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Spatial and temporal aspects of chromatic adaptation and their functional significance for colour constancy

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ABSTRACT

Illumination in natural scenes changes at multiple temporal and spatial scales: slow changes in global illumination occur in the course of a day, and we encounter fast and localised illumination changes when visually exploring the non-uniform light field of three-dimensional scenes; in addition, very long-term chromatic variations may come from the environment, like for example seasonal changes. In this context, I consider the temporal and spatial properties of chromatic adaptation and discuss their functional significance for colour constancy in three-dimensional scenes. A process of fast spatial tuning in chromatic adaptation is proposed as a possible sensory mechanism for linking colour constancy to the spatial structure of a scene. The observed middlewavelength selectivity of this process is particularly suitable for adaptation to the mean chromaticity and the compensation of interreflections in natural scenes. Two types of sensory colour constancy are distinguished, based on the functional differences of their temporal and spatial scales: a slow type, operating at a global scale for the compensation of the ambient illumination; and a fast colour constancy, which is locally restricted and well suited to compensate region-specific variations in the light field of three dimensional scenes.

1. Robust colour: constancy

Colour is one of the most salient features in natural scenes and a powerful cue for many visual tasks: for example, it facilitates signal detection (Chaparro et al., 1993), provides additional cues for figure-ground segmentation (Gegenfurtner & Kiper, 1992; Healy, 1989), feature binding (Mollon, 1989), and the detection of shadows (Kingdom, Beauce, & Hunter, 2004); furthermore, it improves object detection and recognition (Gegenfurtner & Rieger, 2000; Osorio & Vorobyev, 1996; Regan et al., 1998; Summer & Mollon, 2000; Tanaka & Presnell, 1999; Wurm, 1993) and augments our mental representation of objects by enhancing memory (Wichmann, Sharpe, & Gegenfurtner, 2002).

It can therefore be easily appreciated that colour perception, i.e., the cortical representation of chromatic features, needs to be reliable and robust. With the exception of selfluminant bodies like stars or bioluminescence (e.g. photophores of fireflies (*lampyridae*)), vision in natural scenes is derived from surface reflexion. Therefore, the biggest challenge for achieving a robust colour percept is the changing illumination: the spectral composition and intensity of the daylight changes greatly over the course of the day and so do the chromaticities of the surfaces. Furthermore, in three-dimensional scenes, the light field is inhomogeneous, by objects blocking the path of light (shadowing) as well as by secondary illumination through reflexions from other surfaces (inter-reflexions). However, the neuronal computation of colour ensures that objects can be recognised almost independently of changes in illumination (colour constancy; von Helmholtz, 1896). The importance of this phenomenon for the biological function of vision is underlined by the fact that most species with highly developed visual systems posses colour constancy, including other fish and amphibia (e.g. goldfish (Dörr & Neumeyer, 1996), frog (Maximov, 1989)) and invertebrates like bees (Chittka et al., 2014; Werner, Menzel, & Wehrhahn, 1988).

It has to be stressed, though, that the very term *colour constancy* is misleading, because – contraire to it's name – the performance of human (and animal) colour constancy is far from perfect. Depending on the actual experimental conditions and methods (complexity of the visual scene, adaptation time, and instructions), the reported success of colour constancy in two-dimensional structured patterns ranges between 20% in simple two-dimensional arrangements and 85% in three-dimensional, complex surrounds, whereby 100% is defined as perfect colour constancy (values taken from Table 1 in: Foster, 2011; pp. 683–686). It has been argued that a perfect compensation would be disadvantageous, because it would prevent the information about the illumination itself

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(but see Granzier & Valsecchi, 2014); however, it may simply be a consequence of insufficient or incorrect information available from the scene.

2. How is colour constancy achieved?: The importance of scene context

Achieving colour constancy essentially means, to uncover the spectral reflectance $R(\lambda)$ of a surface, which is invariant, from the reflected spectrum $S(\lambda)$, whereby $S(\lambda)$ is the product of $R(\lambda)$ and the spectrum of the illumination $I(\lambda)$ and is therefore variable. As can be easily seen, if neither $S(\lambda)$, nor $I(\lambda)$ are known, as in the case of the retinal input, the spectral reflectance $R(\lambda)$ of a surface cannot be directly derived from this equation. Processing of additional information is needed in order to normalize the signals.

There is general agreement that colour constancy is not the result of a single mechanism, but is achieved by a multitude of processes at all stages of the chromatic pathways (Foster, 2011; Kraft & Brainard, 1999; Maloney, 2002; Smithson, 2005). These include steps of sensory normalization in the retina, which are continued in the LGN and the primary visual cortex as well as input from cognitive stages, from which inferences can be drawn about the scene, the objects within and its light field. For example, recognizing an object with known colour allows inferences about the prevailing illumination (Granzier & Gegenfurtner, 2012); knowledge about the spatial layout of a scene allows its compensation based on previous experience with the light field in such scenes (Bloj, Kersten, & Hurlbert, 1999). However, the relative weight of theses contributions to colour constancy and their constraints still need to be determined. Other examples of useful information obtained in context are specular highlights, which are direct cues to the spectral composition of the illuminant (Lee, 1986), and exploiting higher-order scene-statistics (Golz, 2008; Golz & MacLeod, 2002).

Taken together, this means that all available information is used by the visual system in order to obtain a robust and reliable colour percept. Common to all strategies is the importance of information from local and wider scene context. In other words, colour constancy is a prime example for context related phenomena in colour vision. In the following I will focus on the sensory processes of colour constancy (thereafter called sensory colour constancy), namely context related adaptation, and illuminate the functional significance of their temporal and spatial properties for colour constancy in natural scenes.

The importance of scene context for colour constancy becomes immediately obvious when viewing a single, isolated stimulus (so called void-condition): here, colour corresponds directly to, and therefore changes with, the wavelength composition of the stimulus (Land & McCann, 1971; Valberg & Lange-Malecki, 1990; Zeki, 1983). The role of context for colour constancy has been highlighted by Edwin Land's Mondrian[1] demonstrations: a multicoloured arrangement of rectangular papers, like the one shown in Fig. 1, is illuminated by the light of three independently controlled projector lamps (one for green, red and blue light, each). By measuring the light reflected from each of the patches under different illuminations, Land and McCann (1971) demonstrated that the human perception does not primarily depend on the local light flux emitted from each patch. Extending the concept of constant ratios (Wallach & Galloway, 1946), Land and McCann proposed an algorithm which models colour constancy by computing and integrating local contrast signals (ratios) above a certain threshold across large parts of a visual scene ("Retinex Algorithm" Land, 1986a; Land & McCann, 1971). Daylight changes tend to leave the spatial ratios of light reflected from natural surfaces preserved (Nascimento, Ferreira, & Foster, 2002) and therefore, encoding colour by spatial ratios within the same spectral channels (chromatic and luminance) can indeed be a powerful tool for achieving colour constancy (Foster, Amano, & Nascimento, 2001; Foster & Nascimento, 1994; Hurlbert & Poggio, 1989; Hurlbert & Wolf, 2004; Nascimento, Ferreira, & Foster, 2002; see also review in Shevell & Kingdom, 2008).

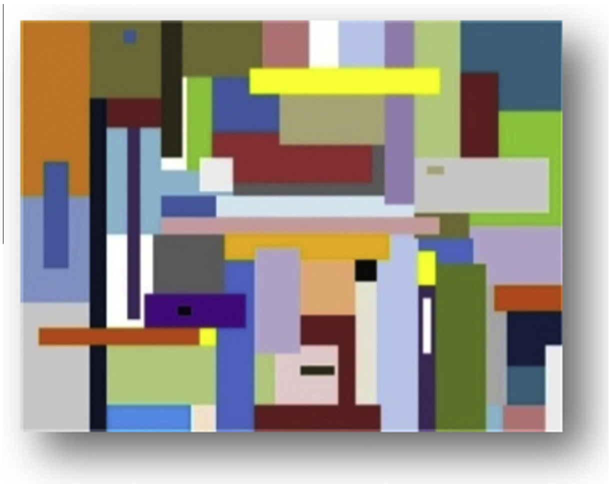

Fig. 1. A Mondrian-pattern.

3. Context in computational models of colour constancy

Computing ratios is also at the heart of many sensory based computational models for colour constancy. The models differ in the type of spatial and temporal filters used for the normalisation. For example, models using the von Kries coefficient law[2] (Ives, 1912; von Kries, 1905) compute local, temporal ratios; the group of Lightness Algorithms (for example the Retinex), on the other hand, computes ratios by spatially extensive operations using different forms of spatio/temporal filtering (see reviews in Foster, 2011; Hurlbert, 1986; Marr, 1976; Smithson, 2005).

The success of all these models critically depends on the selected reference, used for the normalization, mainly on the extent to which the reference signal contains information about the illuminant (allowing a so called "illuminant estimate"). Ideally, this reference would be one that contains the unbiased spectrum of the illuminant. If the chromatic average across all reflectances of a scene is neutral (obeying the so called grey world assumption), it follows that any deviation from a neutral chromaticity is caused by the illuminant and this can be used as a cue to its chromaticity. However, it should be noted that this does not actually *specify* the illuminant, which is a spectral distribution of energy as a function of wavelength, i.e. different metamers can give identical "illuminant chromaticities". The grey world assumption and operations for obtaining a space-average reference are therefore implemented in many algorithms (Buchsbaum, 1980; Land, 1983, 1986a, 1986b); note that for the validity of this argument it is not important that the scene average is actually neutral which is indeed not the case for most scenes, see (Webster & Mollon, 1997a, 1997b), as long as the average reflectance is sufficiently broadband and remains constant.

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[1] Named (not quite correctly) after the dutch neo-plasticistic painter Piet Mondrian (1872–1944).

[2] Scaling of the cone absorptions by a factor which depends on the adapting light; originally developed to model the effect of adaptation to coloured lights, the coefficient law by von Kries (1905), has been modified by Ives (1912) and applied as a possible mechanism for colour constancy.

Following a similar argument, the surface with the highest luminance ("white-patch-assumption") may serve as a reference (Barnard et al., 2002; Brill & West, 1981; Land & McCann, 1971). Even more informative are specular highlights, because they contain the entire and unbiased spectrum of the illuminant (ĎZmura & Lennie, 1986; Lee, 1986). Exploiting higher-order image statistics has also been proposed as yet another method to estimating the illuminant from context information (Golz & MacLeod, 2002).

4. Basic principles: adaptation and encoding contrast

For simplified experimental arrangements like a uniformly illuminated Mondrian, colour constancy can be reasonably well described by low-level processes of sensitivity control, and the encoding of contrast. Both computational principles are integral part of the procedure for normalizing the visual signals, and serve not only to achieve invariance but also, in general, to widen the neurons' dynamic range, to optimize signal detection over a large range of intensities, and to reduce redundancy (efficient coding principle: Atick, Li, & Redlich, 1993; Barlow, 1990; Clifford et al., 2007; Laughlin, 1981; Wark, Lundstrom, & Fairhall, 2007). Experimentally difficult to separate, chromatic adaptation and induction can be understood as parts of the very same normalisation procedure, with chromatic adaptation referring more to its temporal and induction more to its spatial aspects.

In the following, the term chromatic adaptation will be used in a broad sense, for the adjustment of the chromatic system to the prevailing light flux and contrast distribution, including temporal and spatial processes. As such, chromatic adaptation is an important sensory process for obtaining colour constancy.

Psychophysically identified mechanisms of chromatic adaptation comprise multiplicative gain control (von Kries type mechanisms), and repetitive steps of subtractive spatial and temporal filtering with local but also spatially extensive components (either via spatial or temporal mechanisms; two-process model; Geisler, 1983; Hayhoe, Benimoff, & Hood, 1987; Hayhoe & Wenderoth, 1991; Jameson & Hurvich, 1972; Shevell, 1978; Walraven, 1976; Whittle & Challands, 1969).

Correlated physiological processes include light adaptation and contrast gain control and adaptation, which take place, repetitively, at several stages of the visual pathways and at different spatial and temporal scales (reviewed in Carandini & Heeger, 2013; Heeger, 1992; Kohn, 2007).

Retinal light adaptation to mean intensity shifts the neurons' operating range to match the present intensity (equivalent to a "discounting" of the mean luminance; Boynton & Whitten, 1970; Normann & Perlman, 1979; Pugh, Nikonov, & Lamb, 1999; Schneeweis & Schnapf, 1999; Shapley & Endroth-Cugell, 1984; Valeton & van Norren, 1983).

The operation can be modelled by scaling of the receptor signals by their local mean (von Kries adaptation) and as such are a neural measure of local spatio-temporal contrast. In particular with respect to colour constancy, light adaptation is the pre-requirement for the reliable encoding of image contrast over a wide range of light intensities, i.e. obtaining constant ratios.

Light adaptation is immediately followed by contrast gain control/adaptation in the bipolar and ganglion cells (Shapley & Endroth-Cugell, 1984; also see reviews in Carandini & Heeger, 2013; Heeger, 1992; Kohn, 2007), which adjusts the neurons contrast sensitivity with respect to the contrast in the surrounding spatial regions. It involves multiple mechanisms and operates at several time and spatial scales (Bao et al., 2013). This allows the adjustment to very fast changes in local contrast following saccades (Baccus & Meister, 2002; Victor, 1987), as well as adaptation to slower changes in the overall contrast level, resulting from eye- or head-movements (Baccus & Meister, 2002; Brown & Masland, 2001; Kim & Rieke, 2001; Smirnakis et al., 1997; Wark, Fairhall, & Rieke, 2009).

In terms of image processing, contrast adaptation is an important mechanism for increasing coding efficiency because it normalizes the distribution of image contrast so that all response levels are used with equal frequency (Gonzales & Wintz, 1977; Laughlin, 1981; Shannon & Weaver, 1949). In colour perception, contrast adaptation exerts an important influence through adaptation to the temporal modulation of chromatic signals caused by eye-movements across a complex scene (Brown & MacLeod, 1997; Webster, Georgeson, & Webster, 2002; Webster & Mollon, 1994). Colour constancy can be affected by contrast adaptation under conditions where an illumination change goes along with a change in chromatic contrast distribution, i.e. if it results in metamerism (Brown & MacLeod, 1997; Webster & Mollon, 1995). However, in natural environments, image contrast and hence cone ratios have been found to be quite stable across illuminations (Nascimento, Ferreira, & Foster, 2002) and therefore, this effect may not be pronounced in such scenes. On the other hand, the efficiency of chromatic adaptation (and hence colour constancy) is influenced by the spatial structure of the adapting field, in a way, which is reminiscent of contrast gain control (Werner, 2003). Adaptation depends also on the magnitude of image contrast (Werner, 2003) and as such, contrast adaptation will be important for colour constancy by enhancing weak contrast signals (as for example in foggy or distant scenes (Webster, Georgeson, & Webster, 2002)).

Contrast adaptation is not restricted to the retina, but has also been identified as a crucial process in cortical processing (Carandini, Heeger, & Movshon, 1997; Heeger, Simoncelli, & Movshon, 1996; Kouh & Poggio, 2008; Smith, Bair, & Movshon, 2006). For example, it has been implicated as underlying adaptation effects in the spatial domain, like the tilt after-effect (Barlow & Földiak, 1989; Clifford, Wenderoth, & Spehar, 2000) or colour-orientation contingent after-effects (Clifford et al., 2003a; Engel & Furmanski, 2001).

Finally, local cone-contrast has been attributed to the function of double opponent cells in the upper layers of the primary visual cortex (Conway, 2001; Johnson, Hawken, & Shapley, 2001; Michael, 1978; Shapley & Hawken, 2011). Since their responses are characterized by a combination of spatial and chromatic opponency within their receptive fields they can serve as a possible neural substrate for simultaneous as well as successive colour contrast (Conway, Hubel, & Livingstone, 2002; Wachtler, Sejnowski, & Albright, 2003). The very mechanism which leads to colour contrast could potentially also lead to colour constancy, since illumination changes affect the receptive field of double opponent cells uniformly, and therefore will be compensated by the antagonistic responses of centre and surround. However, V1 double opponent cells do not have large receptive fields and their responses do therefore not correlate with the long-range properties of colour constancy. Also, direct evidence for colour constancy in human or monkey V1 is still lacking. Instead, the V4 complex has frequently been suggested as cortical site for colour constancy (Bartels & Zeki, 2000; Rüttiger et al., 1999; Zeki, 1983; Zeki & Marini, 1998); for a discussion of the extended literature on this topic see (Gegenfurtner, 2003; Shapley & Hawken, 2011; Werner et al., 2005).

5. Time-course of chromatic adaptation

Influenced by Land's Mondrian demonstrations, colour constancy is often implicitly assumed to be instantaneous. However, quantitative measurements of the sensory component of colour constancy (chromatic adaptation) show that colour appearance changes for several minutes after switching to a new adaptation regime. For example, Hunt (1950) and Jameson, Hurvich, and

Varner (1979) observed slow processes of up to 5 min to reach a final level of adaptation, whereby 80–90% were reached within the first minute. In general, time-courses consistently show a biphasic characteristic (Fig. 2), with most of the compensation (50–60%) taking place during a fast initial phase (first milliseconds to seconds); this is followed by a slower (several seconds up to minutes) asymptotic approach to a steady state, during which the remaining compensation takes place (the final result depends on experimental parameters). The time-course measured by Fairchild and Lennie could be described as exponential function with a time constant of 8.4 s, taking almost 1 min to complete (Fairchild & Lennie, 1992); a later study revealed the contribution of a fast and a slow mechanism, with time-constants of 1 s for the fast and 40–50 s for the slow component (Fairchild & Reniff, 1995). Using much shorter presentation times, (Rinner & Gegenfurtner, 2000) identified three components, one almost instantaneous (time-constant less than 10 ms), one fast with a time-constant of 40–70 ms and a slow component with a half-life of 20 s.

Werner, Sharpe, and Zrenner (2000) investigated the time-course of chromatic adaptation using adaptation patterns of different spatial complexities (articulated and uniform, equivalent in size, average chromaticity and luminance). The time-courses in both conditions could be described by exponential functions, but differed significantly in their time constants (8 s and 1 s). Modelling the time-course suggested three processes with different time-constants, wavelength- and spatial sensitivity (see Fig. 2): two processes with a combined time-constant of 8 s, which were independent of image articulation; however, in the complex condition, at least one additional process was necessary to explain the first seconds of the time-course of adaptation. This process had a time-constant of less than 200 ms, depended on the presence of image contrast (luminance or chromatic), and was middle-wavelength specific (Werner, 2003; Werner, Sharpe, & Zrenner, 2000). It's presence in dichoptic conditions indicated a cortical locus. After 5 s, it started to decay (or de-adapt), and was no longer effective after 10–20 s.

It is possible that the fast process identified in Werner's study is indeed identical to one of the fast processes described by Rinner and Gegenfurtner (with time constants of 10 ms and 40–70 ms), since the spatial arrangement of their stimulus showed some degree of complexity, i.e. the test-stimulus was displayed as an increment on a uniform background in the centre of a monitor screen, which in turn was seen against another surface (illuminated, uniform wall). However, the difference in presentation times (83 ms in Rinner and Gegenfurtner's study versus 200 ms in Werner's study), makes a definite evaluation difficult.

Notably, it was found in further experiments that the effectiveness of this instantaneous contrast response correlated with the similarity between the spatial features (spatial frequency and orientation) of target area and its surround (Werner, 2003), in way resembling the properties of contrast gain control mechanisms in retina and cortex (e.g. Carandini, Heeger, & Movshon, 1997; Dragoi et al., 2002; Hosoya, Baccus, & Meister, 2005; Moradi & Heeger, 2009; Müller et al., 1999; Sharpee et al., 2006; Smith, Bair, & Movshon, 2006; amongst others). Because these mechanisms work at multiple time scales, including those under 100 ms, it is possible that the instantaneous contrast response was subject to fast adaptation/normalization. As will be shown

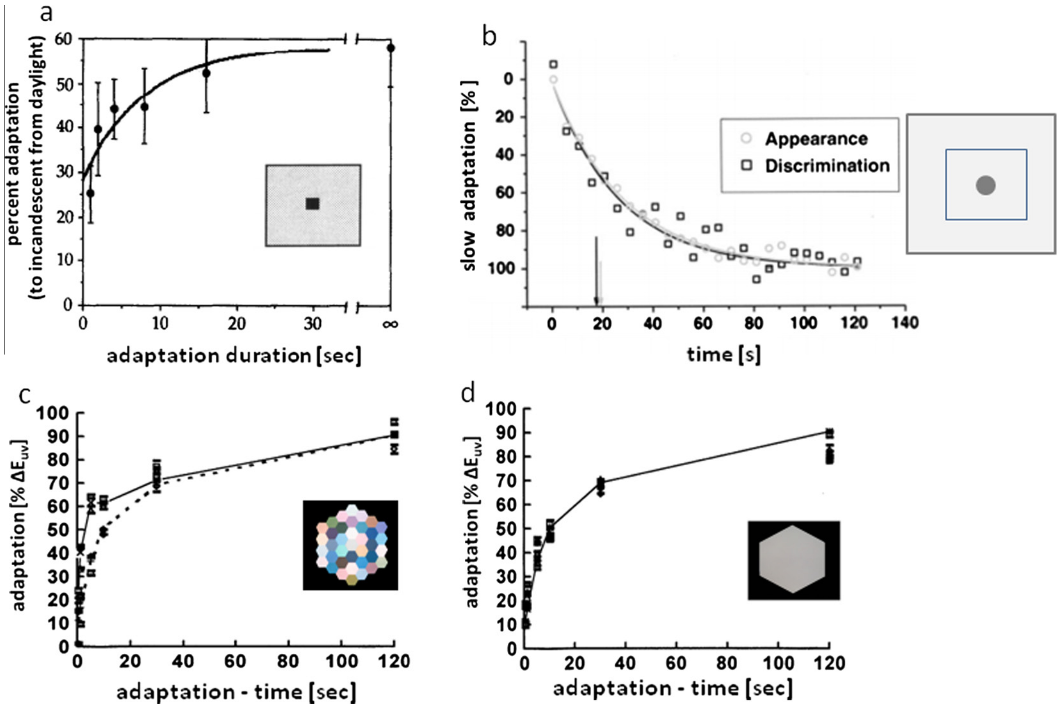

Fig. 2. Comparison of time-course of chromatic adaptation, as measured in independent studies. In all experiments, the stimuli were displayed on a monitor screen, and the observers had to judge the achromatic appearance of a briefly presented central test-patch. Adaptation was quantified by the shift of the achromatic colour locus following a simulated illumination change. Mean luminance, chromaticity and size of adaptation field were comparable, small inserted figures show the type of adapting patterns used; (a) time-course of adaptation to changes from D65 to CIE illuminant A (tungsten light), as measured by Fairchild and Lennie (1992). Adaptation-times were 1 s to 32 s. Size of display: 10 × 7.5°, diameter test-patch 0.25 or 1°; luminance: 25 cd/m^2. (b) Slow component of the time-course measured by Rinner and Gegenfurtner (2000). Adaptation was measured for changes along a red–green and blue–yellow axis and adaptation times of 1–120 s. Size of display: 8 × 10° (monitor)/45 × 64° (surrounding wall); diameter test-patch 4°; luminance: 26 cd/m^2 ; figure shows the decay, data are normalized to 100%; (c) and (d) time-courses measured by Werner, Sharpe, and Zrenner (2000), using an articulated (c) or uniform (d) background. Adaptation times were 200 ms to 120 s. Size of displays: 15.4 × 13.2°, test-patch 2.4 × 2.2°; luminance: 19.3 cd/m^2. In (c), the dotted line refers to shortwavelength (blue) and longwavelength (red) adapting lights, the solid line shows adaptation to middle-wavelength (green, yellow) light; in (d) the time-courses are identical for all adapting lights.

below, this fast component could therefore play a significant role for linking chromatic adaptation to the spatial structure of a scene.

The observation that adaptation occurred significantly faster to middlewavelength light as compared to short- or long-wavelength light (Werner, Sharpe, & Zrenner, 2000; see Fig. 2c) deserves further consideration. Interestingly, the acceleration is not specific for one of the cardinal axes i.e. blue–yellow versus the red–green, nor is it confined to the cardinal axes; rather, it also includes intermediate directions in colour space (yellow–green), suggesting the existence and independent adaptation of multiple colour channels at cortical stages (see also Webster & Mollon, 1991, 1994). Furthermore, it is noteworthy that the fast adaptation to middlewavelength light would not support better colour constancy for changes in daylight phases (Worthey, 1985), in particular towards blue, as recently reported for the discrimination of illumination changes (Pearce et al., 2014). It needs to be emphasized, however, that the middlewavelength preference of adaptation applies to *surface colour*, whereas the reported optimization of colour constancy for blue illumination concerns the *illuminant* itself, and this may indicate a task-specific differentiation of the processes involved. The accelerated adaptation to middlewavelength light, in particular, accommodates for the mean chromaticity of light reflected in natural scenes (e.g. Hendley & Hecht, 1949; Osorio & Bossomaier, 1992; Webster & Mollon, 1997a, 1997b; Nascimento, Ferreira, & Foster, 2002) and potentially supports compensation of local interreflections. At the same time, this may also facilitate object detection by improving the chromatic signal/noise-ratio, since biologically important objects (ripe fruit, water, etc.) reflect mainly in the long- or shortwavelength range of the spectrum (which is more slowly adapted).

In addition to these relatively short-term adaptation processes, adjustments also occur at a very large time scale, as for example demonstrated by the McCollough effect (McCollough, 1965; Vul & MacLeod, 2006) or when wearing tinted lenses/glasses over an extended period of time (Belmore & Shevell, 2011; Neitz et al., 2002). The same effect occurs naturally when adjusting to the changed opacity and chromaticity of the aging lens (Delahunt, Webster, & Werner, 2004). In addition, scene chromaticity may also change at a very slow temporal scale following seasonal changes, and affect colour appearance through contrast adaptation (Webster, Georgeson, & Webster, 2002; Webster & Mollon, 1997a, 1997b). These very-long lasting effects (persisting over days (Jones & Holding, 1975) or even weeks and months (as reported in Vul & MacLeod, 2006)), are additive with respect to short-term adaptation and are thought to involve synaptic plasticity (Belmore & Shevell, 2011; Neitz et al., 2002; Vul & MacLeod, 2006). The exact interaction between the long-term adjustment and short-term adaptation are, however, not fully understood.

Taken together, two properties of the time-course of chromatic adaptation are to be noted: (1) Chromatic adaptation operates at multiple time-scales, ranging from almost instantaneous to minutes; very long-term processes preset the sensitivity of the chromatic system, which is then modulated by fast and intermediate adaptation to the present set of stimuli. (2) The temporal profile depends on the spatial structure of the adapting field, indicating different spatial scales of the contributing mechanisms. In the following, the spatio-temporal aspect of chromatic adaptation will be further investigated.

6. Spatial properties of chromatic adaptation

The contextual influences in adaptation can be spatially very extensive and this seems to be an important factor for achieving colour constancy. For example, Murray et al. (2006) reported for long adaptation times (30–60 s), a substantially higher degree of colour constancy using a 120 deg as compared to a 20 deg adapting field. Hansen, Walter, and Gegenfurtner (2007) found that colour constancy critically depended on the size relation of adapting background and test-patch, i.e. colour constancy was significantly reduced if the context was reduced in relation to the size of the target. Finally, there is direct experimental evidence for the involvement of large-field computations in colour constancy from psychophysical experiments involving split-brain patients, where it could be demonstrated that cross talk between the two hemispheres is necessary to obtain colour constancy (Land et al., 1983). Taken together, these studies demonstrate the importance of the context size for the success of colour constancy.

On the other hand, there are also numerous studies demonstrating more localized effects (in the range of 1 deg) in chromatic adaptation and colour constancy (Fairchild & Lennie, 1992; Granzier, Smeets, & Brenner, 2006; Zaidi, Spehar, & DeBonet, 1998; see also review in Shevell & Kingdom, 2008). It has been suggested therefore, that large field computations might be based on the temporal integration of locally derived signals, via eye-movements (Cornelissen & Brenner, 1990; D'Zmura & Lennie, 1986; Golz, 2010; Shevell, 1980; Zaidi, Spehar, & DeBonet, 1998). Alternatively, the integration of signals across large areas of the visual field could be the function of spatial interactions based on neurons with large receptive fields. Correlates of the psychophysically identified long range interactions, exceeding the more local computations in V1, are the "non-classical" receptive fields of neurons in macaque V4 (Desimone et al., 1993; Schein & Desimone, 1990) and in the infero-temporal cortex (Komatsu et al., 1992; but see also Wachtler, Sejnowski, & Albright, 2003, for remote induction in V1).

An important consequence of spatially extensive operations is that object colours become relatively independent of their immediate local surround; instead, they are more related to the global surround, which is relatively stable within a given visual scene. Furthermore, in natural environments, this global average tends to be spectrally broad (corresponding to the "grey world assumption"). Therefore, large-field computations are an important mechanism for achieving a robust colour code.

In general, stronger adaptation and context influences are observed in patterned ("articulated") than in uniform adaptation fields and this has been attributed to the combined effect of receptive field structure and a temporal modulation of the signals caused by eye movements (Fairchild & Lennie, 1992; Golz, 2010; Werner, Sharpe, & Zrenner, 2000; Zaidi, Spehar, & DeBonet, 1998; Zaidi et al., 1992), as well as the additional information retrievable from an increased number of "colour ratios" (Plet & Gerbino, 2001). This seems to be in contrast to the notion of an equivalent surround (Valberg & Lange-Malecki, 1990). However, both findings can be reconciled if the time-course of colour constancy is taken into account: as the study by Werner, Sharpe, and Zrenner (2000) shows, the enhancement of colour constancy by context complexity is restricted to the first 10 s, and cannot be observed for longer adaptation times.

Numerous psychophysical studies have established the close co-processing of spatial and chromatic information, resulting in mutual influences of colour and form as for example in orientation discrimination (Beaudot & Mullen, 2003; Webster, De Valois, & Switkes, 1990), or in the well known McCollough effect (Barnes et al., 1999; McCollough, 1965). These conjunctions also involve contextual influences (see for example the tilt illusion, (Clifford et al., 2003b), whereby two aspects are to be noted: (1) contextual influences are specific with respect to the similarity of the inducing surround and the induced area; (2) their tuning properties of are subject to adaptation. For example, Barnes, Wei, and Shevell (1999) and Hurlbert and Wolf (2004) showed that chromatic induction is most pronounced if the spatial scale or chromatic texture of inducers and induced area match, but if they differ, induction is reduced. Similarly, chromatic adaptation to middlewavelength light was found to be most pronounced if the spatial frequency and orientation of the adapting background and test-field matched (Fig. 3; Werner, 2003); it is important to note that this was not restricted to a particular set of orientations or spatial frequencies, suggesting a dynamic tuning to the spatial features of the present background. The spatial tuning of chromatic adaptation also includes the depth plane of the adapting pattern (Kraft, Maloney, & Brainard, 2001; Shevell & Miller, 1996; Werner, 2006), although this is not found to the same extent in all experimental paradigms (compare also for induction: Hurlbert & Wolf, 2004).

There is a striking similarity in the temporal and spatial characteristics of the above described selectivity of spatial tuning in adaptation on one side and mechanisms of contrast adaptation on the other (this is also true for chromatic induction, which is not primarily considered here); for example, selective adaptation of cortical neurons to the spatial content of images is well documented (Boynton & Finney, 2003; Dragoi et al., 2002; Müller et al., 1999; Sharpee et al., 2006). On the other hand, spatio-chromatic co-processing has been implicated as a function of multiplexing neurons (e.g. Johnson, Hawken, & Shapley, 2001), and there is some evidence that colour-form contingencies are carried by a specialized class of oriented double opponent cells in V1 and higher cortical areas (in addition to non-oriented colour-selective cells; Engel, 2005; Gheiratmand, Meese, & Mullen, 2013; Seymour et al., 2010; for a detailed review of multiplexing neurons and the function of double opponent cells see Shapley & Hawken, 2011). Spatially selective adaptation in multiplexing neurons is therefore a potential neural correlate for the observed tuning in chromatic adaptation.

7. Conclusions: the functional significance of spatial and temporal properties of chromatic adaptation for colour constancy in natural scenes

In contrast to the "Flat World" of the Mondrian, visual scenes in the real world are three-dimensional, and consequently, have a non-uniform light field, i.e. the spatial distribution of the illumination is non-uniform in terms of its intensity and spectral content. This is because objects obstruct the path of light and cause shadows, light is filtered through e.g. the canopy of trees and reflected from other surfaces, causing multiple, secondary illuminations. Thus, the visual scene is sub-divided into many regions each with a different light environment, as illustrated in Fig. 4. In natural scenes, forest regions in the shadow are typically more greenish yellow, whereas forest regions with direct sunlight tend to be more reddish (Endler, 1993) see also Fig. 4). Thus, the spatial layout and, consequently, coexisting, variable illuminations, pose a serious challenge to colour constancy in natural scenes. Colour mechanisms operating at large spatial scales are useful for the compensation of the overall illumination, but will be detrimental in scenes with complex light fields, because the information from scene average is not equally appropriate for all regions; in the worst case, using information about illumination in region X will lead to incorrect scaling of signals in region Y. Contextual influence, therefore, has to be restricted to regions sharing the same illumination, which is why scene segmentation becomes important for colour constancy in three-dimensional scenes.

There is ample evidence that the spatial layout of scenes influences colour appearance and this has often been attributed to cognition and memory, for example knowledge about scene geometry and the physics of light in a scene (Bloj, Kersten, & Hurlbert, 1999; Boyaci et al., 2006; Doerschner, Boyaci, & Maloney, 2004; Yang & Shevell, 2002), or grouping factors related to the Gestalt concept (Schirillo & Shevell, 2000).

In addition, at a lower processing level, segmentation can be based on exploiting scene statistics. For example, Fine, MacLeod, and Boynton (2003) used colour statistics for grouping/segregating images based on the probability distribution of colour differences within and between surfaces. Similarly, Geisler (2008) and Geisler et al. (2001) successfully exploited the statistics of image contours to segment natural images, based on the direction, orientation and contrast polarity of line elements.

Likewise, the spatial tuning of chromatic adaptation could utilize the distribution of chromatic and spatial features (frequency and orientation) in natural scenes, which are highly correlated between neighbouring patches, but not in more distant patches (Fine, MacLeod, & Boynton, 2003; Tolhurst, Tadmore, & Chao, 1992); this would effectively restrict contextual influences to nearby regions of similar spatial properties. Limiting context influences by segmentation rather than by distance alone (as suggested by Valberg & Lange-Malecki, 1990) is important since it considers object borders. Because these regions would also be likely to have the same illumination, it follows that spatial tuning would be an effective tool to support colour constancy in complex scenes (see Fig. 4).

This is directly illustrated by the results of two studies, where the effect of inconsistent illumination was examined for colour con-

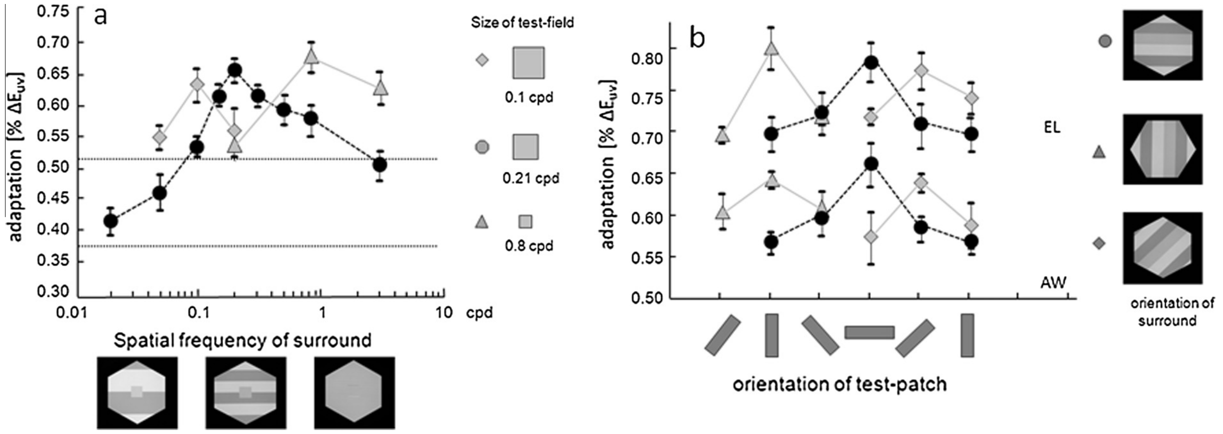

Fig. 3. Spatial tuning in chromatic adaptation. (a) Shows colour constancy performance as a function of the spatial frequency of the background (0.02–3 cpd); different symbols refer to different sizes of the test-patch (0.1–0.8 cpd). (b) Shows colour constancy performance as a function of the orientation of the background, different symbols refer to different orientations of the test-patch (figure modified after Werner, 2003). The test-patterns appeared achromatic under the standard condition ($u' = 0.197$, $v' = 0.468$) and consisted of luminance contrast only ($L_{\min} = 10.3$ cd/m^2, $L_{\max} = 28.3$ cd/m^2, $L_{\text{mean}} = 19.3$ cd/m^2); chromatic adaptation was measured for a 5 s green adapting light; experimental conditions were identical to those shown in Fig. 2c and d.

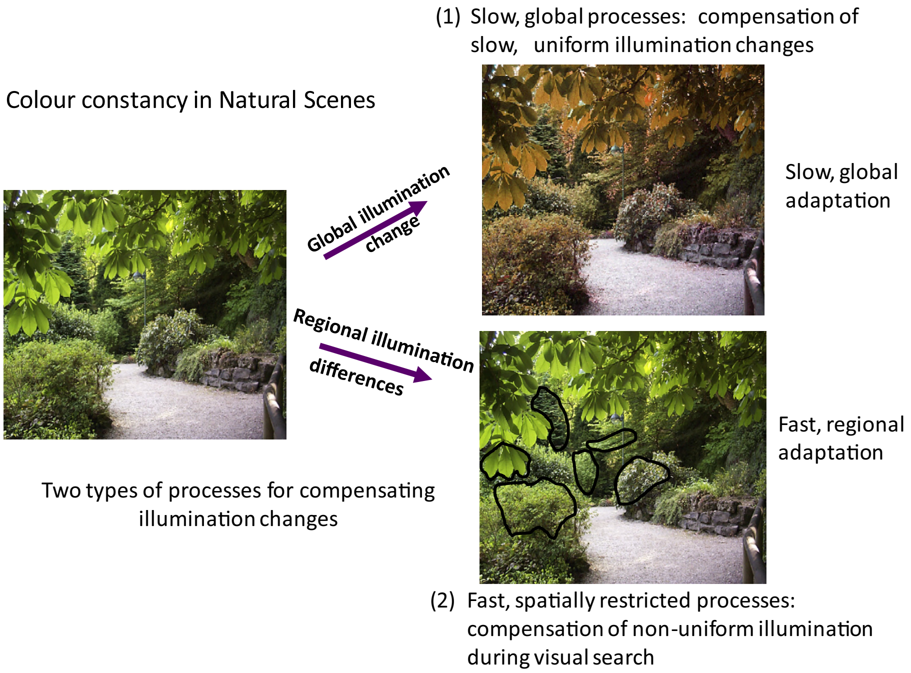

Fig. 4. Types of illumination changes in natural scenes. Left-hand figure illustrates a scene under neutral illumination, upper right-hand figure simulates the effect of a homogenous illumination change towards longer wavelength light; black lines in lower right-hand figure encircle examples of regions with different spatial features (spatial scale and orientation); note that these regions posses similar mean chromaticity, but are likely to have different illumination.

stancy. Werner (2006) presented test patch and surround either in the same depth plane or separated in depth. Following an inconsistent illumination change, colour constancy worsened significantly in the same-depth condition but only marginally in the separated condition, demonstrating the benefit of scene segmentation for colour constancy. Similarly, Smithson and Zaidi (2004) found adaptation to be spatially localized when testing the effect of locally inconsistent illumination in variegated, 2D scene; here, the test-patch (square) and background features (randomly oriented ellipses) were clearly segmented by spatial features (see their Fig. 1). Taken together, the two studies suggest a functional role for selective spatial tuning in chromatic adaptation and colour constancy.

In natural viewing conditions, visual systems encounter illumination changes at several spatial and temporal scales: (1) when visually exploring a three-dimensional scene we encounter locally confined, short-term illumination changes due to the variations in the spectral composition and intensity of the scene's light field; (2) slow and long-lasting (minutes to hours) changes of the overall illumination occur in the course of the day, due to atmospheric changes (weather conditions) or when moving from one habitat to another; (3) in addition, long-lasting changes in the environment occur from seasonal changes or the effect of aging on the optical media in the eye.

It is an attractive idea to consider, within this framework, the spatial and temporal scales of chromatic adaptation. Fast and local mechanisms of light and contrast adaptation/normalisation have been implicated for compensating changes following saccadic eye-movements. The same or similar processes could potentially contribute to fast and spatially restricted chromatic adaptation, while a region of interest is explored, for a few seconds, during visual search; it's selective/dynamic tuning to the spatial image statistics may serve as a tool for the appropriate segmentation of the light field, and provide a possible link between colour constancy and the spatial structure of a scene. The observed middle wavelength selectivity of these processes makes them particularly suitable for the compensation of inter-reflexions in natural scenes because their spectral properties match those of the reflexions from natural surfaces (e.g. leaves, soil; Werner, Sharpe, & Zrenner, 2000). On the other hand, global changes in ambient illumination are well compensated for by slow and large-scale processes of chromatic adaptation, which take between tens of seconds and minutes. Finally, the very long-lasting variations of the chromatic environment require additional long-term re-calibration of the visual system. Clearly, these processes are not independent from one another; for example, short-term adaptation can be understood as a fine-tuning to regions of interest, based on a very long-lasting calibration of the chromatic system. Therefore, for a full account of colour constancy in natural scenes, the interaction and cooperation among these processes needs to be understood and incorporated in models of human colour perception.

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