeared dark yellow for human observers when viewed against the Mondrian pattern. The performance of normally reared monkeys was neither affected by changing the wavelength composition (Figures 3K–3N). However, the vision of the color-deprived monkeys was very much wavelength dominated. They selected the yellow chip, not the red chip, as the target (Figures 3O–3R), indicating that they could not compensate for wavelength composition. They showed no sign of improvement even 9 months after being moved to the normal-animal room.

The color-deprived monkeys could learn brightness matching but could not transfer the learned rule to color matching. For particular sets of stimuli, they could learn to judge color similarity as well as normal monkeys. But, their performance was quite different from those of normal animals when they were tested with other sets of color stimuli. Furthermore, the color-deprived monkeys exhibited severe deficits in the color-constancy task. The deficits were not restored even 9 months after being moved to the normal-animal room, suggesting the existence of critical periods for the development of normal color perception. The color-deprived animals were reared under the monochromatic illuminations where an object color was by no means visible. Objects changed their appearance depending on the wavelength of the illuminating lights. In these surroundings, color constancy could not work at all. Presumably exposure only to these illuminations resulted in the severe deficits in color constancy.

Deficits in color constancy have been shown by lesion studies. Lesions of V4 induced only mild deficits in color discrimination but remarkably disrupted the color constancy [6, 7]. It has been also reported that the responses of V4 neurons correlated with the perceived color rather than the wavelength components reflected from the stimulus surface [8, 9]. Inferior temporal cortex might be responsible for categorical perception of color [10–12]. It has been shown that many neurons in the inferior temporal cortex selectively responded to a range of colors similar to those designated by basic color names [13]. Recent findings showed that some degree of color constancy was processed already in V1 [14, 15]. It remains to be answered how the color deprivation in infancy would disrupt the maturation of these neural circuits.

Table 1. Combination of Stimulus Brightness

Sample or Target (cd/m^2)	Distractors (cd/m^2)
7.45, 12.2	0.11, 46.5
37.7, 46.5	0.11, 7.45
0.11, 0.74	7.45, 46.5

Table 2. Combination of Stimulus Color in CIE Coordinates (x, y)

Sample or Target	Distractor
(0.578, 0.366), (0.563, 0.307)	(0.235, 0.352)
(0.345, 0.553), (0.294, 0.55)	(0.406, 0.218)
(0.191, 0.094), (0.165, 0.118)	(0.479, 0.447)
(0.517, 0.416), (0.445, 0.474)	(0.147, 0.069)
(0.457, 0.246), (0.35, 0.184)	(0.308, 0.575)
(0.252, 0.406), (0.225, 0.308)	(0.608, 0.338)

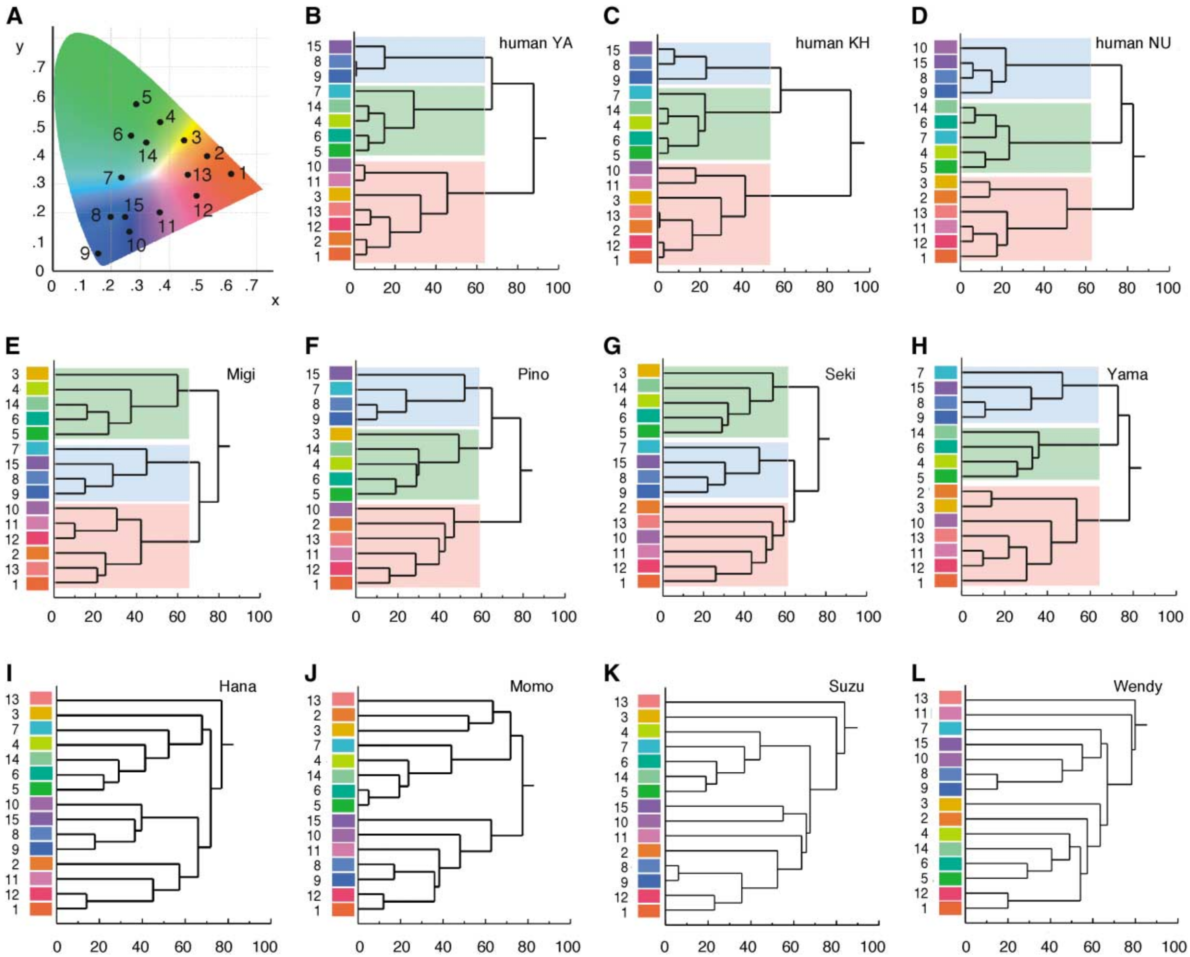

Figure 2. Similarity Judgment

(A) 15 stimuli used in the similarity judgment task were plotted in the CIE 1931 chromaticity diagram. Based on the dissimilarity matrix, a tree cluster analysis was performed to estimate the pattern of clustering of 15 different colors. Dendrograms were also obtained from human data by using the same procedure for comparison (B–D). Note that the dendrograms obtained from normal animals (E–H) are similar to those of a human, but not from the color deprived animals (I–L).

Experimental Procedures

All experimental procedures were approved by the Institutional Animal Use and Care Committee of the National Institute of Advanced Industrial Science and Technology and were performed in compliance with guidelines published by the National Institute of Health (USA).

Subjects

A male and three female Japanese monkeys were used as control animals. They grew up in a normal-animal room, where the sunlight shined into though windows in addition to the illumination of fluorescent lamps. Experimental animals were four female Japanese monkeys. They were reared in a separate room from 1 month after birth. The room was illuminated by arrays of very high luminance light-emitting diodes (LEDs), the peak wavelength of which were 465, 517, 592, and 641 nm and half bandwidth were 26, 35, 18, and 18 nm. These LEDs were commercially available. Average luminance of the floor was 103.5 lx. The wavelength was changed randomly every minute so that all three different retinal cones would be activated in turn. There were lots of imitation flowers in the separate room. The monkeys could play with many colorful toys and dolls in their home cages. A year after birth, they were moved to the normal-animal room and a series of experiments were carried out for 4 months on average. Since then, they have been retrained and tested for color matching and identification tasks at least once a month.

General Procedure

In a matching to sample and a similarity judgment task, stimuli were presented on a CRT display. The background was uniform dark gray (2.6 cd/m^2). The stimuli were filled squares (6.0 $\times$ 6.0 cm). In a color-identification task, color papers (Munsell patches) were used to create Mondorian patterns. In both cases, a transparent touch screen was placed in front of the stimuli. The monkeys sat with their eyes 65 cm from the stimulus plane. In the matching to sample and the similarity judgment task, the sample was first presented. When the monkeys touched the sample, two secondary stimuli were presented at the upper left and upper right of the sample. The monkeys had to touch the correct target to receive a drop of grape juice. These three stimuli were erased when the monkeys touched one of the secondary stimuli. The monkeys performed between 1000 and 5000 trials during each daily session. If correct responses exceeded 95% for three consecutive days, the performance was regarded as reaching criterion level and the experiments proceeded to the next step.

Matching to Sample

The monkeys were first trained on a brightness-matching task. The stimuli were black, gray, and white rectangles, the luminance of

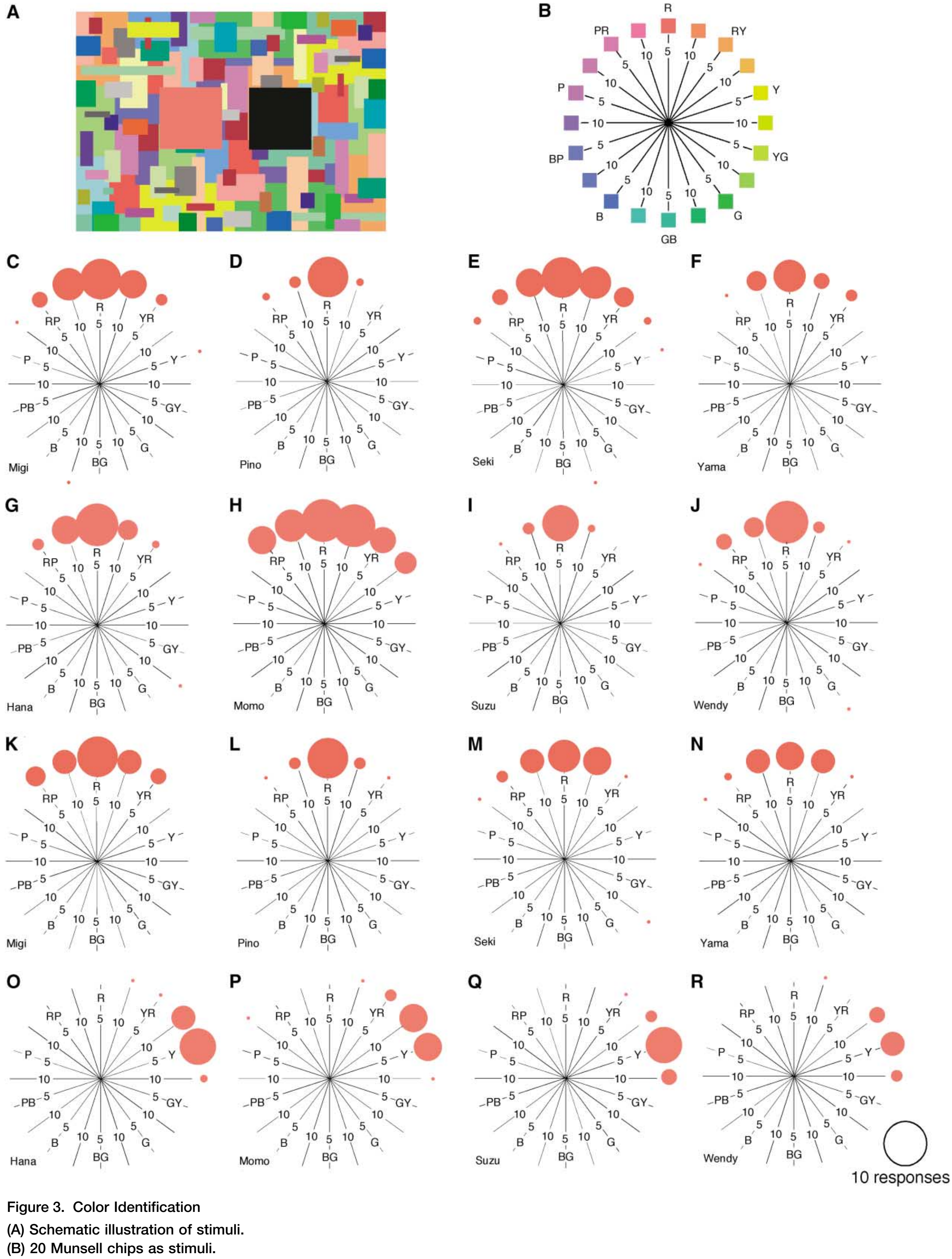

Figure 3. Color Identification

(A) Schematic illustration of stimuli.

(B) 20 Munsell chips as stimuli.

(C–F) Normal monkeys' responses under the illumination where the x and y values of a white chip (N9.5) were 0.331 and 0.331, respectively.

(G–J) Color-deprived monkeys' responses under the same illumination as (C–F).

(K–N) Normal monkeys' responses under the illumination where the x and y values of a yellow chip (5Y) were equivalent to those of a red chip (5R) in (C–J).

(O–R) Color-deprived monkeys' responses under the same illumination as (K–N). Responses to each chip were represented as a diameter of a circle and plotted at the position that corresponds to the Munsell Color Order System.

which was 0.2, 3.5, or 23.0 cd/m^2, respectively. When performance reached criterion, the monkeys were trained on a color-matching task. The stimuli were blue, green, yellow, and red rectangles, the luminance of which was 15.0 $\pm$ 0.2 cd/m^2. The CIE x, y coordinates were (0.147, 0.069), (0.308, 0.575), (0.479, 0.447), and (0.608, 0.338), respectively.

Similarity Judgment

There were 12 combinations of stimulus brightness. The monkeys were rewarded when they touched the one of the secondary stimuli more similar to the sample than the other. When performance reached criterion, they were further trained on similarity judgment with 12 combinations of stimulus color. When performance reached criterion, the judgments were made for every combination of 15 different colors in a test phase. In the test phase, 90% of trials were randomly assigned as training trials and the remaining 10% as test trials. Training trials were exactly the same as those in the training phase. In test trials, 10 responses were obtained for all combinations of the 15 different colors and every response was rewarded. If the monkeys touched the secondary stimulus B for the sample A, then one point was added to dissimilarity scores for the A and secondary stimulus C pair. Based on the dissimilarity matrix, a tree cluster analysis was performed to estimate the pattern of clustering of 15 different colors.

Color Identification

The monkeys were trained on a color-identification task. The stimuli were five Munsell chips—red, yellow, green, blue, and purple—the value and the chroma of which were six and eight, respectively. One out of five colors was presented in conjunction with a black chip against a background of Mondrian patterns. In the dark, a stimulus paper was put on the rear of the translucent touch screen to prevent bending of the paper. The stimulus was then illuminated by arrays of high luminance three-color LEDs. The illumination was turned off when the monkey made a response. The intensity of long- (636 nm), middle- (525 nm), and short-wave (470 nm) light was adjusted so that the x and y values of a white chip (N9.5) would be very close to 0.333 and 0.333, respectively. The target was a red chip. The target color was presented randomly in 50% of trails. They were rewarded if they touched the target color when it was presented or the black chip otherwise. When their performance reached criterion, the monkeys were tested with 20 Munsell chips. In the test phase, 90% of trials were randomly assigned as training trials and the remaining 10% as test trials. Training trials were exactly the same as those in the training phase. In test trials, 10 responses were obtained for all of the 20 chips, and every response was rewarded. The monkeys were also tested in another illumination where the intensity of long-, middle-, and short-wave light was adjusted so that the x and y values of a yellow chip would be the same as those of the red chip in the previous condition.

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