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examined in this task: two were the same animals providing data shown in Figure 1B (cats 1 and 2), and the third (cat 4) was only tested in this task. The results for the three animals are shown in Figure 2B. With cat 1, the maximum step height remained higher than control values and usually higher than the rod height for all time durations we tested. With cat 2, the maximum step height was quite variable during longer pause durations (over 5 seconds) but remained higher than control step height in the majority of trials. With cat 4 there was also some variability, but on most trials the maximum hind leg step height was also higher than the height of the rod and well above control values.

By comparing the step heights when cats pause either immediately in front of an obstacle or straddling an obstacle, we have shown that stepping over an obstacle with the forelegs is necessary to create long-lasting memories to guide the hind legs (Figure 1). We have also shown that visual signals related to the obstacles are not essential for this process (Figure 2). This is strong evidence that a neural signal related to the stepping of the forelegs is responsible for the activation or enhancement of additional structures of the nervous system to produce a long-lasting memory. There are two possible sources of such a signal: the feedback from cutaneous, muscle, and joint afferents which can signal the position of the limb [8]; and the output of motor systems which enhance foreleg flexor activity when stepping over obstacles [9]. We consider the latter hypothesis the most likely as it is consistent with theories of movement control in which motor control signals are used to predict the resulting movement and the associated sensory feedback [10-13].

The significance of this finding is that it clearly provides an example of a signal related to the movement of the limbs (forelegs in this case) being used to update the representation of the location of obstacle close to the body. We believe that the activity from the motor and/or sensory systems provides a positive signal that an obstacle is located between the fore and hind legs, and thus extends the duration of the neural representation of this obstacle until the hind legs step over. This simple behavior provides a convincing example of movement signals being used to update the neural representation of external obstacles and offers a good system to explore the neural structures involved.

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Biological components of sex differences in color preference

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The long history of color preference studies has been described as "bewildering, confused and contradictory" [1]. Although recent studies [1–3] tend to agree on a universal preference for 'blue', the variety and lack of control in measurement methods have made it difficult to extract a systematic, quantitative description of preference. Furthermore, despite abundant evidence for sex differences in other visual domains, and specifically in other tasks of color perception [4,5], there is no conclusive evidence for the existence of sex differences in color preference. This fact is perhaps surprising, given the prevalence and longevity of the notion that little girls differ from boys in preferring 'pink' [6]. Here we report a robust, cross-cultural sex difference in color preference, revealed by a rapid pairedcomparison task. Individual color preference patterns are summarized by weights on the two fundamental neural dimensions that underlie color coding in the human visual system. We find a consistent sex difference in these weights, which, we suggest, may be linked to the evolution of sex-specific behavioral uses of trichromacy.

We employed a simple, forced-choice 'color-picking' task with colorimetrically controlled stimuli separating the relative contributions of hue, saturation and lightness. Observers used a mouse cursor to select, as rapidly as possible, their preferred color from each of a series of pairs of small colored rectangles presented sequentially in the center of an otherwise neutral CRT display. (See Supplemental data available on-line with this issue for details of experimental procedures).

We tested 208 observers, aged 20–26. The main population (171)



Figure 1. Mean hue preference curves.

(A) British subjects. (B) Chinese subjects (±s.e.m.). Hue values are obtained from CIE-LUV coordinates, using the background color as reference white. The horizontal bar indicates only approximately the tested hues and is not an accurate reproduction of the spectrum.

were British Caucasian (79 male). A sub-population (37) were mainland Han Chinese (19 male), the majority having left China for the UK within the past year (range 0.5-3 years). Observers were tested in three different experiments, each of which included the same pair-wise comparisons for a standard group of eight colors (varying hue; saturation 0.5; lightness 80). A subgroup of 90 subjects (28 British females, 25 British males, and the Chinese sub-population), performed the standard experiment twice, with a two-week interval. Here we report results for the standard color group common to all experiments.

We obtained hue preference curves by plotting for each of the eight standard hues the proportion of trials on which it was preferred (Figure 1). We found that hue preference curves do not vary significantly for different lightness and saturation levels (Figure S1 in the Supplemental data). The mean hue preference curves for males and females differ significantly. The average female preference rises steeply to a sustained peak in the reddish-purple region, and falls rapidly in the greenish-vellow region, whereas the male preference is shifted towards blue-green and less pronounced. Although there is a significant main effect of hue for both sexes independently (p < 0.000001 males; p < 0.000001 females) and together (p < 0.000001), the variance in preference over all hues is significantly greater for females versus males (p < 0.00001). Individual female preference curves are also more stable over time, for the subgroup of 90 subjects tested twice (p < 0.002).

The predictability of the individual hue preference curves prompted us to seek more concise descriptors. Principal component analysis reveals that three factors alone explain 79% of the variance across the entire population. The first two factors strongly resemble the cone-opponent contrast components of the stimuli — the fundamental S–(L+M) ('blue–yellow') and L–M ('red–green') neuronal mechanisms which encode colors. We therefore decomposed the hue preference curves in terms of fixed basis functions which explicitly match the two cone-opponent contrast components (see Supplemental data). These account for 70% of the population variance. For sub-populations by sex and nationality, the fixed components account for between 64% (Chinese females) and 72% (British females) of the variance.

Each individual hue preference curve is thereby reduced to two physiologically meaningful weights. While the 'blue-yellow' contrast component accounts for the greatest variance across the population (44.5% S-(L+M); 25.5% L-M), the 'red-green' contrast component accounts for the greater variance within the male population alone (41% L-M; 28% S-(L+M)). Only the 'red-green' weights show a consistent sex difference across all populations. On average, all males give large negative weight to the L-M axis, whereas all females weight it slightly positively (sex difference p < 0.00001). That is, females prefer colors with 'reddish' contrast against the background, whereas males prefer the opposite. On average, all subjects give positive weight to the S-(L+M) contrast component ('bluish' contrasts), with British females weighting it significantly higher than British males (p < 0.00001) (Figure 2).

Although male reaction times are significantly faster on average (1.26 seconds) than female (1.33 seconds) (p < 0.00001), both females and males respond faster to 'bluish' versus 'yellowish' contrasts (reaction times correlate negatively with S-cone-contrast increments of the preferred hue; female r = -0.1061, p < 0.00001; male r = -0.0348, p < 0.01).

Thus, while both males and females share a natural preference for 'bluish' contrasts, the female preference for 'reddish' contrasts further shifts her peak towards the reddish region of the hue circle: girls' preference for pink may have evolved on top of a natural, universal preference for blue. We speculate that this



Figure 2. Decomposition of individual hue preference curves into two cone-contrast components, the weights on which account for differences between sexes and cultures.

(A) Cone-contrast components of the eight standard colors as a function of CIE-LUV hue angle (radians), used as basis functions to extract individual hue preference weights. Left: S-(L+M) contrast. Right: L-M contrast. (B) Mean weights for S-(L+M) contrast component. (C) Mean weights for L-M contrast component. Means are for the entire population ('All'; 98 males; 110 females) and constituent sub-populations separately ('UK'; 79 males; 92 females) ('China'; 19 males; 18 females). Significant differences based on independent two-sample t-tests are marked with asterisks; error bars are s.e.m.

sex difference arose from sexspecific functional specializations in the evolutionary division of labour. The hunter-gatherer theory proposes that female brains should be specialized for gathering-related tasks and is supported by studies of visual spatial abilities [7]. Trichromacy and the L-M opponent channel are 'modern' adaptations in primate evolution thought to have evolved to facilitate the identification of ripe, yellow fruit or edible red leaves embedded in green foliage [8]. It is therefore plausible that, in specializing for gathering, the female brain honed the trichromatic adaptations, and these underpin the female preference for objects 'redder' than the background. As a gatherer, the female would also need to be more aware of color information than the hunter. This requirement would emerge as greater certainty and more stability in female color preference, which we find. An alternative explanation

for the evolution of trichromacy is the need to discriminate subtle changes in skin color due to emotional states and social-sexual signals [9]; again, females may have honed these adaptations for their roles as care-givers and 'empathizers' [10].

As further support for the 'female brain' hypotheses, we find that observers' femininity scores on the Bem Sex Role inventory correlate significantly with L-M cone-contrast component weights for all subjects (rho = 0.333; p < 0.002), but not with S cone-contrast weights, for the tested subgroup of 90 subjects. Within cultures, for the Chinese sub-population, masculinity correlates negatively with L-M cone-contrast component (r = -0.531; p = 0.019) whereas for the British sub-population, femininity correlates positively with L-M cone-contrast weight (r = 0.437; p = 0.002).

Our results demonstrate robust sex differences in color preference, which are consistent with the evolution of sex-specific behavioral uses of trichromacy. Yet while these differences may be innate, they may also be modulated by cultural context or individual experience. In China, red is the color of 'good luck', and our Chinese subpopulation gives stronger weighting for reddish colors than the British. Color preference patterns are nonetheless systematically governed by sensory encoding, and, to a significant extent, predictable.

Supplemental data

Supplemental data, including experimental procedures, are available at http:// www.current-biology.com/cgi/content/ full/17/16/R623/DC1

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