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Latitude-of-birth and season-of-birth effects on human color vision in the Arctic

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Abstract

Extreme natural ambient light reduction, in both energy and range of wavelength spectrum, occurs during the winter season at very high latitudes (above the Arctic Circle or 66°32′ North) that in turn results in increased exposure to artificial lighting. In contrast, during the summer months, the sun remains above the horizon and there is no darkness or night. Little is known about these extreme changes in light exposure on human visual perception. Measuring color discriminations with the FM100 Test revealed that Norwegians born above the Arctic Circle were less sensitive to yellow-green, green, and green-blue spectrum differences whereas they were more sensitive to hue variations in the purple range than individuals born below the Arctic Circle. Additionally, it was found that the Norwegian individuals born above the Arctic Circle and during autumn showed an overall decrease in color sensitivity, whereas those born in the summer showed a relative increase. All participants were adults and their color vision was tested in the same location (i.e., in Tromsø at 69.7° North). These findings are consistent with the idea that there is a measurable impact on colour vision as adults of the photic environment that individuals born above the Arctic Circle and in the autumn experienced during infancy, namely a reduction in exposure to direct sunlight and an increase in exposure to twilight and artificial lighting.
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1. Introduction

In Norway, most of the population lives below the Arctic Circle, an imaginary line at latitude 66°32′ North, with only 10.2% (approximately 460,000 inhabitants) living above the Arctic Circle. In this part of the world, seasonal swings of sunlight are extreme and for a period during the winter season there is a complete absence of direct sunlight, called *mørketid* ("dark time" in Norwegian), whereas during the summer months the sun remains above the horizon through the night (the *midnattsol* or "midnight sun" period). For example, at 69.7° of latitude, in the city of Tromsø, where the present study was conducted, the sun disappeared below the horizon on the 25th of November 2006, only to reappear on the 21st of January 2007; whereas the whole disc of the sun remained above the horizon for 24 h a day from the 18th of May 2006 until the 26th of July 2006. In contrast, in Oslo (59°55′ North), during the same winter and summer periods, the duration of daylight and of darkness ranges, respectively, from 5 to 6 h each day. This continued absence or presence of natural sunlight at this northern latitude is also accompanied by either an extended exposure to artificial lighting in the winter (e.g., tungsten or fluorescent) or minimal use of it during the summer months.

Little is known about the impact of extended periods of absence or presence of sunlight and of its compensation

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with artificial lighting on many aspects of human physiology and behavior and practically nothing is known about its influence on human color vision. At latitudes above the Arctic Circle, during the polar night in which only twilight illuminates the sky, the prevalent ambient light is blue (Ørbæk, 2006), due to the Rayleigh scattering of sunlight reaching the earth's atmosphere from below the horizon (e.g., the so-called "civil" twilight corresponds to a position of the sun of $\approx -6°$ in relation to the horizon). Moreover, at latitudes above the Arctic Circle, snow covers much of the landscape during the winter period and this effectively mirrors the light from the sky by reflecting almost 90% of all incoming scattered solar radiation (Ørbæk, 2006).

Humans can show remarkably long-lasting adaptation effects to natural sunlight; for example, an hour spent reading in natural bright sunlight causes a shift in color matches lasting for several hours (Jordan & Mollon, 1995a, 1997, 1995b). Also, only half an hour exposure to monochromatic light can cause a long-lasting 'protan' shift (Jordan & Mollon, 1998). In all of the cases described by Jordan and Mollon, color matches always returned to pre-adapted levels. However, it is unknown whether protracted exposures to natural sunlight and protracted periods of reduction in energy and range of the visible light spectrum may cause irreversible alterations in spectral sensitivity, especially when these changes in ambient light occur during developmental periods for color vision.

Indeed, it is well known that abnormal visual environments can result in anatomical and physiological changes within the mammalian visual system and impair visual function. Animal studies have shown that limiting early visual exposure (e.g., contours of one orientation, monocular information) makes neural cells predominantly responsive to those features that are prevalent in the degraded environment (e.g., Blakemore & Cooper, 1970; Fagiolini, Pizzorusso, Berardi, Domenici, & Maffei, 1994; Katz & Shatz, 1996; Prusky, West, & Douglas, 2000; White, Coppola, & Fitzpatrick, 2001; Wiesel & Hubel, 1963). Animals reared in monochromatic light can show abnormal neural substrates (e.g., Petry & Kelly, 1991) and loss of hue discrimination (Sperling, Wright, & Mills, 1991). Intense blue light exposure in monkeys can result in irreversible damage to the "blue" cones, as attested by the lack of recovery over many years and neurophysiological evidence of degeneration of retinal cones (Sperling, Johnson, & Harwerth, 1980). However, some primate studies have not found effects of monochromatic rearing on color sensitivity (e.g., Brenner, Cornelissen, & Nuboer, 1990; Shi, Neitz, & Jacobs, 1987). The examination of visual pigments in non-human vertebrate species living in natural, less extreme, environments show that the maximum absorption curves generally correspond to the most common wavelengths of light found in the habitat, while minimum sensitivities correspond to segments of the spectrum which are rare or absent (Lythgoe, 1979).

In human adults, the proportion of L and M cones can be strikingly different between individuals (Roorda & Wil-liams, 1999) and the number and arrangement of cones can place a limit on human vision. However, the neural locus of the developmental changes in color vision is still unknown and most likely reflects an initial general deficiency for all color vision mechanisms (Adams, Courage, & Mercer, 1994). Research on infants has shown that two-months-old can discriminate reds, oranges, blue-greens and blues from a white surround but fail in two regions centered in the yellow/green and mid-purple ranges (Teller, 1998; Teller, Peeples, & Sekel, 1998; cf. Dobson, 1976). Pulos, Teller, and Buck (1980) suggested that one key difference between adults and infants in color vision may be described as an immaturity of the infant's short-wavelength sensitive mechanism (cf. Ohnishi, 1993). By three or four months, infants show evidence of discriminating all chromatic hues but the development of the ability to detect green and the yellow appears to progress more slowly than other colors (Adams, Courage, & Mercer, 1991, 1994).

In sum, there are reasons to believe that sunlight deprivation and the specific changes in the color spectrum of ambient light, as well as protracted use of artificial lighting, could affect human color vision, especially when these occur during infancy (cf. Quinn, Shin, Maguire, & Stone, 1999). If in humans color vision is still developing after birth until around three months (Adams et al., 1994), then "sensitive periods" (Bornstein, 1989) for color vision may occur during these initial months of life. In the present study, we demonstrate the existence of individual differences in color vision in the adult life of Norwegian individuals, all residents at the same latitude, who were born either below or above the Arctic Circle and in different seasons. Our starting hypothesis was that the lack of an adequate amount of natural sunlight stimulation for an extended period of time during winter would affect the human visual system and/or its development. However, the increased use of artificial lighting, consisting of incandescent light or tungsten lamps (mainly in private buildings) and fluorescent lamps (mainly in public buildings), may compensate the reduction in sunlight during winter; nevertheless, all types of artificial lighting differ in energy from sunlight and provide a restricted range of the sunlight's composition of electro-magnetic wavelengths that can naturally stimulate the human eye (Livingstone, 2002).

We hypothesized that the perceptual process that is most immature at birth and/or the one supporting the late developing hues (e.g., yellow/green) are most likely to be disrupted by changes in ambient light during development. However, additional considerations about the photic regime above the Arctic Circle, that is, highest exposure to twilight at latitudes between 60° and 80° (Ørbæk, 2006), would also lead us to predict an increased sensitivity for the shortest wavelength hues of twilight (like indigo and purple). Finally, given that artificial lighting could partially compensate the reduction of sunlight energy and those wavelengths of ambient light that are missing during *mørketid* (i.e., all above the shortest), we predicted that the largest error rates would occur in those regions of the

visible color spectrum where the energy of incandescent or fluorescent light is the poorest compared to sunlight energy (i.e., for wavelengths ranging from 460–530 nm, or blue-green, to 560–600 nm or green-yellow; Livingstone, 2002).

Differences in color discrimination skills of Norwegians 'born above the Arctic Circle' (above-AC) and Norwegians 'born below the Arctic Circle' (below-AC), as well as a 'control' group of French and English participants, were revealed by the use of the Farnsworth-Munsell 100 Hue Test (FM100), which can measure slight individual differences within the normal range of color vision (Farnsworth, 1957). The participant's task is to arrange or order movable hues so that they provide a gradual progression of color. Participants were tested individually during the 2002–2004 period and testing sessions were evenly distributed within each year. None of the participants was an immigrant or born of immigrant parents; however, we do not have information about the indigenous ethnic composition of our groups and official statistics in Norway do not register ethnicity. The original indigenous population of Norway (the Saami people, of Asian descent, estimated to be about 40,000 in total) is more prevalent in the northern and central regions of Norway (Cavalli-Sforza, Menozzi, & Piazza, 1994). At any rate, the number of Saami within the general population (≈1%) is small and it is unlikely that it differed between the present groups of participants. Moreover, previous studies (Reimchen, 1987, p. 7) showed that this indigenous group has a color deficient frequency of 6.2%, comparable to that of non-indigenous Scandinavians. Also, women are generally better at color discriminations than men (mainly because of variations in the number of visual pigment genes per X chromosome; Jameson, Highnote, & Wasserman, 2001), therefore care

was taken that similar proportions of female participants would be included in the above-AC and below-AC groups. Smoking has also been reported to (negatively) affect color vision (Bimler & Kirkland, 2004a), but each group had comparable proportions of individuals who reported smoking (see Table 1). Similarly, individuals with dark/light eye color were balanced across groups, since it has been shown that iris color can affect performance in the FM100 (Dain, Cassimaty, & Psarakis, 2004; Woo & Lee, 2002).

Age is another variable that can strongly affect performance on the FM100: performance improves from infancy to about 20 years and then gradually deteriorates; at both ends of the age range, individuals show a slight 'tritan' deficiency (Dain, 2004). In the younger group this is attributable to a late developing blue-yellow system, whereas in the older group it reflects non-pathologic age-related increases of the optical density of the intraocular crystalline lens (Dain, 2004). Individual differences in the density of macular pigment can affect FM100 performance, which can cause population differences in FM100 performance between, for example, Caucasians (especially if blue-eyed) and Asians (Bornstein, 1973; Dain et al., 2004; Woo & Lee, 2002). In this study, the Norwegian participants were non-immigrant individuals of comparable age and they did not differ in prevalence of specific iris colors (see Table 1).

2. Methods

2.1. Participants

There were 260 Norwegian individuals who volunteered to participate in a study on color vision. At the time of testing, these participants had been residents of the city of Tromsø for at least a year; 95% of these were students at the University of Tromsø, the rest being administrative staff;

Table 1
Grouped biographical data

| | Participants | | |
	Born above Arctic Circle	Born below Arctic Circle	Control group
N	125	127	41
Mean age	26.1 (6.5)	27.7 (5.7)	26.9 (6.8)
Females/males	77/48	67/60	14/18
Latitude-of-birth (range)	66°–71° North	58°–66° North	40°–58° North
Season-of-birth (N)			
Autumn	34	37	—
Winter	32	25	
Spring	36	37	
Summer	22	29	
Years of schooling	15.8 (1.4)	15.0 (1.6)	15.9 (1.7)
Eye color (%)			
Blue	60.0	65.0	43.7
Brown	20.1	19.2	39.6
Green	19.2	22.8	16.6
% Smokers (daily use)	20%	17%	—
Years spent in birthplace	14.9 (8.1)	15.9 (8.6)	20.6 (8.6)
Years spent in Tromsø	11.1 (9.1)	12.0 (9.1)	—
% Born in coastal locations	75.3%	69.4%	—
FM100 total errors	57.7 (34)	54.0 (29)	34.1 (28)
Ishihara plates errors	1.05 (1.5)	0.88 (0.9)	—

Standard deviations are in brackets.

all were Norwegian citizens with Norwegian as their first language. Of these 260 Norwegian participants, eight were excluded from the analyses due to their unequivocally pathological responses on the color vision tests. Hence, the descriptions and analyses below will apply only to the remaining 252 participants (see Table 1).

In addition, a small "control" group of European participants ($N = 41$) was included in the study (see Table 1). These were individuals in the same age range of the Norwegians and they were recruited and tested in London (UK) and Strasbourg (France).

2.2. Tests

The Farnsworth-Munsell 100 Hue Test (GretagMacbeth©) consists of four sets of plastic caps in which the colors are mounted. There are a total of 85 moveable caps of the same brightness representing hues along the complete human "circular" color space (equally in all strengths from neutral to high purity). The task is to rearrange the caps, from an initial random arrangement, according to color similarity between two fixed reference caps. The error score for a cap is calculated as the sum of the differences between the caps adjacent to it; hence the minimum error score ($=2$) is different from zero. Scoring of errors was performed according to the standardized FM100 hue scoring system, using the GretagMacbeth© software as well as a WEB-based scoring software developed by Béla Török (http://www.torok.info/fm100/). FM100 performance depends on ambient's illuminance (Bowman, 1978), which was therefore held constant in the present study by administering the test in a windowless room and by placing the caps on a table under a halogen lamp (about 6500° Kelvin illumination). The same test box was shipped to London and to Strasbourg, where control participants could be tested with exactly the same hues seen by the Norwegian participants.

In addition, the Norwegian participants received a color discrimination test with the Pseudoisochromatic Ishihara Plates (Dain, 2004; Ishihara, 1951). The Ishihara Plates (published by the American Optical Corporation, Beck Engraving Company©) are commonly used for the identification of congenital red-green deficiencies and consist of 14 pseudoisochromatic plates made of colored circles of various sizes, representing double-digit numbers inscribed inside a circle. Participants must name each of the numbers. Omissions and incorrect responses are recorded on a score sheet by the experimenter. Incorrect responses to 4 or fewer plates indicates normal vision, whereas incorrect responses to 5 or more plates indicates defective red-green vision; however, high error scores in the test do not identify the type of red-green defect or the amount of defect. Only four of the above-AC participants (1 female) showed abnormal scores as well as 2 male below-AC participants. Within the normal range of performance, there were no overall error differences between the two groups ($p = .32$). Hence, we report these results only in Table 1.

2.3. Questionnaire

A questionnaire was administered after the color vision tests to collect relevant biographical data, i.e., age, sex, place of birth, number of years spent in the place of birth, eye color, smoking habits.

2.4. Statistical analyses

Performance in the FM100 Test ranged widely (2–220) and of the original 260 Norwegian participants, 8 had error scores above the 99th percentile for normative data for participants 20–29 of age (Verriest, Van Laetham, & Uvijls, 1982). These outliers (scores >150) were excluded from the analyses, which included only the 252 participants with a normal range of color vision. However, when this trimmed data set was in turn compared with a WEB-based scoring software (http://www.torok.info/fm100/), which compares each individual's score to Kinnear and Sahraie (2002) norms, we identified another 26 individuals (born above the Arctic Circle: $N = 14$; born below the Arctic Circle: $N = 12$) who had borderline pathological color vision. However, these individuals were not excluded

from the analyses presented below and preliminary tests confirmed that their exclusion did not modify the effects described in the following analyses.

Individual scores for each of the 85 caps in the FM100 Test were first obtained. In a first exploratory analysis, we performed a repeated-measure ANOVA (performed with Statview© software) with latitude-of-birth and season-of-birth used as between-subjects factors and the 10 step color subdivisions and the 85 caps in the FM100 Test as the within-subject factor. Although differences in the FM100 data are typically compared with non-parametric tests (e.g., the Mann–Whitney test), FM scores vary according to an interval scale and range from a minimum score of 2 to scores approaching 200. The main advantage of applying the repeated-measure ANOVA to the present data is that this statistical method allows the simultaneous evaluation of multiple factors and their interactions. This is important for the present study since we need to specifically evaluate whether the factors of latitude-of-birth and season-of-birth interact with one another and for specific ranges of color. In addition, we computed Cohen's d to express the effect size of the differences between two groups (Cohen, 1988). Conventionally, an effect size (ES) $d < 0.2$ is considered small, ES: $0.2 < d < 0.6$ is considered medium, and ES: $d < 0.7$ is considered a large effect size. Such effect sizes can be interpreted in terms of the percent of non-overlap of one group's scores with those of the other group (Cohen, 1988). For example, a ES: $d = 0.0$ indicates that the distribution of scores of the two groups overlap completely; whereas a ES: $d = 0.8$ indicates a non-overlap of 47.4% in the two distributions.

For one repeated-measure ANOVA, the 85 caps' scores were also averaged within each the 10 step color subdivisions of the Munsell color circle (i.e., red, red-yellow, yellow, yellow-green, green, green-blue, blue, blue-purple, purple, purple-red) and latitude-of-birth and season-of-birth were used as between-subjects factors and the 10 step color subdivisions as the within-subject factor. Confidence intervals (95%) for between-subjects design were computed and shown in Figs. 2–4 so as to reveal which mean scores differed reliably among the participants groups. The Ishihara test scores were also submitted to Mann–Whitney U test with the above-AC and below-AC participant groups as the between-subjects factor. The Mann–Whitney U test is the non-parametric version of "unpaired t-test." Since this test does not look at the observations but instead considers their ranks, it is resistant to outliers in either of the groups being compared.

Finally, we used the WEB-based scoring software for the Farnsworth-Munsell 100 Hue (http://www.torok.info/fm100/) to compute "Vingrys" analyses of the present data and thus we obtained the angle, major radius, minor radius, selectivity index and confusion index for each individual's score. The mean performance in each of these measurements for the above-AC and below-AC participant groups was then submitted to Mann–Whitney U tests.

3. Results

We first submitted the Ishihara test scores to a Mann–Whitney U test with the above-AC and below-AC participant groups as the between-subjects factor (above-AC: mean = 1.05, SD = 1.5; below-AC: mean = 0.88, SD = 0.96). This analysis revealed no significant difference between the groups, $z = -0.37$, $p = .69$. An ANOVA with season-of-birth (spring, summer, autumn, winter) as the between-subjects factor also showed no differences, $F(3, 206) = .2$, $p = .88$. However, the error scores in the Ishihara plates test were moderately correlated with total error scores in the FM100 ($R = 0.27$; $p < .0001$).

An exploratory repeated-measure ANOVA with sex of participant (female, male) latitude-of-birth (above-AC, below-AC) and season-of-birth (spring, summer, autumn, winter) as between-subjects factors and the Specific Hues

(85 colored caps) in the FM100 color circle as the within-subject factor revealed a main effect of Specific Hues, $F(84, 20748) = 100.8$, $p < .0001$. In addition, there was a main effect of sex, $F(1, 235) = 3.6$, $p = .05$; that is, females (mean error = 2.625, SD = 1.006) made fewer errors than males (mean error = 2.715, SD = 1.073). There were no other significant main effects. However, the Specific Hues factor interacted with latitude-of-birth, $F(84, 19740) = 2.3$, $p < .0001$, and season-of-birth, $F(252, 19740) = 1.3$, $p = .004$. Fig. 1 illustrates the interaction of latitude-of-birth with the discrimination of the Specific Hues. The above-AC group's average mid-point of error scores was at cap: 39 (SD = 13); whereas the below-AC group's average mid-point was at cap: 45 (SD = 27); each average mid-point was outside of the 95% confidence intervals of the other.

To further explore and clarify the above effects, FM100 error scores were averaged within the 10 step color subdivisions of the Munsell color circle and a new repeated-measure ANOVA with latitude-of-birth (above-AC, below-AC) and season-of-birth (spring, summer, autumn, winter) as between-subjects factors was performed. There were no significant main effects. Latitude-of-birth had a significant effect on discriminations within Specific Hue categories, $F(9, 2196) = 5.1$, $p < .0001$. Specifically, above-AC participants made significantly more errors when arranging yellow-green (Cohen's $d = 0.46$), green (Cohen's $d = 0.22$), and green-blue hues (Cohen's $d = 0.32$) than below-AC participants (see Fig. 2). In addition, above-AC individuals made significantly fewer errors in arranging purple (Cohen's $d = 0.32$) and purple-red hues (Cohen's $d = 0.31$) than below-AC individuals. We also
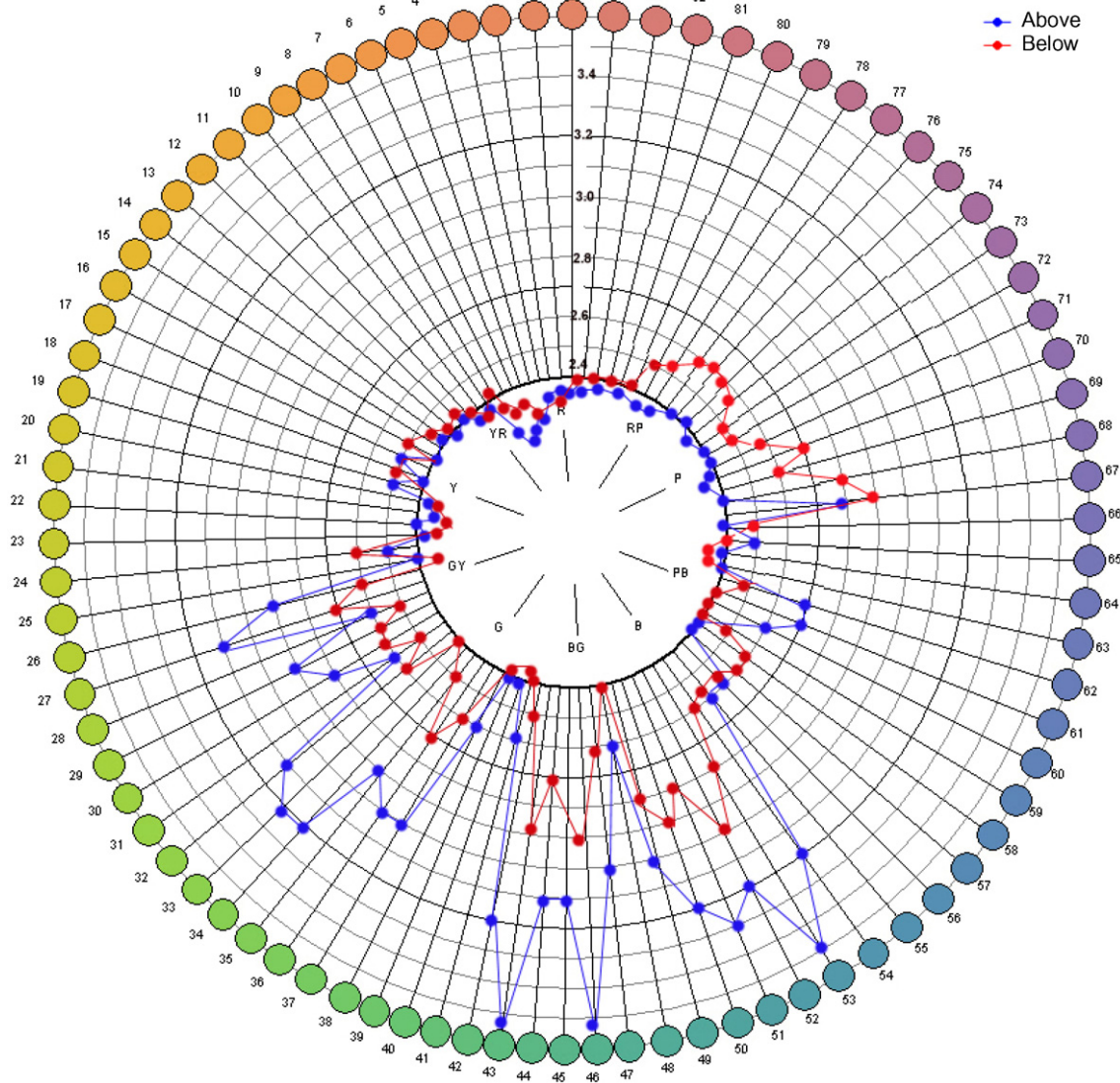

Fig. 1. Errors in the FM100 Test for the 85 colored caps of the Munsell color circle. Blue circles show mean scores for participants ($N = 125$) born above the Arctic Circle ($>66°33'$ North) and red circles show mean scores for participants ($N = 127$) born below the Arctic Circle (AC). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)
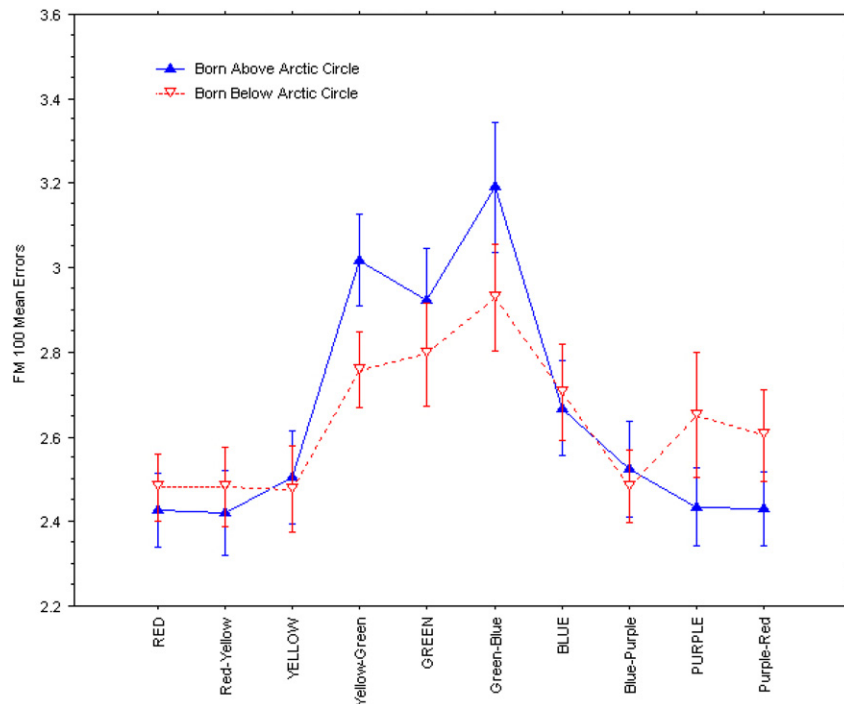
Fig. 2. Errors in the FM100 Test averaged within each the 10 steps color subdivisions of the Munsell color system. Blue triangles show scores for participants ($N = 125$) born above the Arctic Circle (>66°33′ North) and red triangles show scores for participants ($N = 127$) born below the Arctic Circle (AC). Bars show the 95% confidence intervals for between-subjects design. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

identified a subgroup ($N = 32$) of above-AC individuals whose families moved to a residence below the Arctic Circle during childhood (i.e., age <10 years). We confirmed that this smaller group also differed from the below-AC participants in showing more green-blue discrimination errors ($p < .05$) and fewer errors for purple hues ($p < .05$). Remarkably, a regression analysis of green-blue discrimination errors and years spent in the birthplace revealed no relationship (slope = 0.02, $p = .41$). Thus, it appears that permanence in the Arctic within the initial period of life, perhaps neonatal, may be sufficient to affect color discrimination in the adult life.

We also assessed whether amount of snowfall, which is high in the Arctic regions, and the related increase of phototoxic UV light reflectance could have influenced the effects attributed above to latitude-of-birth. Hence we performed an analysis of covariance with 'numbers of days with snow' as the covariate (range = 5–220), 'latitude-of-birth' as the between-subjects variable, and averaged FM100 scores for yellow-green, green, and green-blue hues (i.e., the ''worst hues'' for the above-AC group) of the corresponding participants as the dependent variable. This revealed that latitude ($F(1, 208) = 4.4$, $p = .04$) remained a significant predictor of decrements in color discrimination whereas snowfall played no significant role, $F(1, 208) = 1.04$, $p = .31$.

Season-of-birth yielded an interactive effect on specific colors' discrimination, $F(27, 2196) = 1.6$, $p = .035$. That is, there was an increase in errors for green-blue (Cohen's $d = 0.63$) and yellow-green hues (Cohen's $d = 0.37$) in indi-

viduals born in the autumn and in the winter compared to those born in summer (see Fig. 3a), whereas marginal differences were found for individuals born during the autumn and spring seasons for blue and blue-purple hues (see Fig. 3b). Thus, the season-of-birth effects occurred for regions of the color spectrum that largely overlapped those also affected by latitude-of-birth (e.g., greenish and purplish colors). However, the season-of-birth effect on green failed to reach significance (Fig. 3), but this was already marginally significant for latitude-of-birth (Fig. 2). We surmise that the season-of-birth null finding for green may be due to the reduced statistical power due to the small N's of subjects in each season group.

In addition, latitude-of-birth also interacted with season-of-birth, $F(3, 244) = 2.9$, $p = .039$. As Fig. 4 illustrates, below-AC individuals showed no season-of-birth effects, whereas the above-AC individuals born in the summer had significantly lower overall error scores. Above-AC individuals born in the autumn also had significantly higher overall error scores. Interestingly, there was no higher order interaction effects of latitude-of-birth, season-of-birth, and Specific Hues ($p = .65$); thus suggesting that better performance among above-AC participants for color purple and their worse performance for the green-blue colors was not attributable to different individuals born in the summer or winter, respectively.

To summarize the findings so far, the above-AC and below-AC groups had similar profiles of error rates across hues but the above-AC and below-AC groups showed significant differences for some Specific Hues, as revealed by
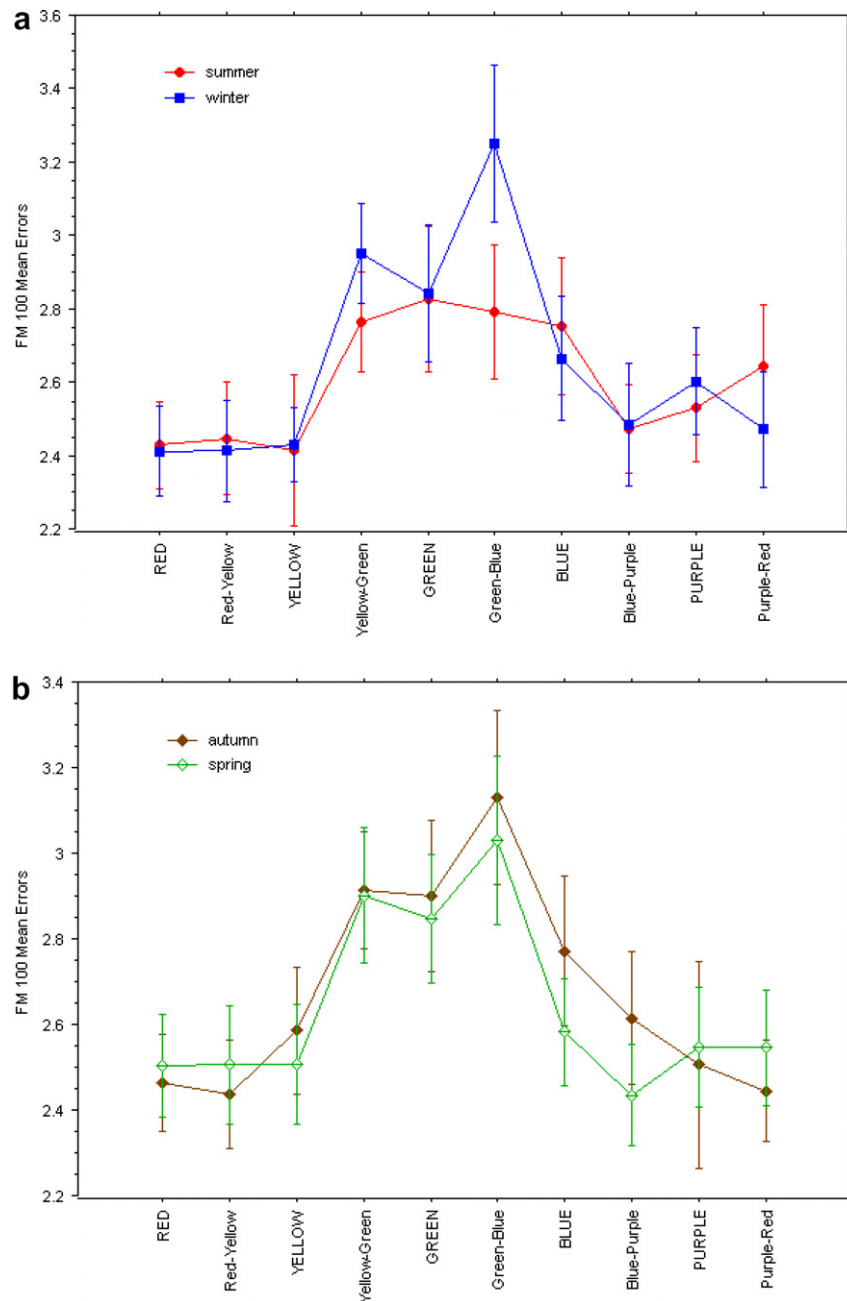
Fig. 3. (a) Errors in the FM100 Test averaged within each the 10 steps color subdivisions of the Munsell color system. Squares show scores for participants born in the winter ($N = 57$), and circles show scores for participants born in the summer ($N = 51$). Bars show the 95% confidence intervals for between-subjects design. (b) Errors in the FM100 Test averaged within each the 10 steps color subdivisions of the Munsell color system. Filled diamonds show scores for participants born in the autumn ($N = 71$), open diamonds show scores for participants born in the spring ($N = 73$). Bars show the 95% confidence intervals for between-subjects design.

the significant interaction of latitude-of-birth and Specific Hues. In addition, individuals born in different seasons (collapsed over latitude-of-birth) also had similar profiles of error rates but, as revealed by a significant interaction of season-of-birth and Specific Hues, there were significant performance differences for some Specific Hues in relation to season. However, the interaction displayed in Fig. 4 shows that season-of-birth plays an additional role by modulating the overall color performance of the above-AC group (but not that of the below-AC group).

The European control group had an average total FM100 score consistent with published norms for the same age groups (Verriest et al., 1982), but made fewer errors in color discriminations in comparison with both the above-AC and below-AC groups, while the total FM100 error scores did not differ between the two Norwegian groups (see Table 1). To further explore whether differences between the European control group and the two Norwegian groups occurred for specific colors, we performed an additional repeated-measures ANOVA with Geography
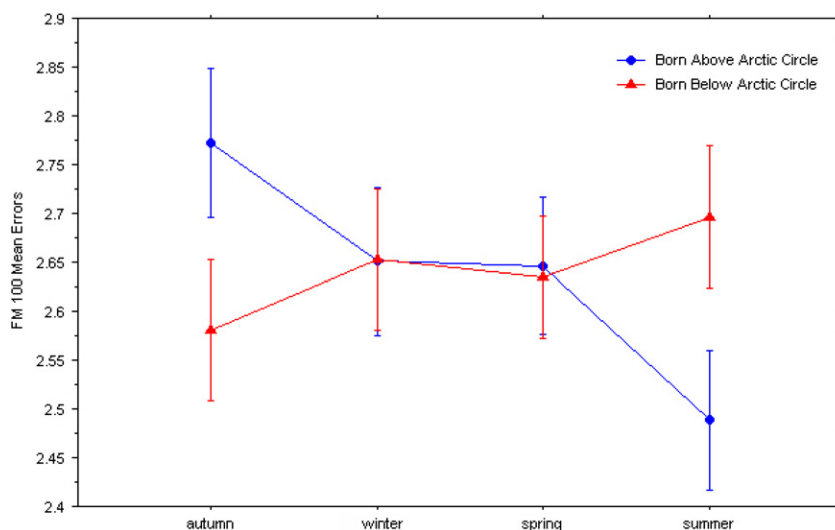
Fig. 4. Errors in the FM100 Test averaged within each season. Blue circles show scores for participants ($N = 125$) born above the Arctic Circle ($>66°33'$ North) and red triangles show scores for participants ($N = 127$) born below the Arctic Circle. Bars show the 95% confidence for between-subjects designs. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

(Europeans, above-AC Norwegians, below-AC Norwegians) as the between-subjects factor and the 10 colors subdivisions of the Munsell color circle as the within-subject factor. This analysis revealed a significant interactive effect of Geography and colors, $F(18, 2610) = 6.3$, $p < .0001$. When 95% confidence intervals were computed, it was found that the Europeans had significantly lower error rates than both Norwegian groups for all colors except yellow, blue, and blue-purple. However, one has to be cautious in interpreting these findings since the European group was considerably smaller ($N = 41$) than either of the Norwegian groups.

Finally, by use of a computer-scoring program we obtained, for each Norwegian participant's FM100 performance, measurements according to the moment of inertia method (Vingrys & King-Smith, 1988), so as to further analyze for difference in the confusion index and specificity index as well as in the angle or the direction of the errors. These scores were then averaged for each participant group (above-AC versus below-AC). If the present results reflect the deficit in one of three cone types, one would predict (i.e., when the selectivity index is larger than 1.65), the following angles in degrees: P = from -2 to 29; D = from -30 to -2; T = from -90 to -65. However, since we had removed from our analyses those six individuals with the strongest evidence for pathology, none of the participants included in the analyses had negative angular values. Note also that, in the present study, very few of the FM100 error scores were above the 95th percentile of normal participants (Verriest et al., 1982). In fact, among all the participants, only 2.3% had a selectivity index larger than 1.65 (Vingrys & King-Smith, 1988); that is, 4 participants in the above-AC group and 2 in the below-AC.

Specifically, the obtained measurements according to the moment of inertia method were the following: angle (above-AC = 49.95, SD = 13.4; below-AC = 48.07,

SD = 14.56), major radius (above-AC = 3.59, SD = 0.66; below-AC = 3.59, SD = 0.59), minor radius (above-AC = 2.72, SD = 0.59; below-AC = 2.67, SD = 0.37), selectivity index (above-AC = 1.38, SD = 0.26; below-AC = 1.35, SD = 0.15) and confusion index (above-AC = 1.48, SD = 0.51; below-AC = 1.42, SD = 0.23). The mean performance in each of these measurements for the two participant groups was then submitted to Mann–Whitney U tests. Remarkably, none of these scores reached a significant difference ($-0.08 < z < 0.42$; $0.51 < p < .93$). Dain and colleagues (2004) pointed out that few color vectors are available in normal arrangements and these can show highly variable angles; thus, a "Vingrys" analysis of the direction of normal error scores in the FM100 can be problematic.

According to Farnsworth (1957), protanomals and protanopes (P) show defects on the FM100 specifically for those caps ranging from 14–24 to 62–70; deuteranomals and deuternanopes (D) for caps ranging 12–20 to 56–61; tritanomals and tritanopes (T) for caps ranging 2–6 to 46–52. In contrast, the differences we observed were not only within the normal range of FM100 performance, but the larger error scores of above-AC participants compared to below-AC occurred specifically for those caps ranging from 22–31 to 38–51, whereas the lower error scores of above-AC participants compared to below-AC occurred for caps 68–82. Thus, there was marginal overlap between the present pattern of errors and those of the classic cone defect types.

4. Discussion

Although sensitivity to color would seem to constitute a very relevant part of the information defining objects in the environment, there exist large individual differences among humans in color sensitivity. Little is known about differ-

ences in color vision that depend on characteristics of the individuals' environment. Geographical latitude has emerged as one of the factors that can affect color vision (Reimchen, 1987) and, in turn, the color lexicon (Bornstein, 1973; Brown & Lindsey, 2004; Lindsey & Brown, 2002). In the present study, we found that a large group of residents of one town in the Norwegian Arctic, but born at various latitudes, showed differences in color vision discriminations that depended on whether their place of birth was located either above or below the Arctic Circle. Such a subdivision was motivated by the fact periods of darkness/sunlight lasting longer than the circadian cycle only occur above 66°32′ of latitude. In such periods the lack of sunlight needs to be compensated by use of artificial lighting (e.g., tungsten and fluorescent). Further, during mørketid, when the sun is positioned a few degrees below the horizon, only the shortest wavelengths (purple/indigo) are scattered through the sky during part of the "day".

The observed differences in color vision were subtle and they occurred within the normal range of human performance, at least as measured with the FM100 (see Fig. 1). Although the differences were small, the two groups of individuals born above or below the Arctic Circle differed more from each other in several regions of the spectrum (e.g., yellow-green: mean errors score difference = 0.256; green-blue: mean errors score difference = 0.253) than, for example, the two sexes differed in their overall FM100 scores (i.e., mean errors score sex difference = 0.09). Specifically, we found that individuals born above the Arctic Circle were on average worse in discriminating such greenish hues (Fig. 2). In contrast, individuals born above the Arctic Circle showed relatively better discrimination of hues within the purple range of the spectrum (see Fig. 2). Interestingly, research on infants has shown that two months old can discriminate reds, oranges, blue-greens and blues from a white surround but fail in two regions centered in the yellow/green and mid-purple (Teller, 1998; Teller et al., 1998; cf. Dobson, 1976). Considering that greenish hues (i.e., yellow-green and green-blue) and purple hues were the regions of the color spectrum where significant differences were observed in the present study, we surmise that the extended periods of normal development for these hues may result in greater susceptibility to the effects of the light environment during infancy than for other regions of the human color spectrum.

In addition, we found effects of the season-of-birth of our Norwegian participants. That is, individuals born in the autumn or winter showed significantly larger error rates than participants born in the other seasons (see Fig. 3a) and individuals born in the summer showed significantly better performance for purplish hues than participants born in the other seasons. Thus, the season-of-birth effects occurred for regions of the color spectrum that largely overlapped those also affected by latitude-of-birth (e.g., greenish and purplish colors). Most interestingly, it was the group of above-AC individuals born in the autumn that showed the lowest overall color performance (see Fig. 4).

Remarkably, protracted residence at the latitude-of-birth did not exacerbate the individual differences described above for Specific Hues. Thus, the environmental impact on color vision may act early in infancy, in all likelihood during the first months of life. Indeed, the first months of life for those born in autumn and winter would coincide with the least exposure to direct sunlight (mørketid) and the most exposure to twilight. One intriguing possibility is that such an exposure to nearly monochromatic natural light (twilight) could have been the causal factor in the selective improvement of color visual discrimination within a selected range of the spectrum. In general, the "photic regime" (cf. Lythgoe, 1979) or the colors that are prevalent in the ambient (either outdoors or indoors) can influence the relative sensitivity of the color visual system of species that are resident in a specific environment. Such adjustment to the photic regime may have been either selected in each species by natural selection or they may result, at least in species whose nervous system is immature at birth, as an adaptation of the developing visual system. All species that are indigenous to the Arctic environment show a seasonal pattern of mating and reproduction, but humans are not a reproductively seasonal species and their offspring are remarkably immature for an extended period after birth, so that different environments may have a tangible impact on human development.

Also, the relatively better performance across the whole color spectrum of above-AC individuals born in the summer, compared to all of the other seasons (Fig. 4), suggests that early exposure to midnattsol may provide optimal levels of light stimulation in this group for the development of color vision mechanisms. In fact, at latitudes above the Arctic Circle, although the autumn and spring seasons (i.e., the months around the two equinoxes) would have a daylight cycle that is not very different from that of, for instance, central Europe, the levels of solar irradiation (W/m^2) would be sensibly lower. Hence, the continuous presence of sunlight in the summer months may make a difference for a developing visual system.

In addition, in present-day Norway, electric artificial lighting supplements the lack of natural light during mørketid; hence, the observed changes in color discrimination within specific regions of the color spectrum may reflect the combined effect of the narrowing of the spectrum of natural light towards the short wavelengths and the concomitant protracted exposure to (mainly) incandescent light. Artificial lighting of tungsten lamps has a relative energy that is lowest for short-wavelengths and highest (approximating the energy of natural sunlight) for the long-wavelengths (i.e., above 600 nm; cf. Livingstone, 2002). Also, the increase in relative energy of tungsten to wavelength is approximately linear, whereas fluorescent lamps have an irregular profile of relative energy over wavelengths, but fluorescent lamps typically approximate sunlight's energy only for wavelengths between 600 and 620 nm (that is in the 'orange' part of the spectrum). In sum, the protracted exposure in the indoors environment,

during the winter period, to the irregular energy profile over the range of wavelengths of different types of artificial lighting could also be a contributing causal factor. Indeed, we predicted that the largest error rates (see Figs. 2 and 3) would occur in those regions of the visible color spectrum where the energy of incandescent or fluorescent light is poorest compared to sunlight energy (i.e., for wavelengths ranging from 460–530 nm, or green-blue, to 560-600 nm or yellow-green; Livingstone, 2002). Furthermore, we had speculated that the unusually high exposure to twilight among above-AC individuals compared to below-AC could result in a photic regime that is beneficial to visual discriminations of the shortest wavelengths (indigo-purple).

Levels of annual insolation of UV-B light can also be ruled out as a causal factor in the present study. According to the UV-B phototoxicity hypothesis (Davies, Laws, Corbett, & Jerrett, 1998; Javitt & Taylor, 1995; Zigman, Datiles, & Torczynski, 1979), higher energy UV photons lead to changes in the optical density of the intraocular crystalline lens and, thus, may cause gradual brunescence and eventually cataracts (Dolin, 1994; Werner, 1991; Young, 1991). However, UV doses are inversely proportional to latitude and color vision within the green-blue range of the spectrum should be best among people living at increasingly higher latitudes. Indeed, solar irradiation is nearly absent during mørketid or winter time (i.e., from late November until early January) the range = 0–10 W/m^2, (*Institutt for informatikk, Universitetet i Tromsø, 2005*). In the spring season of 2005 solar irradiation in Tromso ranged 100–1200 W/m^2; in the summer the range was 300–1200 W/m^2; in the autumn the range was 200–800 W/m^2. Moreover, the Daily effective UV doses in Tromsø range approximately 500–1000 J m^2 lower than those in Oslo (Johnsen et al., 2002) and the Arctic "ozone hole" does not extend over Norway. Decreased UV doses should be associated with better performance in discrimination of green-blue hues but our findings show the inverse relationship, with good performance in the purple range and for overall scores of individuals born in the summer, and no dose-dependent effect of permanence in the Arctic after birth. One should also note that there are no variations in basic color terms among Norwegian dialects and separate terms are available for *blue* and *green* (cf. Lindsey & Brown, 2002).

However, UV radiation can also be reflected from the ground and fresh snow can reflect up to 88% (Stojanovic & Nitter, 2001). Indeed, snowfall is higher in urban areas of northern Norway compared to those in central or southern Norway (e.g., the average number of days with snow depth 5 cm or more, period 1971–2000, was 91 in Oslo and 16 in Bergen but it was 188 in Tromsø and 194 in Karasjok; *Metereologisk Institutt*). In addition, Norwegian northerners may have a more "outdoorish" lifestyle (*Statistics Norway*). The amount of outdoor activities could modulate exposure to albedo from water or snow; but water albedo is unlikely to play any causal role (similar

proportions of participants in each group were born in a location near the coast, see Table 1). Also, altitude plays no significant role for the present findings since the large proportion of participants in the sample was born and lives near sea level (see Table 1). However, snowfall could considerably increase UV light reflectance during the Arctic spring and, at the northernmost latitudes, in the early summer as well. Yet, an analysis of covariance with 'numbers of days with snow' as the covariate revealed that latitude was a significant predictor of decrements in color discrimination whereas snowfall played no significant role.

Nevertheless, differential exposure to water/snow albedo or the outdoorish lifestyle of Norwegians may play a role in explaining the significant increase in color discrimination errors of both Norwegian groups compared to the European group for nearly all colors (exceptions were yellow, blue, and bluish purple). Another possible cause for the lower performance of Norwegians compared to Europeans may be due to some peculiarities in the diet of Norwegians. However, there does not seem any specific lack of nutrients or excesses in their diet compared to other European populations, as the mean dietary intake of vitamins and minerals among Norwegians exceeded the recommended values (Johansson, Solvoll, Bjørneboe, & Drevon, 1997). Given that colour vision is known to be vulnerable to neurotoxins (e.g., Mergler, Bowler, & Cone, 1990) and that a number of persistent organic pollutants are transported by sea currents into the Arctic, one could hypothesize that, trough the consumption of seafood, several neurotoxins may enter into the human food chain. Indeed, the intake of fish, in particular of fatty fish, can affect colour vision in fish-eating populations (e.g., Neuringer, 2000; Stamler, Mergler, Abdelouahab, Vanier, & Chan, 2006). However, the same quantity of fatty fish appears to be consumed at different latitudes (Døving, 1997; Meltzer, Bergsten, & Stigum, 2002). Among other substances' intakes, alcohol consumption has also shown to be related to impairment of colour vision (e.g., Cruz-Coke & Varela, 1966). Yet, the above-AC regions' consumption of pure alcohol per person is well below the national mean (Statistisk sentralbyrå/*Statistics Norway, 2005*) and the mean Norwegian consumption of pure alcohol per person is low compared to other European countries (Statens institutt for rusmiddelforskning/ Norwegian Institute for Alcohol & Drug Research, 2005). Thus, neither fish nor alcohol consumption would seem to be likely causal factors for the latitudinal and (especially) the seasonal effects observed in the present study.

Another explanation for the difference between the Norwegians and the Europeans could be found in evolutionary adaptations among early populations that originally settled at different latitudes. In humans, color vision may have undergone considerable "selection relaxation" (Pickford, 1963) and the natural selection on color vision may have also differentially relaxed among peoples that resided in different habitats (Post, 1962). In particular, early hunter-gatherers living in the extremely harsh environment of the northern continental tundra or in the dimly lit circum-

polar regions and misty maritime environments may have been under rather different selective pressures for their visual abilities than those that promoted trichromacy for frugivory or folivory in tropical environments (cf. Sumner & Mollon, 2003; Surridge, Osorio, & Mundy, 2003). Reimchen (1987) has specifically hypothesized a relationship between human color vision deficiencies and atmospheric twilight. Specifically, color vision deficiencies might represent evolutionary adaptations among early northern populations for hunting and gathering during the low light intensities encountered at twilight. This is apparently in contrast to Post (1962) observation of a general lower incidence (1/4) of color deficiencies in hunting peoples compared to agricultural and industrial societies, which suggests that natural selection may remove color vision defectives in hunting populations. However, red-green insensitive individuals can detect relatively smaller differences in brightness of colors than normal individuals (Adam, 1969) and this is particularly true at reduced light intensity (Hurvich, 1981).

Indeed, Reimchen (1987) found that the percentage of red-green insensitive individuals in the world's population increases exponentially (range = 1–10% of R–G deficients) with geographic latitude ($R = 0.69$, $P < 0.001$) as well as with total hours of twilight per year ($R = 0.55$, $P < 0.001$). Interestingly, the duration of ''civil'' twilight (i.e., light deriving from a sun's position of $\approx -6°$ in relation to the horizon) is highest between 60° and 80° of latitude and it peaks at 70° (i.e., Tromsø's latitude) adding about 1100 h of light per year to the half a year's daylight period of 4392 h (Ørbæk, 2006). Moreover, the duration of ''nautical'' twilight (i.e., a sun's position of $\approx -12°$) and of ''astronomical'' twilight (i.e., a sun's position of $\approx -18°$), which are also the highest between 70° and 90° of latitude, would add together another 1000 h of dim purplish light to the sky. It is then possible that the differences observed in the present study between the Norwegian group and the central European group reflected similar color vision adaptations of populations during their evolutionary past. However, the data summarized by Reimchen (1987) showed minimal differences (range = 0.5–1.5%) between France and the UK compared to Norway and it seems especially unlikely that this account would explain the observed differences within Norway. In fact, in present-day Norwegian society there is plenty of geographical mobility and Norwegian southerners and northerners share to a great extent the same evolutionary past; most importantly, in the present study, we did not observe a difference in terms of percentage of red-green deficiencies, as measured with the Ishihara Plates, between the Norwegians born above/below the Arctic Circle. Interestingly, the percentage of red-green deficiencies as measured in our sample with the Ishihara (i.e., 3%) was rather low compared to what one would have expected from Reimchen's (1987) review (i.e., 7.5%) or predictions; this contrast may be due to differences in the color tests used in the various studies. In fact, Waaler (1927) estimated a prevalence of color deficits in Norwegians of 8% among males and 0.4% among the females; hence a prevalence of 4.2% in the whole population.

To conclude, the present study is mainly descriptive and we cannot propose in this context specific mechanisms for the observed differences. These may reflect substrate changes at the retinal level or at a post-receptor level. We know that newborns are responsive to red but fail to discriminate the blue hues from achromatic backgrounds and are also very poor at discriminating green and yellow hues (Pulos et al., 1980; Varner, Cook, Schneck, McDonald, & Teller, 1985). By three months, however, infants show evidence of discriminating all chromatic hues but green and yellow appears to progress more slowly. It is then interesting that some of the hues where above-AC participants differed the most from below-AC participants corresponded to the yellow-green part of the spectrum.

One can speculate whether changes in lens or macular pigment or receptor sensitivity could predict the present patterns of errors. However, receptor losses or weaknesses would predict that the errors fall along axes rather than one pole of the circle; but there was no sign of this in the plots. In fact, we suggest that group differences in levels of pre-retinal screening due to either macular pigment or iris color (cf. Dain et al., 2004; Woo & Lee, 2002) were unlikely to have played a role for the present results. First of all, there was no difference in iris color frequency between the two groups. Second, although we did not directly measure macular density, it is known that increasing macular density results in a shift in the tritan direction of errors (Moreland & Dain, 1995; Rodieck, 1973). However, the differences we observed did not clearly correspond to a 'tritan' pattern or that of other cone defect types. There was only very marginal overlap between the present pattern of errors and those of the classic cone defect types, according to either the classic analysis of FM100 data or the moment of inertia method (Vingrys & King-Smith, 1988).

In sum, if the changes we observed occurred at the receptor level, it is likely that these did not represent losses or strong functional alterations of a specific type of cone, since these would give rise to different patterns of errors than those we found. Thus, it remains unclear which neural factor would lead to the highly selective effects that we found for different hues and, specifically, what factors would be behind a lower sensitivity to green while simultaneously sensitivity to purple is relatively enhanced. In general, the neural locus of the developmental changes in color vision is still unknown and the neural locus of the color differences in color vision reported in the present study must remain speculative until physiological, optometric, and molecular genetics studies can be conducted.

Acknowledgments

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