



Cortical communication and the comparison of colors

John Mollon¹ and Marina Danilova^{1,2}

The hues or the colorimetric purities of a pair of colored targets can be compared with similar precision whether the targets are juxtaposed or fall at well-separated positions in the visual field. This is the case even if the stimuli are 10° apart and fall in opposite hemifields. What could be the neural processes that underlie such comparisons? We are led to ask whether the long-range, white-matter tracts of the brain constitute a *neural net* (where representations are embodied in the weightings and signs of connections between the nodes of the net) or a *communication network* (where the same physical substrate carries different information from moment to moment).

Addresses

¹ Department of Psychology, University of Cambridge, Downing St., Cambridge, CB2 3EB, United Kingdom

² I. P. Pavlov Institute of Physiology, Russian Academy of Sciences, nab. Makarova 6, St. Petersburg, 199034, Russia

Corresponding author: Mollon, John (jm123@cam.ac.uk)

Current Opinion in Behavioral Sciences 2019, **30**:203–209

This review comes from a themed issue on **Visual perception**

Edited by **Hannah E Smithson** and **John S Werner**

For a complete overview see the [Issue](#) and the [Editorial](#)

Available online 7th November 2019

<https://doi.org/10.1016/j.cobeha.2019.10.002>

2352-1546/ 2019 Elsevier Ltd. All rights reserved.

Introduction

In most people's lifetime, there is at least one happy period when they are refurbishing a house or apartment. A common domestic task at such times is that of matching colors using a swatch of samples of paint, fabric or carpet. Sometimes it is physically possible to superpose the sample on the surface being matched, but sometimes it is physically difficult to bring the two together. How precisely and how accurately can we match or discriminate colors? And does our discrimination deteriorate when the two stimuli lie at a distance from one another in the visual field?

The first of these questions has been intensively studied, and there exist well-honed formulae to predict the visibility of color differences for practical purposes [1*]. A fundamental finding, for example, is that discrimination is finest when the discriminanda are close in chromaticity to that of the illumination to which one is adapted. But the second question — the effect of spatial separation — is only

occasionally discussed [2,3*,4]. It is on this latter issue that we concentrate here. Our psychophysical results lead us to ask what kind of network is the brain and what protocols govern transmission over the white matter tracts that connect different cortical areas. There is strong current interest in the 'connectome' [5*,6,7], but there is relatively little recent discussion of the distinction we make here between a *neural net* and a *communication network*.

The comparison of colors at a distance

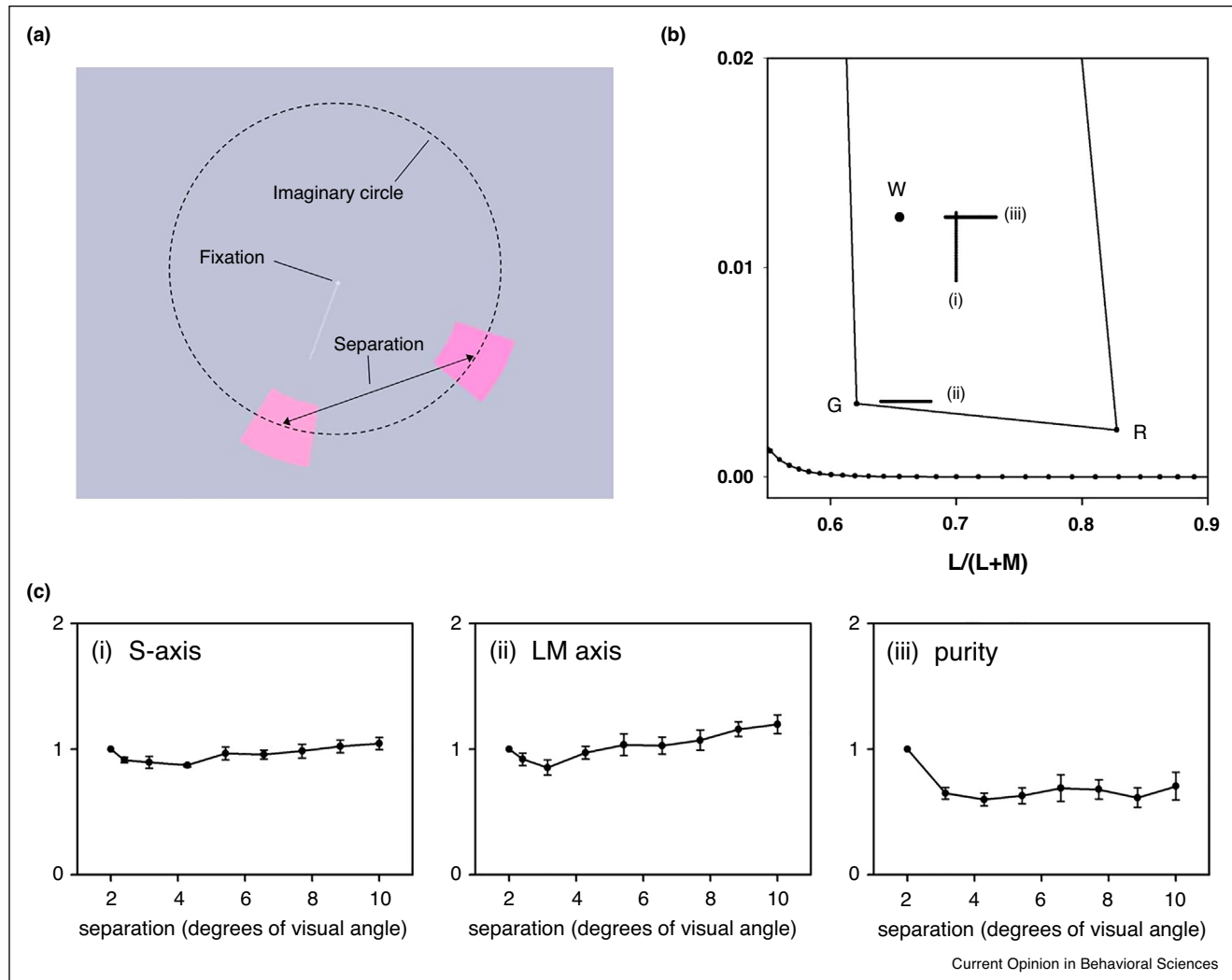
In the case of luminance, discrimination is optimal when the discriminanda are touching one another and it deteriorates quickly as the stimuli are separated in space [4,8]. Yet this is not always the case for color.

Figure 1 shows results from experiments in which the discriminanda varied along different axes of color space [3*,9]. Panel (a) illustrates the arrangement of stimuli. The participant is adapted to a steady white field. In order to hold eccentricity constant while the separation of the stimuli is varied, the stimulus patches are sectors of an annulus, and their midpoints lie on an imaginary circle of radius 5° of visual angle. The patches are 2° wide at their midpoints and are brief (<200 ms) — too brief for a saccade from one to the other. A concurrent white marker indicates which patch is to be reported, relative to the other. In different blocks of trials, the spatial separation of the patches can vary from the case where they are touching to the case where they lie 10° apart on opposite sides of the fixation point. However, although separation is held constant within a block, from trial to trial the yoked positions of the two patches fall at random places on the imaginary circle.

An adaptive psychophysical procedure is used to measure the difference in chromaticity that allows the patches to be discriminated with a probability of 79.4% correct [3*]. To ensure that the participants do actively compare the two stimuli (rather than making absolute judgments of just one of them), there is not a fixed reference chromaticity. Rather, the reference chromaticity is jittered over a range that is large relative to the threshold; and what is adjusted by the adaptive procedure is the factor by which the variable stimulus differs from the reference.

In three separate experiments we used discriminanda that varied in different directions of color space. The first two cases were for discrimination of hue: (i) The excitation of the short-wave (S) cones was varied while the ratio of excitation of the long-wave (L) and middle-wave (M) cones was held constant; and (ii) The excitation of the S cones was held constant, while the relative excitation of L and M cones ($L/(L + M)$) was varied.

Figure 1



(a) Typical stimulus arrangement for our experiments. The participant fixates a central white dot, and the target patches – the ‘discriminanda’ – fall on an imaginary circle of diameter 10° . A white bar marker, concurrent with the discriminanda, indicates which patch is to be judged as, say, ‘more saturated’. **(b)** A local region of a MacLeod-Boynton chromaticity diagram [10]. The ordinates of this diagram are thought to correspond to two physiological signals – cone ratios – extracted at an early stage of the visual system [30]. ‘G’ and ‘R’ indicate the green and red phosphors of the display, and the dotted line shows part of the spectrum locus. The vertical and horizontal lines marked (i)–(iii) indicate the approximate ranges of chromaticities tested in the three experiments. The present diagram is strictly schematic, since different white points were used in the different experiments (Equal-energy white versus Illuminant D65) and since chromaticity was jittered within ranges that were chosen on the basis of preliminary measurements for each participant. **(c)** The separate panels show the relationship between normalized threshold and the spatial separation of the two patches. The left and middle panels show results for hue discrimination along lines parallel to the vertical (i) and horizontal (ii) ordinates of the MacLeod-Boynton diagram; and the right-hand panel shows results for purity discrimination along an axis where the ratio of long-wave to middle-wave cone excitation is varied (iii). The data are averaged across participants and the error bars represent standard errors based on between-subject variance. To allow comparison of the different axes, the thresholds in each case are scaled relative to the threshold when the edges of the discriminanda are touching.

The third data set (iii) was for variation in colorimetric purity along a line radiating from the white point and increasing in the ratio L/M , with short-wave excitation held constant. (The subjective correlate of colorimetric purity is saturation.)

The schematic MacLeod-Boynton chromaticity diagram [10] of Figure 1b shows the approximate ranges of

chromaticities used in the three experiments: The vertical and horizontal lines marked (i), (ii) and (iii) correspond to the three types of variation described above.

Figure 1c shows the measured thresholds, scaled so that the value is 1.0 when the stimulus patches are touching, that is, when their midpoints are separated by two degrees of visual angle. The three data sets all tell a similar story: Thresholds

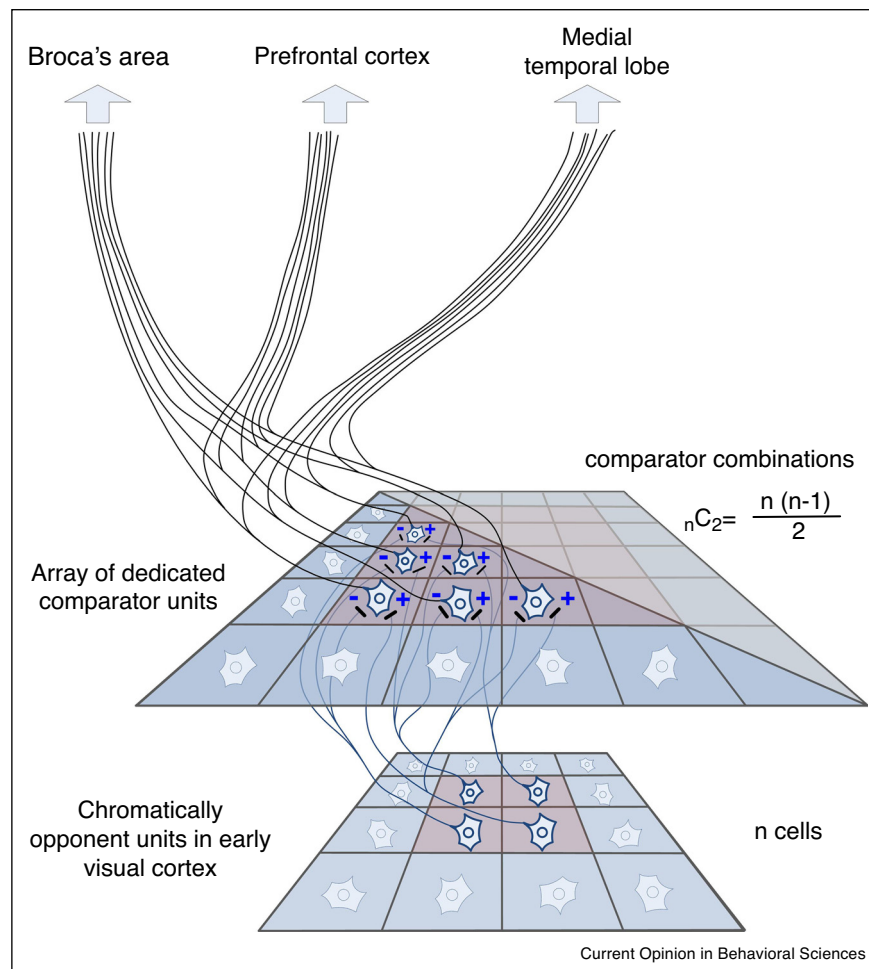
deteriorate very little as the stimuli are increasingly separated up to ten degrees of visual angle (even though in the latter case, they often fall into opposite hemifields.) In all three data sets, to a greater or lesser extent, discrimination is better at a small separation than when the discriminanda touch each other, a result that recalls a similar phenomenon observed in foveal vision [2,11] (This 'gap effect' is to be distinguished from the 'gap effect' discussed in the literature on oculomotor saccades.)

It turns out that there are several other visual attributes (e.g. speed, spatial frequency) that similarly can be discriminated with almost equal accuracy whether they are juxtaposed or are 10° apart [3*]. What could be the anatomical basis for such performance?

Dedicated neural comparators?

In the case of luminance, where discrimination does deteriorate rapidly with separation, we may suppose that the observer relies on a local difference signal originating in a cell with a center-surround receptive field, a cell that draws opposed excitatory and inhibitory signals from nearby regions of the visual field. But it is difficult to imagine that discrimination of stimuli at any two arbitrary positions in the field is mediated by an array of dedicated comparator neurons of this kind. Such 'dipole operators', with two, separated receptive fields, have occasionally been postulated [12], and in Figure 2 we sketch a model of this kind. As an explanation of the results considered above, such a model faces a number of problems:

Figure 2



A model in which discriminations are performed by dedicated 'comparator units'. At the lower level, representing early visual cortex, chromatically opponent cells draw their inputs from local areas of the visual field. At the second level, there is a dedicated comparator unit for each possible pairing of cells at the first stage. Each comparator unit draws opposed excitatory and inhibitory inputs from the paired lower-order cells. So for n cells at the lower level, $(n(n-1))/2$ comparators are required (and the matrix of comparators would need to be doubled if only positive ratios are signaled by each comparator — as is usually assumed to be the case for midget ganglion cells in the retina). A further array of dedicated projections is then needed to convey the results of the comparison forwards to other parts of the cortex that might need the information.

- (a) There is a combinatorial explosion in the number of dipole operators required to accommodate all possible pairings within the visual field. And separate arrays of dipole operators would be needed for (a minimum of two) dimensions of chromaticity, as well as several other dimensions, such as speed and spatial frequency. It might be objected that receptive fields become larger in more anterior parts of pre-striate cortex and so discrimination might be based on the responses of such cells. This is unlikely. If a neuron is to subserve one of our comparison tasks, it is not enough that it should integrate inputs for a given sensory attribute over a large area. Rather, it must signal the difference, or the ratio, of the values of the attribute in two, specific, local, and arbitrarily chosen patches of its receptive field; and it must preserve the sign of the difference. Thus far, chromatically-specific neurons with such properties have not been described in pre-striate cortex.
- (b) The many dedicated connections require a significant bulk of ‘wiring’ — myelinated and unmyelinated axons; and the volume of wiring is known to be a critical constraint in the design of the brain [13].
- (c) Thirdly, there is what we term the problem of ‘junk mail’. (Unless some additional neural apparatus is postulated) the model requires each local hypercolumn in, say, V1 continuously to radiate signals about each sensory attribute to a large array of comparators — even though this broadcast information is only occasionally needed in the course of life. This is no way to run a brain, since every action potential is costly [14^{**},15].
- (d) Perhaps the deepest problem is an extension of (a). If the result of the comparison is embodied in the activity of a dedicated comparator unit, then — for each comparator unit — a further array of dedicated connections is required to carry the information forwards to any other part of the brain that might require it for the purposes of association, decision or response. This is a general — and seldom considered — problem with the hypothesis of gnostic units or grandmother cells: If words, faces, tools, concepts and comparisons are represented centrally only by the activity of dedicated neurons — an idea implicit in much of contemporary neuroscience [16,17] — then the information can be made available to other parts of the brain only by a large network of specific connections. The problem is not solved, and is possibly exacerbated, by assuming the traditional alternative to gnostic units — representation by a dedicated pattern of activity in a local ensemble of neurons: In the latter case, the distributed representation has itself to be carried forward by a projection of dedicated axons.

A communication network?

In the general class of models considered in the preceding section, the brain is taken to be a *neural net*, in the

sense this term is used in modern computer science. Individual nodes have a fixed response that depends on the signs and the weightings of their current connections. Although the latter are modifiable and although the ‘meanings’ of particular nodes may be difficult to interpret, especially in hidden layers, the response of a node is determinate for a given stimulus at a given time [18].

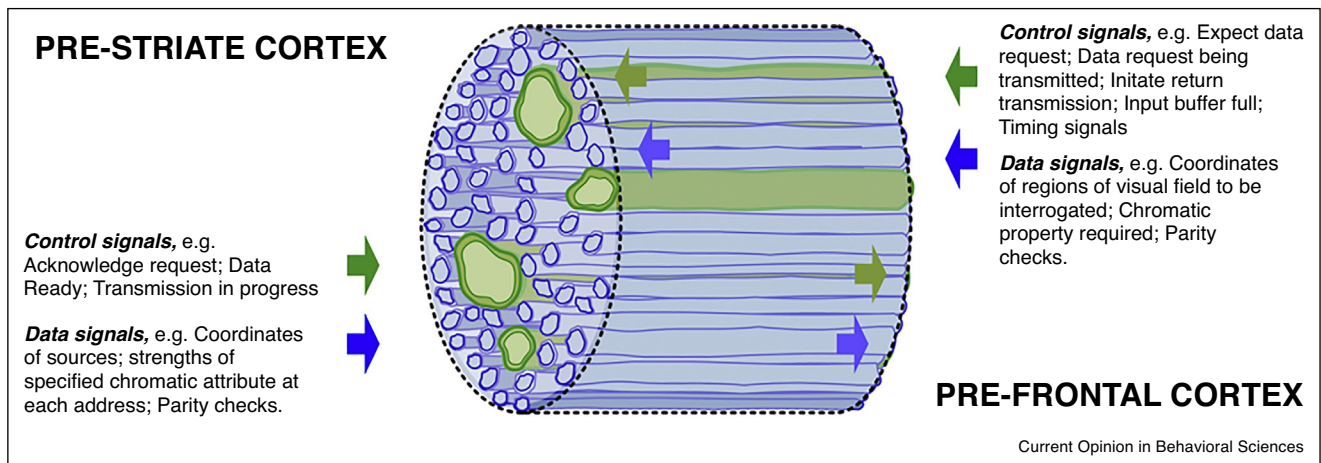
Neural nets may well offer a model for early stages of sensory analysis. But is the whole brain a neural net? The alternative is a *communication network* where the same physical substrate carries different information from moment to moment [19^{**}]. The manmade Internet offers such a model. In the case of the Internet, what are physically transmitted are ones and zeroes, but at any instant the local sequence of bits may represent a pixel, a number, an alphanumeric character or details of the source address, destination address and other control signals. Local cortical modules may resemble neural nets, but the required bandwidth of the intervening fasciculi would be vastly reduced if the fasciculi constituted a communication network. The distinction made in this essay, between two types of network, may be seen in the larger context of the classical debate between Connectionism and Symbolic AI [20].

As a communication network, the white matter of the human brain is likely to be very much more parallel in architecture than is the Internet. In modern man-made networks, fiber optics allow high-speed serial transmission. In contrast, since axonal transmission is slow and since action potentials are limited in the precision of timing and in their maximal frequency, the baud rate of an individual axon cannot be high. Our illustrative model of a neuronal communication network (Figure 3), is therefore based — very loosely — on the parallel architecture of a ‘Small Computer System Interface’ (SCSI). In many white-matter fasciculi, there is a distribution of axon diameters [21–23]. In our — strictly illustrative — model of a ‘cerebral bus’, we suggest that smaller fibers carry data, while the larger fibers carry control signals. Larger fibers have more rapid transmission and are energetically more costly [21]. Since they are also rarer, we tentatively suggest that they carry the simpler, but indispensable, ‘hand-shaking’ signals, such as ‘INPUT BUFFER FULL’. A cerebral bus, of course, will differ from even a SCSI bus in two important ways: The lines — the individual axons — are not bidirectional; and the data signals, at least, may well be analogue rather than digital.

The anatomical site at which colors are compared

Curiously, it is seldom asked where the comparison of colors is performed, that is, where is it that the internal

Figure 3



A cross-section of part of a 'cerebral bus'. This might be, say, part of the inferior fronto-occipital fasciculus, delivering information from different parts of the visual field to the prefrontal cortex. In all white-matter tracts there is range of axon diameters [23] and in this illustrative example (of what is a large generic class of models) we assign *Control* signals to the minority types of large axons, which have faster transmission, and we assign *Data* signals to the many smaller axons. *Control* signals subserve the 'handshaking' between transmitter and receiver that has been proved a necessary feature of almost all man-made communication networks [19**]. If in fact the larger axons do carry control signals, then a testable hypothesis might be that their signals are more stereotyped than those of the smaller, data-carrying axons.

representations of the two signals brought together and collated? If the decision depended on an array of dedicated comparator neurons in one of the pre-striate areas concerned with color and if the stimuli fall in opposite hemifields, then transmission across the corpus callosum would be necessary for one of the two signals; and so some degradation of that signal might be expected, relative to the case where both signals originate within one hemisphere. In fact, providing care is taken not to bias the observer's attention, the precision of comparison of hue is the same whether the discriminanda fall in the same hemifield or in opposite ones [24].

Our own suggestion is that encoded representations of separated stimuli are independently transmitted over a 'cerebral bus' to the prefrontal cortex of one or other hemisphere; and that it is only there that the two representations are collated and compared in the form of abstract codes. The inferior occipito-frontal fasciculus would be a candidate path to carry this chromatic information forwards [25]. Diffusion tensor imaging has shown that the inferior occipito-frontal fasciculus of each hemisphere contains not only a component that originates in the ipsilateral occipital lobe but also a second component that originates in the contralateral occipital lobe and passes through the posterior corpus callosum [26]. If in fact the representations of colors are collated in prefrontal cortex, then the number of synapses is the same, and transmission distance very similar, for between-hemifield and for within-hemifield

comparisons. So there is no reason to expect that one of the two signals in the inter-hemifield case might be subject to additional degradation or additional delay.

Questions that are not being asked about communication within the brain

If, as we suggest, the long-range white-matter tracts of the brain constitute a communication network rather than a neural net, then many interesting questions immediately offer themselves. The most prominent, of course, is the format in which information is being transmitted — the long-sought 'neural code'. But there are many other questions that an engineer might ask about a man-made communication network [19**]:

- (i) Is information transmitted only on request, as on the Internet? This would be, in essence, the basis for selective attention. The reason that brains are likely to adopt this arrangement — we suggest — is the raw cost of broadcasting unnecessary action potentials [14**,15].
- (ii) Is data transmission continuous or does it occur in fixed packets that might be sent by alternative routes, not only in case of damage to part of the network, but also during normal operation — as on the man-made Internet [27]?
- (iii) Are addresses encoded separately from data? Are for example, the two types of information transmitted by parallel fibers?

- (iv) What error checks are there to detect corrupted messages?
- (v) How is the speed of transmission matched to that of the receiver? Is the currently available buffer space signaled back from the receiver to the transmitter? Do pathologies arise from failures of control mechanisms of this and the previous type?

Some of these secondary questions might be tackled before the actual data code is understood. For example, if our hypothesis were correct, single-unit recording from the large axons of major fasciculi might reveal ‘control’ signals that are sparser and more stereotyped than the data signals carried by other axons. Histological examination of the terminations of the tracts might reveal structures that are analogous to the hubs of a man-made network. In this context, it is interesting that an unusual class of giant pyramidal cells have been described in layer III of the parastriate cortex at the terminations of callosal fibers [28]. It is here that the translations from one type of code to another may take place, perhaps by the mediation of dynamic synapses [29]. It will be instructive to compare the terminations of large and small fibres.

Conclusions

Straightforward psychophysical experiments show that observers can discriminate the hues and the purities of parafoveal colors with similar precision whether the discriminanda are juxtaposed or are 10° apart and fall in opposite hemifields. There is no agreed model of how (or where) this comparison is performed. Consideration of possible models leads us to ask whether the long-range tracts of the brain constitute a *neural net* (where representations are embodied in the nodes of the net, in the weightings and signs of connections between nodes) or a *communication network*, where the same physical substrate carries different information from moment to moment. We have argued in favor of the latter.

Conflict of interest statement

Nothing declared.

Acknowledgements

Supported by BBSRC (BB/S000623/1) and Wellcome Trust (082378/Z/07/Z). We thank Dr Chie Takahashi for her kind assistance in the preparation of this paper.

References and recommended reading

Papers of particular interest, published within the period of review, have been highlighted as:

- of special interest
- of outstanding interest

1. Fairchild MD *et al.*: **Color models and systems**. In *Handbook of Color Psychology*. Edited by Elliot AJ. Cambridge University Press; 2015:9-26

An authoritative introduction to the concepts of color science and the properties of color spaces.

2. Saeedi H, Kandi SJ: **How anisotropy of CIELAB color space affects the separation effect: an experimental study**. *J Opt Soc Am* 2019, **36**:51-60.
 3. Danilova MV, Mollon JD: **Cerebral iconics: how are visual stimuli represented centrally in the human brain?** *J Opt Technol* 2018, **85**:515-520
- A recent paper that gives more experimental detail of how our psychophysical data are obtained.
4. Traub AC, Balinkin I: **Proximity factor in the Judd color difference formula**. *J Opt Soc Am* 1961, **51**:755-760.
 5. Bassett D, Sporns O: **Network neuroscience**. *Nat Neurosci* 2017, **20**:353-364
- This paper, and the following two, offer accessible introductions to neuroscientific applications of network theory.
6. Navlakha S *et al.*: **Network design and the brain**. *Trends Cogn Sci* 2018, **22**:64-78.
 7. Bassett DS *et al.*: **On the nature and use of models in network neuroscience**. *Nat Rev* 2018, **19**:566-578.
 8. Le Grand Y: **Sur la précision en photométrie visuelle**. *Revue d'optique théorique et instrumentale* 1933, **12**:145-159.
 9. Danilova MV, Mollon JD: **The comparison of spatially separated colours**. *Vis Res* 2006, **46**:823-836.
 10. MacLeod DIA, Boynton RM: **Chromaticity diagram showing cone excitation by stimuli of equal luminance**. *J Opt Soc Am* 1979, **69**:1183-1186.
 11. Eskew RT: **The gap effect revisited: slow changes in chromatic sensitivity as affected by luminance and chromatic borders**. *Vis Res* 1989, **29**:717-729.
 12. Balas BJ, Sinha P: *Dissociated Dipoles: Image Representation via Non-local Comparisons*. MIT; 2003.
 13. Chklovskii DB, Koulakov AA: **Maps in the brain: what can we learn from them?** *Annu Rev Neurosci* 2004, **27**:369-392.
 14. Sterling P, Laughlin SB: *Principles of Neural Design*. MIT; 2015
- distinguished and readable essay on how the morphology and the biophysics of neurons are constrained by energy limitations and by the type of information carried.
15. Lennie P: **The cost of cortical computation**. *Curr Biol* 2003, **13**:493-497.
 16. Coltheart M: **Grandmother cells and the distinction between local and distributed representation**. *Lang Cogn Neurosci* 2017, **32**:350-358.
 17. Thomas E, French R: **Grandmother cells: much ado about nothing**. *Lang Cogn Neurosci* 2017, **32**:342-349.
 18. Yamins DL, DiCarlo JJ: **Using goal-driven deep learning models to understand sensory cortex**. *Nat Neurosci* 2016, **19**:356-365.
 19. Tanenbaum AS, Wetherall DJ: *Computer Networks*. Pearson; 2014
- This is a standard text on communication networks (as opposed to neural nets). It has centrally influenced the proposals put forward by the present authors.
20. Boden MA: *Mind as Machine: A History of Cognitive Science*. Oxford University Press; 2006.
 21. Perge JA *et al.*: **Why do axons differ in caliber?** *J Neurosci* 2012, **32**:626-638.
 22. Aboitiz F *et al.*: **Fiber composition of the human corpus callosum**. *Brain Res* 1992, **598**:143-153.
 23. Liewald D *et al.*: **Distribution of axon diameters in cortical white matter: an electron-microscopic study on three human brains and a macaque**. *Biol Cybern* 2014, **108**:541-557.
 24. Danilova MV, Mollon JD: **The symmetry of visual fields in chromatic discrimination**. *Brain Cogn* 2009, **69**:39-46.
 25. Takemura H *et al.*: **Occipital white matter tracts in human and macaque**. *Cereb Cortex* 2017, **27**:3346-3359.

26. Sherbondy A *et al.*: **Exploring connectivity of the brain's white matter with dynamic queries.** *IEEE Trans Vis Comput Graph* 2005, **11**:419-430.
27. Graham DJ: **Routing in the brain.** *Front Comput Neurosc* 2014, **8**.
28. Braak E, Braak H: **On layer III pyramidal cells in the parastriate borderzone of man.** *J Hirnforsch* 1985, **26**:117-125.
29. Liaw JS, Berger TW: **Dynamic synapse: a new concept of neural representation and computation.** *Hippocampus* 1996, **6**:591-600.
30. Viénot F: **Cone fundamentals: A model for the future of colorimetry.** *Light Res Technol* 2016, **48**:5-13
• A tutorial guide to the construction of chromaticity diagrams of the MacLeod-Boynton type.