McCollough effect: A neural network model based on source separation

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McCollough effects (MEs) are a group of visual contingent aftereffects that involve colour and contour. These effects have been the subject of a large body of literature concerning their properties and theoretical accounts, but the mechanisms underlying the ME have never been fully clarified. We make the assumption that a general adaptive neural process tending to maintain independent dimensions in visual perception could account for the ME. The proposed neural network model generating the ME, though of minimal complexity, can reproduce various detailed experimental results (such as the tilt effect contingent to colour) and above all it accounts for the distinctive long temporal persistence of this aftereffect.

MCCOLLOUGH EFFECT: PHENOMENOLOGY, CHARACTERISTICS, AND PROCESSING LEVEL

In 1965 Celeste McCollough reported a colour aftereffect dependent on orientation. It was produced by exposing subjects to a grating of vertical black stripes on an orange background, which alternated every few seconds with a horizontal grating on a blue ground. After 2 to 4 min, when subjects viewed a test display of black and white vertical and horizontal gratings side by side, most of them reported seeing a desaturated blue green on the background of the vertical grating and orange on the horizontal one. The effect could persist for up to an hour or more and the colours would exchange place on the gratings if the test stimuli or the subject's head were rotated 90 degrees, disappearing altogether at approximately 45 degrees. The same phenomenon was observed if red and green complementary colours were substituted for orange and blue ones. Since McCollough's article, subsequent research showed that a variety of features, other than orientation, contingently elicits a colour aftereffect following pairing with colour (for a review, see Allan & Siegel, 1997a, b; Humphrey, 1998; Skowbo, Timney, Gentry, & Morant, 1975; Stromeyer, 1978). The McCollough effect (hereafter, ME) has also been observed in young children (Meyer, Coleman, Dwyer, & Lehman, 1982), monkeys (Macquire, Meyer, & Baizer, 1980), and pigeons (Roberts, 1984).

Three features distinguish the ME from classical aftereffects. Whereas the latter are one-dimensional and rather short-lived, the ME associates two visual dimensions and can last for hours, days, or even weeks (Jones & Holding, 1975), depending on adaptation duration and on stimulation after adaptation (MacKay & MacKay, 1975; Skowbo, Timney, Gentry, & Morant, 1974). The third feature concerns the reciprocity of effects between dimensions. In the framework of a McCollough effect based on colour and orientation, the reciprocity of effects is observed through the existence of a tilt effect contingent on colour. For example, after subjects have looked at red stripes tilted clockwise off vertical and green stripes tilted equally but counterclockwise, the vertical test stripes appeared to be tilted counterclockwise when red but clockwise when green (Held & Shattuck, 1971).

Concerning the processing level involved in the ME, many aspects of the effect suggest that the mechanisms mediating the ME operate at an early level of visual processing in the primary visual cortex, or even earlier in the visual pathway. For example, the ME does not transfer from one eye to the other (McCollough, 1965; Savoy, 1984), is sensitive to wavelength rather than to colour *per se* (Thompson & Latchford, 1986; Webster, Day, & Willenberg, 1988), and patients suffering from a profound visual agnosia (due to a diffuse damage in the peristriate areas of the visual cortex) or from a cortical blindness, experience the ME (Humphrey, Goodale, Corbetta, & Aglioti, 1995; Humphrey, Goodale, & Gurnsey, 1991). However, other studies found that high-level

factors such as transparency (Watanabe, Zimmerman, & Cavanagh, 1992) or linguistic factors (Allen, Siegel, Collins, & MacQueen, 1989) can influence the ME. Magnetic resonance imaging experiments presented evidence that the perception of the ME correlates with increased activation in extrastriate visual areas, such as the lingual and fusiform gyri (Barnes et al., 1999; Humphrey, James, Gati, Menon, & Goodale, 1999), and even in the ventrolateral prefrontal cortex (Barnes et al., 1999). It is not clear, however, whether these cortical regions are implicated in the ME adaptation process *per se* or whether the activity in these cortical regions reflects only colour perception. Therefore, to this day, the question of the locus in the visual system of the mechanisms mediating the ME is not completely settled.

HYPOTHETICAL MECHANISMS UNDERLYING THE MCCOLLOUGH EFFECT

The nature of the adaptation underlying the McCollough effect is not clear. Having shown that the ME had functional characteristics similar to the aftereffect stemming from adaptation to chromatic fringes produced by prismatic spectacles (Hay, Pick, & Rosser, 1963), McCollough (1965) suggested that both effects could be explained by the colour adaptation of orientation-specific edge detectors which "respond with decreased sensitivity to those wavelengths with which they have recently been most strongly stimulated" (p. 1115). However, she did not clarify the functional mechanisms of this adaptation. Thereafter, three main functional hypotheses or models have been proposed.

The first and most common model of the ME relies on neural fatigue. It refers to the general fact that repeated stimulation with a pattern can fatigue neural mechanisms that encode the pattern. In the case of the ME, repeated presentation of the chromatic grating would fatigue the neurons that simultaneously code orientation and colour, as found in monkey striate cortex (e.g., Hubel & Wiesel, 1968; Leventhal, Thompson, Liu, Newman, & Ault, 1993; Michael, 1978). However, the neural fatigue model is hardly plausible. It cannot account for the two major functional characteristics of the ME: its duration (which is generally considered to be much longer than the recovery time of simple neural processes) and the reverse effect.

Because of its very long decay and its dependency on post adaptation stimulation, many investigators have gravitated towards some form of associative learning model to explain the McCollough effect (see Siegel & Allan, 1992). One of the earliest associative accounts was formulated in terms of Pavlovian conditioning (Allan & Siegel, 1986; Murch, 1976). According to this theoretical framework, the colour is the unconditioned stimulus, the feature paired with the colour (for example, grid orientation) is the conditioned stimulus, and the colour-opponent response elicited by the colour is the unconditioned response. After some pairings, the conditioned stimulus alone (achromatic grid) elicits

the colour aftereffect as a conditioned response. The issue of whether the ME results from a classical conditioning or not has been debated extensively at a variety of levels and is still a matter of controversy (see for a review, Allan & Siegel, 1993, 1997a, b; Dodwell & Humphrey, 1990, 1993; Humphrey, Herbert, Hazlewood, & Stewart, 1998; Siegel & Allan, 1998; Skowbo, 1986). As emphasized by Humphrey (1998), one problem with the debate is that it appears that the terms and concepts of the conditioning account are quite flexible and can seemingly be accommodated to diverse findings. Such flexibility makes it very difficult to propose crucial experiments that could potentially show the account to be false.

Classical conditioning is not the only type of associative model to have been proposed for the ME. Notably, Barlow (1990; Barlow & Foldiac, 1989) suggested a decorrelation model[1] in which the ME would result from an increase in inhibition between units coding colour and units coding orientation. Roughly speaking, the McCollough effect could be explained as follows. During the induction phase, when a vertical black and red grating is shown, neurons coding redness and neurons coding verticality are activated simultaneously, and the strength of the mutual inhibition between these neurons increases. In the test phase, when a vertical black-and-white grating is shown, the "verticality" neurons inhibit the redness neurons, so the lack of redness biases the output of the colour system towards green. According to Barlow (1990, 1997), the dynamics of mutual inhibition between colour and orientation would be a specific case of a more general principle called the "law of repulsion". It states that when two stimuli (in the same modality of sensation and/or in similar regions of the sensory field) frequently occur together, their representations in the brain repel, meaning that one representation discourages or inhibits the other so that each is weaker than when presented alone. It is supposed that the degree of repulsion is constantly modifiable ("anti-Hebbian" rule) and therefore represents the average strength of the association between the two stimuli over some period in the past. We agree with the valuable assumption that the ME could be a particular outcome of a more general principle of neural signal decorrelation. However, this assumption was not quantitatively specified sufficiently and was not confronted with detailed simulations.

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[1]Dodwell and Humphrey (1990) proposed a model of the ME close to Barlow's. In relation to the adaptation level principle of Helson (1964) and the error correcting device mechanism of Andrews (1964), Dodwell and Humphrey suggested that the ME plays a role in adjusting the internal representation of the world to conform with the statistical properties of the environment. In perceptual environments, correlations between colour and orientation are usually zero. In the ME, colour and orientation are highly correlated. The model assumes that the ME is generated because the zero correlation between colour and orientation that exists in the long run is violated. To maintain the internal representation of the long run correlation between the two dimensions to zero, the visual system recalibrates by decorrelating colour and orientation.

AIM OF THE RESEARCH

In an earlier study (Ans, Hérault, & Jutten, 1985; Hérault & Ans, 1984), we introduced an adaptive neural network able to extract statistically independent sources, a priori unknown, from a set of multidimensional input patterns. Our neural model had basic principles and general objectives similar to that of Barlow (1990; Barlow & Foldiac, 1989). The latter was widely explored in the framework of brain cognition, whereas our model (initially oriented towards neural decoding) was developed in the framework of source separation in signal processing and in particular initiated a new procedure of data analysis: the Independent Component Analysis (Charkani & Hérault, 1995; Hérault & Jutten, 1986; Jutten, Hérault, & Comon, 1991). However, what essentially distinguishes the two approaches is that Barlow uses a *decorrelation* principle of neural signals, whereas we use a more constraining principle of *independence* (indeed, two uncorrelated entities are not necessarily independent). Barlow and colleagues had the promising idea of linking together the decorrelation principle and the ME. Starting from this idea, we propose in the present paper, using the synaptic plasticity rule proposed by Hérault and Ans (1984), a detailed neural network simulation of the ME that, despite its minimal complexity, reproduces various experimental results, such as the tilt effect contingent to colour and the temporal resistance of the ME. As we will show, this later property, a rather distinctive feature of the ME, cannot result from a simple decorrelation principle.

THE MODEL

The neural network architecture (Figure 1) is composed of a set of colour units and a set of orientation units. Each colour unit is connected to all orientation units, each of them being in turn connected to all colour units. There is no intra connection within the two sets. The input patterns are composed of two parts, a colour part and an orientation part. Here the colour input has only a red (R) and a green (G) component, which specifically connects the corresponding colour unit (fixed weight equals one). The colour input is supposed to originate from an opponent colour system so that the red and green input components cannot be simultaneously active. The colour of an external stimulus is simply characterized by a given amplitude (ranging from 0 to 1) of only one of the colour components. In simulations a red stimulus will be coded by ($R = 1$, $G = 0$) and a green one by ($R = 0$, $G = 1$).

The components of the orientation input pattern are assumed to originate from filters tuned to specific orientations. To perform simulations, one preferred orientation component was chosen for each 10 degrees, ranging from $-80°$ to $90°$, with a gaussian response (maximum 1, half-height bandwidth $25°$). The orientation input pattern therefore has 18 components, the vertical
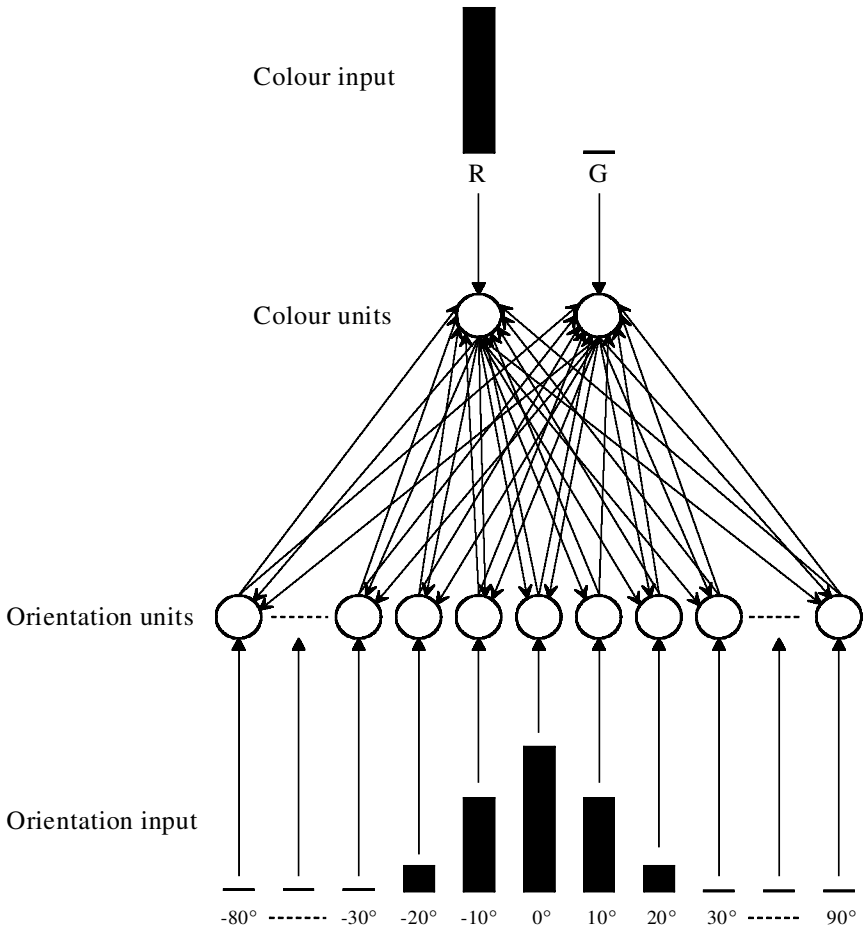
Figure 1.   Neural network architecture underlying the McCollough effect in which the input pattern corresponds to a red vertical grating.

and horizontal components being respectively coded by 0° and 90° (negative value coding for orientations tilted to the left of the vertical). As for colour components, each input orientation component specifically connects the corresponding unit (fixed weight equals one) of the 18 orientation units of the network. For example, Figure 1 shows the input pattern corresponding to a red-vertical stimulus.

There are a total of 20 processing units that are numbered from 1 to 20. The first two units ($i = 1, 2$) are colour units and the other ($i = 3, 4, …, 20$) are orientation units. Similarly, for an input pattern, denoted $P = (p_1, p_2, p_3, …, p_i, …, p_{20})$, the first two components p_i are the colour components and the others are the orientation ones. When an input pattern P is presented to the network, the induced

activity of each unit i, denoted o_i, is computed in the following way. The activation of the unit i, denoted a_i, is first computed as:

$$a_i = p_i + \sum_{j \in C} w_{ij} o_j \tag{1}$$

where w_{ij} represents the connection weight from unit j to unit i, the weighted sum runs over the set C of units j that are connected to unit i. In fact, if the unit i is of colour type, then C is simply the set of orientation units, and conversely. The effective output activity o_i of each unit i is a non-linear function of its activation (see Figure 2):

$$o_i = \sigma(a_i) \quad \text{with } \sigma(a_i) = 0 \text{ for } a_i < 0 \quad \text{and } \sigma(a_i) = 1 - e^{-a_i} \text{ for } a_i \geq 0 \tag{2}$$

The output activity of the network has to be computed recursively until its activity stabilizes. In practice, while maintaining the current specific input pattern, 30 recursive computation steps are used for calculating the stabilized activity induced by the input. The resulting stabilized output activity of each unit i, which is induced at time t by a given input pattern $P(t)$, is denoted $o_i(t)$.

Each time t a pattern $P(t)$ occurs, each network connection weight $w_{ij}(t)$ from unit j to unit i is modified according to the following adaptive rule:

$$\Delta w_{ij}(t) = -\alpha o_i^3(t) \, [o_j(t) - \hat{o}_j(t)] \tag{3}$$

where α is the adaptation rate parameter and $\hat{o}_j$ denotes an estimate of the mean value of o_j, calculated as:
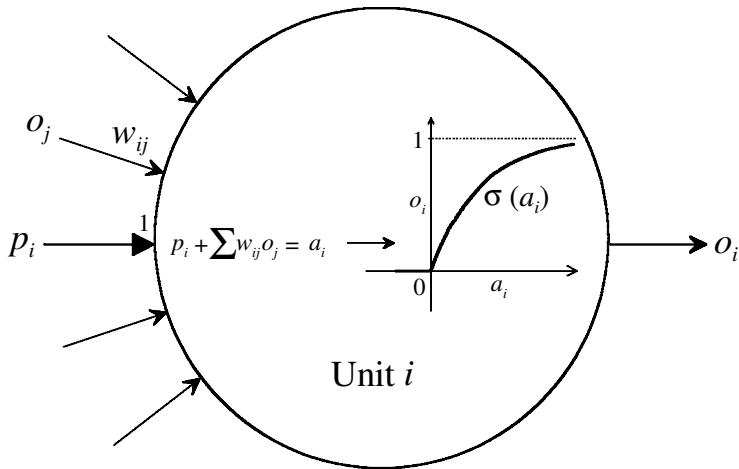

Figure 2.   A network processing unit i, where p_i is a specific component of a given input pattern (fixed connection weight = 1), o_j are the inputs from the other processing units (with modifiable weights w_{ij}), a_i is the unit i activation (weighted sum of all its inputs), o_i is the resulting unit output activity computed as a non-linear function σ of its activation ($o_i = \sigma(a_i)$).

$$\hat{o}_j(t) = \hat{o}_j(t-1) + \tau[o_j(t) - \hat{o}_j(t-1)] \tag{4}$$

Expression (4) is formally a low-pass filter with a time constant τ of the pre-synaptic activity. Hence the pre-synaptic part in (3) is a high-pass filter. In all simulations the two parameter values will be taken as: $\alpha = 10^{-3}$ and $\tau = 0.1$. The adaptive rule (3) is a variant of a rule originally introduced by Hérault and Ans (1984) that was used for extracting independent sources from a set of multidimensional neural patterns (in the original version, the pre-synaptic part of the rule was a sigmoid function of the high-pass filter, a function unnecessary for the present study). Expression (3) is roughly an anti-Hebbian rule (minus sign), except that the post-synaptic part is a non-linear function of the unit output activity. It will be shown below that the account of this non-linearity is essential to reproduce the persistence in time of the ME aftereffect.

SIMULATIONS

The McCollough effect

Two inducing input patterns are considered: the red-vertical input (R, $0°$), as depicted in Figure 1, and the green-horizontal input (G, $90°$), that is, $(R = 0, G = 1)$ with its orientation part of the same form as that in Figure 1, except that it is centred on the $90°$ component. These two patterns are alternatively presented to the network during the induction period. For each presentation, and after the network activity has stabilized, the modifiable connection weights (initially set to zero) are updated according to the adaptive rule (3). Once the induction phase is completed, two test patterns are presented to the network: either the achromatic-vertical (A, $0°$) or the achromatic-horizontal (A, $90°$) input, the achromatic nature of these patterns being coded by $(R = 0, G = 0)$. After an induction time $t = 5000$ (this same induction time, evaluated in an arbitrary time scale, will be used in all simulations), the colour output of the network is $(R = 0, G = 0.189)$ in response to the (A, $0°$) test pattern, and symmetrically the colour output is $(R = 0.189, G = 0)$ for the (A, $90°$) test pattern. If it is considered that before the induction phase the maximum activity reached by a unit is 0.632 (since in expression (2), $\sigma(1) = 1 - e^{-1} = 0.632$), then the colour aftereffect that emerges from the network in test is equal to roughly 30% of the maximum colour value. So, after induction, the emergent "illusive" colour may be called rather "greenish" (or "reddish"). McCollough (1965) reported that the ME decreases as the orientation of the achromatic test grid moves away from the inducing orientation and finally vanishes when the orientation test reaches $45°$. Corresponding simulations performed with the network account also for this vanishing phenomena (Figure 3).
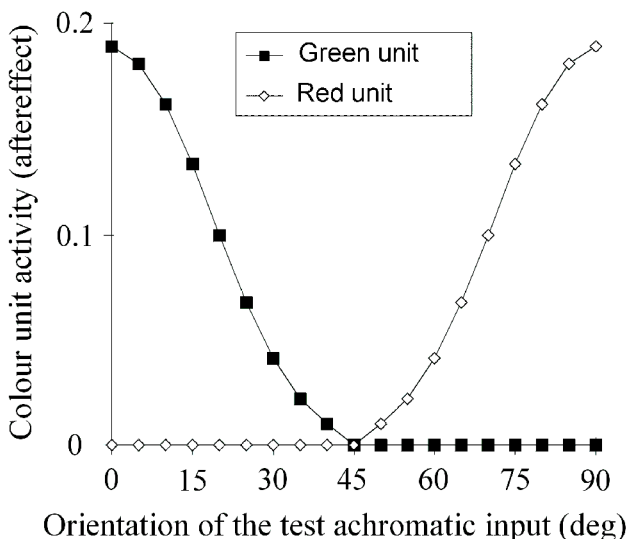
Figure 3.   Simulation of the ME variation as a function of orientation of the test achromatic input.

Temporal resistance of the McCollough effect

An essential feature characterizing the ME is its persistence with time. To high-light this temporal resistance the network, once adapted, has next to be faced with input patterns reflecting a continually changing ecological environment. To simulate a desadaptation phase with this goal in mind, it is supposed simply that the input pattern components come from filters sharing a receptive field that contains contours whose colour and orientation change randomly with time. For the colour input part (which was earlier considered as coming from an opponent colour system) the only active component at a given desadaptation time t is taken at random with probability .5. The magnitude of the selected col-our component is also taken at random according to a normal law. With regard to the orientation input part, a cluster of three orientations is considered as potentially occurring in the receptive field at each desadaptation time t, every one being randomly selected between $-90°$ and $90°$ uniformly. The three ele-mentary responses of the gaussian filters corresponding to the three selected orientations are weighted by a random factor according to a normal law, which amounts to taking into account one, two, or three more or less blurred edges occurring by chance in the receptive field. Finally, the orientation input pattern that actually activates the network is the average of these three weighted filter responses. For both the colour and the orientation parts of the de-adapting input patterns, the random magnitudes are computed using the same normal law (mean = 0.2, standard deviation = 0.1), rejecting generated values that are nega-tive or greater than one.

After the adaptation period the network is then faced with the above desadaptation process. In Figure 4a the variation of the green colour unit activity, in the course of the desadaptation phase, is plotted at regular time intervals when the network is tested with the achromatic-vertical input pattern. It is observed that, from its adaptation value ($G = 0.189$), the magnitude of the aftereffect decreases very slowly with time and vanishes at $t = 18.10^5$, which corresponds to 360 times the induction time ($t = 5000$). Obviously, the same holds true for the slow decrease of the red colour aftereffect when the network is tested with the achromatic-horizontal input pattern in the course of the desadaptation phase. A high temporal resistance therefore emerges from the model. Once desadaptation is completed, all the modifiable connection weights within the network are close to zero, which is consistent with the zero initial value that was taken for the connection weights before the induction period. Indeed, before induction, the network has to be initially considered as simulating a living visual structure previously faced with input patterns reflecting a continually changing ecological environment.

As emphasized earlier, the adaptive rule (3) governing the connection weight plasticity has a non-linear post-synaptic part. As one could wonder about this assumption, it is well-advised to check the neural system behaviour when the post-synaptic part of the adaptive rule is taken as linear, that is, simply replacing in expression (3) the post-synaptic factor $o_i^3(t)$ by $o_i(t)$, which is written:
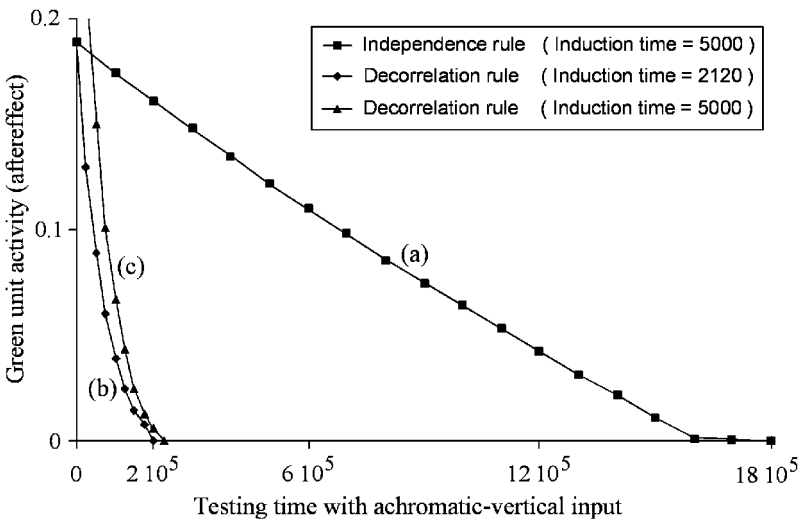

Figure 4.   Simulation of the ME decreasing (green unit activity, for example) in the course of the desadaptation period as a function of testing times with an achromatic-vertical input. (a) Case in which adaptation was previously performed using the independence rule (induction time = 5000). (b) Adaptation with the decorrelation rule (induction time = 2120). (c) Adaptation with the decorrelation rule (induction time = 5000).

$$\Delta w_{ij}(t) = -\alpha\, o_i(t)\,[o_j(t) - \hat{o}_j(t)] \tag{5}$$

Expression (5), which is in its principle similar to the rule used by Barlow (1990; Barlow & Foldiac, 1989), tends to generate uncorrelated network outputs, whereas the rule (3) used in this paper tends to produce independent outputs which is a more constraining task: independent entities are inevitably decorrelated but the reverse is not necessarily true. The decorrelation rule (5) tends to annul a two-order moment whereas the independence rule (3) tends to annul *all* the two-, three-, and four-order moments. When the adaptation period is performed using the same parameters but with the decorrelation rule a similar aftereffect is still observed. However, an essential difference appears in the temporal persistence of the aftereffect. To compare the desadaptation durations obtained with the two rules, the induction period using the decorrelation rule is stopped at the time ($t = 2120$) when the magnitude of the colour aftereffect reaches the same value (0.189) as that obtained with the independence rule. It was also verified that for this same aftereffect magnitude, the connection weights induced by one rule were very close to those induced by the second. Figure 4b shows that the temporal resistance of the aftereffect related to the decorrelation rule *is much shorter* than that observed in Figure 4a which is related to the independence rule. A control simulation was also performed with the decorrelation rule for which the adaptation time was the same as that taken in all simulations with the independence rule ($t = 5000$). At the end of the induction period the aftereffect magnitude was equal to 1.71 times the above reference value (0.189) and the induced connection weights were also higher in the same ratio. The time course of the subsequent desadaptation phase (Figure 4c) was virtually as short as that in Figure 4b. Although the comparison between the two rules can now be made with exactly the same parameters, it must be noticed that this comparison is however very unfavourable for the independence rule. Indeed, in Figure 4a the desadaptation process starts with an aftereffect amplitude and connection weights which are lower than those related to Figure 4c. It is therefore manifest that the adaptive independence rule is more suitable than the decorrelation rule to account for the distinctive temporal resistance of the ME.

However, as shown by Skowbo et al. (1975) and Stromeyer (1969), it is possible to considerably reduce the desadaptation duration, which can be even shorter than the adaptation duration, if it is presented to the subjects colour-orientation patterns that are the inverse of the inducing patterns. In simulations, once adapted on the (R, 0°) and (G, 90°) inputs as previously, the desadaptation period now consists in presenting to the network the (R, 90°) and (G, 0°) input patterns alternatively. Simulation results (Figure 5) show that the desadaptation time is actually slightly shorter than the adaptation duration and, in any case, much shorter than that related to the desadaptation process performed with input patterns reflecting a continually changing ecological environment (Figure 4a).
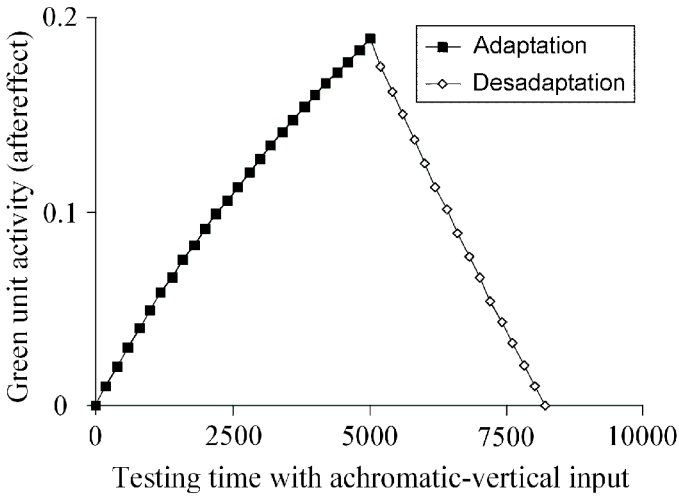
Figure 5. Simulation comparing adaptation and desadaptation durations when desadaptation is induced by alternating colour-orientation inputs (red-horizontal and green-vertical) that are the reverse of the alternating inducing inputs (red-vertical and green-horizontal). As in Figure 4, the magnitude of the aftereffect (green unit activity, for example) is plotted as a function of testing times with an achromatic-vertical input.

A reverse aftereffect: From colour to orientation

An interesting aftereffect from colour to orientation was reported by Held and Shattuck (1971). In an inducing period, subjects were presented with red stripes tilted clockwise off vertical and green stripes tilted equally but counterclockwise. Next, in the testing phase, vertical stripes appeared tilted counterclockwise when red but clockwise when green. As the angle between induction stripes and the vertical test stripe was increased from $0°$ to $75°$, the magnitude of the tilt aftereffect rapidly increased to a peak between $10°$ and $15°$ and then dropped close to zero at about $40°$. In order to show that these aftereffects, from colour to orientation, could in fact originate from the same process at the root of the basic ME (from orientation to colour), we performed the corresponding simulations on the same network accounting for the ME (same input coding and parameters). An induction phase, for a given angle θ on both sides of the vertical, consists of presenting alternatively to the network the input patterns corresponding to $(R, +\theta)$ and $(G, -\theta)$, with the same θ during the induction time $t = 5000$. Next, a red-vertical (or a green-vertical) input pattern is presented to the network in test and a tilt indicator, denoted S, that combines the activity of the $0°$ orientation unit and the activities of its two adjacent orientation units (i.e., the $-10°$ and $+10°$ units) is computed. More formally, if o_{-10}, o_0 and o_{10} denote respectively the output activities in test of the $-10°$, $0°$ and $+10°$ orientations units, then the tilt indicator S is computed as:

$$S = 60 \, (-10°. \, o_{-10} + 0°. \, o_0 + 10°. \, o_{10}) \, / \, (o_{-10} + o_0 + o_{10}) \qquad (6)$$

It is reasoned that the barycentre tilt indicator S should reflect a stimulus appearing tilted clockwise when $S > 0$, tilted counterclockwise when $S < 0$, and vertical when $S = 0$. The multiplicative factor 60 is here introduced to convert degrees in minutes of arc.

The different induction periods, each of them with a given pair of adapting input patterns $(R, +\theta)$ and $(G, -\theta)$, are performed over the network for $\theta = 0°$, $5°$, $10°$, $15°$, $20°$, $25°$, $30°$, $40°$, $50°$, $60°$, and $75°$. When the red-vertical input pattern is presented in test after each induction phase, the corresponding tilt indicators $S(\theta)$ have values that are negative or null, hence reflecting a stimulus appearing tilted counterclockwise. Conversely, for the green-vertical input test, the corresponding $S(\theta)$ tilt indicators have the same magnitudes as in the preceding case but with their signs inversed (i.e., positive or null values) reflecting the appearance of a stimulus tilted clockwise. These colour-to-orientation aftereffects are therefore compatible with those obtained on human subjects. In Figure 6, the different values of $S(\theta)$, computed in the case of a green-vertical input test, are plotted as a function of the angle θ taken in each induction period. The corresponding aftereffect magnitudes related to two human subjects are also plotted for comparison (experimental data expressed in minutes of arc, adapted from Held & Shattuck, 1971).
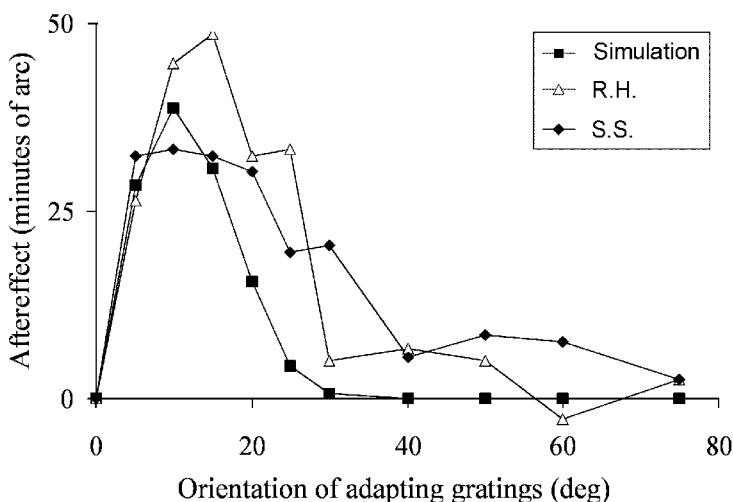

Figure 6.   Aftereffect magnitude, from colour to orientation, as a function of the orientation of adapting gratings. Comparison is made between model simulation and human experimental results (two participants RH and SS; adapted from Held & Shattuck, 1971).

DISCUSSION

The aim of our research was to show that a general adaptive neural process which tends to extract independent dimensions in visual perception could account for the ME. The neural system, of minimal complexity, works with only two parameters that can be chosen within a wide range without altering its basic behaviour. The number of orientation filters, their tuning values and bandwidths, are not critical and can be chosen within any reasonable range. Nevertheless, the model has the ability to reproduce a set of various experimental results, some very accurately as the above reverse aftereffect, and especially accounts for the long temporal resistance of the ME that is one of its main distinctive features not yet explained in literature.[2]

Since McCollough (1965), various extensions of the ME have been reported, notably the possible manifestation of a colour aftereffect on a non-inducing grating orthogonal to the inducing grating, referred to as the "indirect McCollough effect" (IME) by Dodwell and Humphrey (1990). For example, it has been found that viewing a red-vertical grating alternating with a green homogeneous field, not only produces the ME on a vertical achromatic grating, but also produces a colour aftereffect on a horizontal non-inducing achromatic grating: The horizontal grating appears pinkish (IME). Can our model account for the IME? The adaptive rule (3) requires a variation on both colour and orientation during adaptation to produce an aftereffect, whereas in the IME there is only one inducing orientation. One way to obtain an orientation variation in the IME is to postulate that during adaptation, orthogonal orientation to that of the inducing grating is present one way or another. Let us simply underline that this assumption fits in with the explanation of the IME proposed by Humphrey, Dodwell, and Emerson (1989; see also Dodwell & Humphrey, 1990; Humphrey et al., 1998). Here, the authors suggest that orientation coding acts in an opponent manner somewhat analogous to that of colour (see Campbell & Maffei, 1971; Heeley, 1979; MacKay, 1961, for experimental arguments of such a functional eventuality). When a subject fixates on a grating at a certain orientation, neural mechanisms that respond fully to that orientation become fatigued, as do mechanisms that code for colour. When the grating is removed, the opponent process serves to create a relative increase in signals from mechanisms that respond fully to a grating at an orthogonal orientation, thus creating an antagonistic rebound at the orthogonal orientation. For the authors, this orthogonal rebound is paired with the complementary coloured homogeneous field that is alternated with chromatic grating and could serve as the basis of the IME induction. If in the model we assume that this orthogonal orientation

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[2]Von der Malsburg's feature-extracting neural network was extended and applied to the McCollough effect by Montalvo (1976). Though this model used a set of 11 parameters, no attempt was made to account for the long persistence of the aftereffect and the reverse effect.

rebound emerges during the inducing period in the form of a weak amplitude input, then we are placed in the case of the classical ME except that the indirect aftereffect produced by this virtual input will be less than the direct one. In short, our model does not explain the IME *per se*, but it highlights some constraints consistent with explanations proposed in literature.

What is at the root of the ME in our neural model? To understand this aftereffect better, it is sufficient to consider only the vertical and horizontal components of orientation input patterns, components respectively noted V and H later. In this simplified case, the two considered inducing input patterns (red-vertical) and (green-horizontal) can be respectively expressed as $[R = 1, G = 0, V = 1, H = 0]$ and $[R = 0, G = 1, V = 0, H = 1]$. During induction, where these two inducing input patterns are alternatively presented to the network, the components R and V (respectively G and H) are *positively* correlated, whereas R and H (respectively G and V) are *negatively* correlated. Because of its minus sign, the adaptive rule (3) (or the rule (5)) will tend to *decrease* connection weights between unit activities positively correlated and to *increase* weights between negatively correlated activities. Since the induction period starts with null connection weights, the weights w_{RV} and w_{VR} (respectively w_{GH} and w_{HG}) will become negative (corresponding to *inhibitory* connections) and the weights w_{RH} and w_{HR} (*respe*ctively w_{GV} and w_{VG}) will become positive (corresponding to *excitatory* connections). This induced connectivity is schematically represented in Figure 7a. After the induction period, when a test pattern is presented, say the (achromatic-vertical) input = $[R = 0, G = 0, V = 1, H = 0]$, it is easy to realise in Figure 7b that the green unit alone will be positively activated by the input pattern, the red unit being inhibited, hence silent. In the same way, the achromatic-horizontal input would activate the red unit alone. This constitutes the basic process proposed to understand the ME.

Barlow (1990; Barlow & Foldiac, 1989) claimed that a principle of mutual inhibition between dimensions, which he called the "repulsion law", was at the root of the ME. This originates from the fact that, in the model proposed by Barlow, it is implicitly assumed that each dimension is coded by only one unit: one unit for the different real-valued magnitudes taken by the colour dimension and one unit for the real-valued magnitudes of the orientation dimension. In this case, it is indeed possible to account for the ME in terms of mutual inhibition between units coding dimensions. However, we think that it is more neurobiologically realistic to consider that the different values of a same dimension are respectively coded by a number of *distinct* tuned units, as commonly described in visual perception literature. In this case, and as shown earlier, it is rather the mutual excitation process (that we could call the "attraction law"), and not the "repulsion law", that induces the ME. On the other hand, though the ME could in fact be obtained in the framework of this attraction principle, when using the linear decorrelation rule (5) similar to that used by Barlow, it is worth noting that of the two rules discussed, it is only the
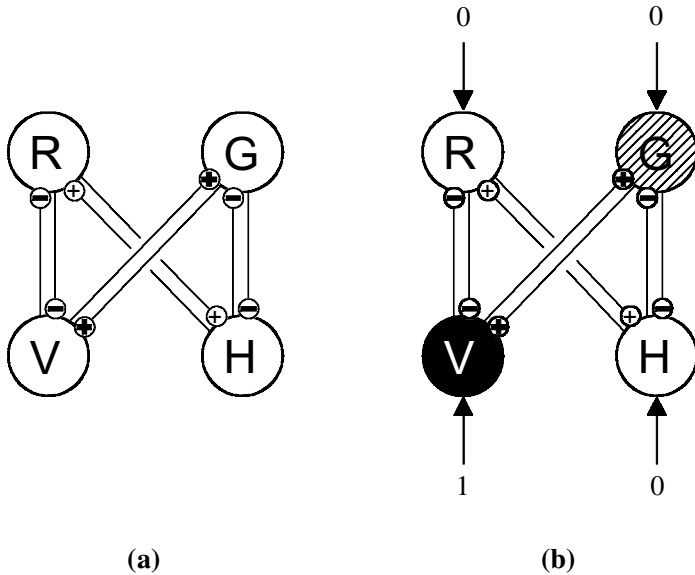
(a)   **(b)**

Figure 7.   Outline of the basic principle of the model. (a) Once the adaptation period is completed, the mutual connection weights between colour and orientation units, *jointly* activated during adaptation, had become inhibitory. On the other hand, the mutual connection weights between colour and orientation units, *alternatively* activated during adaptation, had become excitatory. (b) When the achromatic-vertical input is subsequently presented in test, only the green unit will be positively activated by the excitatory link, hence simulating the basic McCollough aftereffect.

non-linear independence rule (3) that is able to account for the long temporal resistance of the aftereffect. Non-linearity should not be viewed as a stronger assumption than the linear one because non-linearity is the rule rather than the exception in living systems. In fact, linearity is easier only for mathematicians.

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