On the cortical mapping function – Visual space, cortical space, and crowding

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ARTICLE INFO

Keywords:
Cortical map
Logarithmic map
Cortical magnification factor
Cortical location function
Visual cortex
M-scaling
E\(_2\) value
Retinotopy
Retinotopic centre
M\(_0\)
Bouma’s law
Crowding
Critical distance
Myths
Visual field
Local/global

ABSTRACT

The retino-cortical visual pathway is retinotopically organized: Neighbourhood relationships on the retina are preserved in the mapping. Size relationships in that mapping are also highly regular: The size of a patch in the visual field that maps onto a cortical patch of fixed size follows, along any radius and over a wide range, simply a linear function with retinal eccentricity. As a consequence, the mapping of retinal to cortical locations follows a logarithmic function along that radius. While this has already been shown by Fischer (1973, Vision Research, 13, 2113–2120), the link between the linear function – which describes the local behaviour by the cortical magnification factor \(M\) – and the logarithmic location function for the global behaviour, has never been made explicit.

The present paper provides such a link as a set of ready-to-use equations using Levi and Klein’s \(E_2\) nomenclature, and examples for their validity and applicability in the mapping literature are discussed. The equations allow estimating \(M\) in the retinotopic centre; values thus derived from the literature show enormous, hitherto unnoticed, variability. A new structural parameter, \(d_0\), is proposed to characterize the cortical map, as a counterpart to \(E_2\) it shows much more stability. One pitfall is discussed and spelt out, namely the common myth that a pure logarithmic function, without constant term, will give an adequate map. The correct equations are finally extended to describe the cortical map of Bouma’s law on visual crowding. The result contradicts recent suggestions that critical crowding distance corresponds to constant cortical distance.

1. Introduction

One of the most beautiful organizational principles of the human brain is that of topographical mapping. Whilst perhaps universal to the brain, its regularity is most apparent for the three primary senses mediated through the thalamus – sight, hearing, and touch – i.e., in retinotopy, tonotopy, and somatotopy. For the visual domain with which we are concerned here, the regularity of topography is particularly striking and is at a level that lends itself to mathematical description by analytic functions. The seminal papers by Fischer (1973) and Schwartz (1977, 1980) derive the complex logarithm as a suitable function for mapping the location in the visual field to the location of its projection’s in (a flat-map of) the primary visual cortex, by which the visual field’s polar-coordinate grid gets mapped onto a rectilinear cortical grid. The log function’s image domain – the complex plane – is reinterpreted thereby as a two-dimensional real plane.\(^1\) As Schwartz explains in the two papers, the rationale for employing the log function in the radial direction is that its first derivative is an inverse-linear function, the latter implicit in the cortical magnification concept for the visual field as proposed by Daniel and Whitteridge (1961). Expressed more directly, the integral of an inverse linear function is the logarithmic function. Intuitively, summing-up (integrating over) little steps on the cortical map, where each step obeys cortical magnification, will result in the log mapping.

Schwartz’s (1977, 1980) papers with the complex-log mapping have become rather popular in visual psychophysics and visual neurophysiology. Van Essen, Newsome and Maunsell (1984), e.g., use it for explaining the topography of the macaque’s primary visual cortex, writing “Along the axis corresponding to constant polar angle, magnification is inversely proportional to eccentricity, and hence distance is proportional to the logarithm of eccentricity (x \(\propto\) log E)” (p. 437). Levi, Klein and Aitsebaomo (1985, Fig. 14) and Virsu et al. (1987, Fig. 7) plot

Abbreviations: CMF, \(M\), Cortical magnification factor; MAR, Minimal angle of resolution; LGN, Lateral geniculate nucleus.

\(^1\) Note that the elegance of the complex-log representation is deceiving in that not all properties of the complex plane have a counterpart in the 2D real plane (which is undesirable for a mathematical representation). For example, the square of a value on the upper vertical meridian does not correspond to a value on the left horizontal meridian, as would be implied by \(i^2 = -1\).
psychophysical thresholds in terms of cortical units. As another example, Klein and Levi (1987) derive from the log rule that, if spatial vernier-acuity offsets map onto a constant cortical representation, vernier offsets will depend linearly on eccentricity in the visual field (see the last section). Horton and Hoyt (1991) use it to point out that the well-known inverse-linear function for the cortical magnification factor $M$ (CMF) follows from a log-spaced cortical map. Engel et al. (1997, Fig. 9, Fig. 12; 1994, Fig. 2), and Larsson and Heeger (2006), use the log function implicitly when they use an exponential for the inverse location function (which corresponds to a log forward mapping). Duncan and Boynton (2003) fit their fMRI activity maps for the V1 topology using Schwartz’s complex-log mapping. The most advanced development is Schira, Tyler, Spehar and Breakspear’s (2010) closed-form expression for the cortical maps, at the same time accommodating for the horizontal-vertical anisotropy and preserving cortical area constancy across meridians by an added shear function.

While Fischer’s and Schwartz’s papers present the mathematical relationships (with examples for their application), Klein and Levi (1987) provide an empirical link between psychophysical data and location on the cortical map. For characterizing the inverse-linear CMF-vs-eccentricity function, they use a concept they had developed earlier for psychophysical results (Levi, Klein, & Atsbehaumo, 1984; Levi et al., 1985): The slope of that linear function, when normalized to the foveal value, can be quantified by a single number, called $E_2$. The concept is illustrated graphically in Fig. 2B below: In an x-y plot vs eccentricity, $E_2$ is the (negative) x-axis intercept or, alternatively, the (positive) eccentricity value at which the foveal value is incremented by itself (i.e., doubles). Klein and Levi (1987) further bridge the gap to proportionality when they show that relationships become simpler and more accurate when the data are not treated as a function of eccentricity $E$ itself, but of a transformed eccentricity, $E^*$, referred to as effective eccentricity, $E^* = E + E_2$. The linear cortical magnification function thereby turns into proportionality. In the cortical map, locations – i.e. distances from the retinotopic centre – are then proportional to the logarithm of effective eccentricity, $x \propto \log (E + E_2)$. The approach is verified by showing the empirical data both as thresholds and in cortical units (Klein & Levi, 1987, Fig. 5).

However, the papers discussed so far have not yet fully exploited the tight mathematical link between the linear and the logarithmic law for its empirical use. While the basic mathematical form of the mapping function – $\log (E)$ or $\log (E + E_2)$ – is drawn upon and made use of, further parameters are left free to vary and to be determined by fitting to the data. The derivations in the present paper take the log-mapping approach one step further. Unlike these and other papers (discussed below), the parameters for the logarithmic map are here obtained by mathematical derivation from the linear law. In a neuroscience context, that law will be the inverse of the CMF. For the psychophysicist, measures of low-level visual-perceptual function like the minimal angle of resolution (MAR) can be an approximation. In both cases, Levi and Klein’s $E_2$ concept is the basis here. We thereby arrive at a set of fully explicit equations that allow converting the linear, local-behaviour law of the CMF, specified by $E_2$, to a description of the global behaviour, the location on the cortical map. These equations are the message of the paper. In a next step, the empirical data for the cortical maps from neuroanatomy are then used to verify the correctness of these parametric equations. This approach represents a more principled one than before. It further places additional constraints on the describing function, thus adding to its reliability.

Instead of the complex log we here consider the simpler case of the real-valued, 1D mapping, where $\text{eccentricity}$ in the visual field, expressed in degrees of visual angle along a radius, is mapped onto the distance of its representation from the retinotopic centre, expressed in millimetres. The resulting real-valued logarithmic function shall be called the \textit{cortical location function}. Taking the 1D case implies no loss of generality; the function is generalized to the 2D case by simply writing it as a vector function. Compared to the complex log, the real function has the added advantage of allowing separate parameters for the horizontal and vertical meridian, required to meet the visual field’s horizontal-vertical anisotropy.

Once these relationships for the cortical location function are established, they need to be verified by empirical data. We use data from the literature and our own for this (D’Souza, Auer, Strasburger, Frahm, & Lee, 2016). It turns out that not only do the fits work excellently, and even better than the original fits, but that the constraints imposed by the parametric equations can also be used for the long-standing problem of improving estimates for the foveal CMF (called $M_0$). Another issue addressed there are attempts to become independent of the retinotopic centre’s location. That centre’s exact location appears to be difficult to find (it is often specified only approximately), and some authors like to use some other reference location instead. It turns out, however, that while equations can be referenced to some other location than the centre, true independence from the latter cannot be achieved.

In the context of these derivations, I propose a new metric, $d_2$, measured in millimetres, for characterizing the cortical map. It is the equivalent of $E_2$ (which is measured in degrees visual angle). Like $E_2$, $d_2$ allows specifying the steepness of the CMF’s change with location in the cortical map, e.g. for quantifying the horizontal-vertical anisotropy or even for comparisons between species.

In another section, it is further argued that the simplified version ($x \propto \log E$) – which is not uncommon in the fMRI literature – needs to be avoided and that the full version with a constant term added in the log’s argument needs to be employed (i.e., $x \propto \log (E + c)$). There is further apparently confusion about what does and what does not represent the required constant term, which adds to a common myth that omitting the term simplifies matters.

Finally, the cortical location function can be used, perhaps unexpectedly, to derive the cortical distances in visual crowding. Crowding happens when neighbouring patterns to a target stimulus are closer than a critical distance; that critical distance can be described by Bouma’s law (Bouma, 1970; Strasburger, Harvey, & Rentschler, 1991; Pelli, Palomares, & Majaj, 2004; Pelli & Tillman, 2008; Whitney & Levi, 2011; Strasburger, 2020). We thus arrive at a cortical version of Bouma’s law. While this has been done before (Levi et al., 1985; Motter & Simoni, 2007; Pelli, 2008; Nandy & Tjan, 2012; Strasburger, Rentschler, & Jüttner, 2011; Strasburger & Malania, 2013), the present derivations go beyond those in that they include the fovea and provide the derivations.

2. Concepts

Peripheral vision is unlike central vision as Ptolemy (90–168) already noted. Yet just how it is different is still a puzzling question. The goal here is to draw the attention to the highly systematic organization of the early neural processing stages by deriving equations that describe its architecture. But before doing so we need to be explicit on a number of concepts that are the foundation for what follows.

The \textbf{linear law and the hyperbola graph}. Four types of analytic functions are central for describing functional dependencies on eccentricity – in the visual field or in retinotopic areas: linear and inverse-linear, and logarithmic and exponential. Their graphs look entirely different yet the first and second two are effectively equivalent. Let’s start with the first pair (the second pair follows in Fig. 3).

The linear law starts with Aubert and Foerster (1857): Spatial resolution increases linearly with retinal eccentricity. It is still the conceptual standard and it corresponds to what is now called M-scaling when based on cortical magnification (Virsu & Rovamo, 1979; Virsu et al., 1987) or the change of local spatial scale when the scaling factor is not thus constrained (Watson, 1987). Examples for the linear law are shown in Figs. 1A and 2A. However, soon after it also became popular to use the inverse of minimum size instead, i.e. acuity, in an attempt to make the sensory decline more graphic (e.g. Fick, 1898, shown in Fig. 1B). And, since the inverse-linear function’s graph is close to a hyperbola, we arrive at the well-known hyperbola-like function of, e.g., acuity vs. distances from the retinal centre.
eccentricity seen in most textbooks, or in Oesterberg’s (1935) equally well-known cone-density graph. Examples for the cortical map are in Dougherty et al. (2003, Fig. 5) and Harvey and Dumoulin (2011, Fig. 4B), shown in Fig. 1C and 1D.

Yet, graphic as it may be, the hyperbola graph does not lend itself to a comparison of decline parameters. Weymouth (1958) therefore already argued for using the linear graph, introducing the concept of the minimal angle of resolution (MAR) as a general measure of size threshold. Weymouth summarized how the MAR and other spatial visual performance parameters depend on retinal eccentricity (Fig. 1A). Importantly, Weymouth stressed the mandatory use of a non-zero, positive y-axis intercept for these functions (Weymouth, 1958, p. 109). This will be a major point here; it is related to the necessity of a constant term in the cortical-location function emphasised in this paper.

Cortical magnification. Daniel and Whitteridge (1961) and Cowey and Rolls (1974) introduced cortical magnification as a quantitative concept for retinotopic mapping, which, for a given visual-field location, summarizes functional density along the retino-cortical pathway into a single number. The (linear) cortical magnification factor (CMF, or M), was defined as the diameter in the primary visual cortex onto which 1 deg of the visual field projects. Enlarging peripherally presented stimuli by M turns out to counter performance decline to a large degree for many visual tasks (reviewed, e.g., by Virsu et al., 1987); it was thus suggested as a general means of equalizing visual performance across the visual field (Rovamo & Virsu, 1979). Even though this so-called strong hypothesis was soon dismissed (e.g. Westheimer, 1982, p. 161), the strong tie between cortical distances and low-level psychophysical tasks is still striking.

The relationship between the early visual architecture and psychophysical tasks is still a matter of debate. In contrast, the manner in which the CMF varies with eccentricity is largely agreed upon: M decreases with eccentricity – following approximately a hyperbola (Fig. 1C and D) – and its inverse increases linearly (Schwartz, 1980; Van Essen et al., 1984; Tolhurst & Ling, 1988; Horton & Hoyt, 1991, Slotnick, Klein, Carney, & Sutter, 2001, Duncan & Boynton, 2003; Larsson & Heeger, 2006; Schira, Wade, & Tyler, 2007). Fig. 2A shows a few examples for the latter. Note that in the figure there is one function from psychophysics shown along with the anatomical estimates (Rovamo & Virsu, 1979; Virsu & Rovamo, 1979; Virsu et al., 1987). Note also that all functions need to have a positive y-axis intercept, be it ever so slight, because otherwise M were infinite in the centre.

Nonlinear equations. Empirical data typically fit the linear concept

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**Fig. 1.** Examples for the linear and the inverse-linear (approx. hyperbola) graph. Even though the two are equivalent, their intuitive interpretation is different, the linear graph indicating a shallow performance decline and the inverse-linear graph a steep decline (Rosenholtz, 2016; Strasburger 2020). A. MAR for various visual performance parameters; Weymouth (1958, Fig. 13). B. Visual acuity; Fick (1898, Fig. 2). C. Cortical magnification factor M; Dougherty et al. (2003, Fig. 5; error bars: SE). A hyperbola graph with axis intercept M₀ has been added. D. Same; Harvey and Dumoulin, 2011, Fig. 4B; colours denote cortical areas (see inset; error bars: SD). In C and D note the steep incline toward the retinotopic centre and that no data are obtained there. The central value M₀ is therefore difficult to derive from those graphs.

**Fig. 2.** A. The inverse of the cortical magnification factor or, equivalently, the size of a patch in the visual field that projects onto a patch of constant size in the cortex, as a function of eccentricity in the visual field (reproduced from Strasburger et al., 2011 for illustration). All functions show a mostly linear behaviour. Their slope is quite similar, with the exception of Van Essen et al.’s (1984) data for the macaque. Note that Rovamo & Virsu’s function is based on psychophysical data. Note also that all functions need a positive y-axis intercept, be it ever so slight, because otherwise M were infinite in the centre.

Nonlinear equations. Empirical data typically fit the linear concept
quite well in the considered range of about 40° eccentricity, but, nevertheless, fits can sometimes be improved numerically by introducing a slight nonlinearity (Table 1). Rovamo, Virsu, and Näsänen (1978), as an example, used a polynomial by adding a small 3rd-order term; Van Essen et al. (1984), Tolhurst and Ling (1988), and Sereno et al. (1995) increased the exponent of the linear term slightly above 1. That latter innocent looking change gives rise to severe difficulties, however (see Section 3.4.5). Virsu and Hari (1996) used a sine function, based on geometrical considerations. That function is still close to linear up to medium eccentricities though; it is interesting because it can be extended to eccentricities larger than 90° (cf. Strasburger, 2020).

The E2 concept. For a quick comparison of eccentricity functions, Levi et al. (1984, p. 794) introduced the E2 concept by pointing out the specific eccentricity at which the respective foveal value doubles (Fig. 2B). More generally, E2 is the eccentricity increment at which y increases by the foveal value. i.e., at eccentricity E2 the foveal value is doubled and at twice E2 is tripled. As a graphic aide, E2 is also the distance from the origin of where the linear function crosses the eccentricity axis. E2 is most often used for psychophysical tasks but lends itself equally well for describing the anatomical function (Levi et al., 1985, Table 1; Klein & Levi, 1987; Horton & Hoyt, 1991; Dougherty et al., 2003). Eq. (1) states the corresponding equation.

\[ M^{-1}/M_0^{-1} = E/E_2 + 1 \]  

In that equation is measured in /mm (one might call it the retinal magnification factor: it corresponds to the receptive field size of a cortical neuron on the retina). The function’s slope is given by \(1/\text{M}_0E_2\), so when these functions are normalized to the foveal value, the slope is 1/E2. Larger E2 thus corresponds to shallower slope. Parameter E2 captures an important property of the functions (how they increase) in a single measurement. Summaries of values were reported by Levi et al. (1984), Levi et al. (1985), Klein and Levi (1987), Toet and Levi (1992), or more recently by Strasburger et al. (2011, Tables 4–6). These reported E2 values vary widely between different visual functions. They also vary considerably for functions that seem directly comparable to each other (for example, E2 for vernier acuity: 0.62–0.8; for \(M^{-1}\): 0.77–0.82 or even 3.67 in Dougherty et al., 2003; for Landolt-C acuity: 1.0–2.6; letter acuity: 2.3–3.3; gratings: 2.5–3.0). On the other hand, E2 can also be surprisingly similar for tasks that seem entirely unrelated, like for example the E2 of 1.22 for the perceived travel extent in the fine-grain movement illusion (Foster et al. 1981). Note also E2’s limitations: by its definition, it works best at small eccentricities for example.

**M-scaling.** The left-hand ratio in eq. (1), \(M^{-1}/M_0^{-1}\), is the ratio by which a peripherally seen stimulus needs to be size-scaled to occupy cortical space equal to a foveal stimulus. So the equation can be rewritten as

\[ S/S_0 = E/E_2 + 1, \]  

where \(S\) is scaled size and \(S_0\) is the size at the fovea’s centre. Eq. (2) is the psychophysical counterpart to eq. (1). \(S_0\) can be considered the size-scaling unit in the visual field, and \(E_2\) the locational scaling unit. If \(E_2\) refers to the cortical map, this is the concept of M-scaling. If \(E_2\) in the equation refers to some other eccentricity function, this corresponds to a more abstract way of size scaling, called local scale (Watson, 1987).

**The cortical location function.** Fischer (1973), Schwartz (1977), Schwartz (1980) proposed the complex log function for mapping the visual field to the cortical area. The key property of interest for that mapping is the behaviour along a radius (from the fovea centre) in the visual field; the simpler real-valued log function can thus be used instead of the complex logarithm. This, then, maps the eccentricity in the visual field to the distance from the retinotopic centre on the cortical map (Fig. 3B). Neuroscience papers often prefer to show the inverse function (i.e. mirrored along the diagonal with the x- and y-axis interchanged, thus going “backwards” from cortical distance to eccentricity), which is the exponential function shown schematically in Fig. 3A.

**The constant term.** Schwartz (1980) has discussed two versions of the function that differ in whether there is a constant term present; the difference is illustrated in the graphs (Fig. 3). The version without the constant is often considered simpler and is thus often (inappropriately) preferred. A point in the following will be that that simplicity is deceiving and can lead to wrong conclusions – and to more complicated equations. Note that the constant term is at different places in the equations: For the exponential function in figure part (A) it is added to the exponential, for the logarithmic function in (B) it is within the log’s argument. As will be seen later, the constant term in both cases corresponds to the positive y-intercept of the linear function (Fig. 2B).

**Retinal and the retinotopic centre.** There is an important difference in difficulty between measuring at the fovea’s exact centre and at the cortical retinotopic counterpart. Whereas psychophysical measurements at the fovea are particularly simple and reliable, determining the exact retinotopic centre and the CMF at that location, \(M_0\) and \(M_0/S_0\) is the most difficult and \(M_0/S_0\)’s value is mostly extrapolated from peripheral values. The consequences of this include different strategies in research concerning the centre.

**Anisotropy.** A few words on the visual field’s anisotropy are found in the appendix.

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### Table 1

| Equation | Source | Comments |
|----------|--------|----------|
| \( M^{-1} - M_0^{-1}/(1 + aE) \) | Cowey and Rolls (1974) | Inverse-linear equation (using data from Wertheim, 1894) |
| \( M^{-1} - M_0^{-1}/(1 + E/E_2) \) | Levi et al. (1985, Table 1); Klein and Levi (1987); Horton and Hoyt (1991); Dougherty et al. (2003) | Inverse-linear equation using \(E_2\). |
| \( M^{-1} - M_0^{-1}/(1 + aE + bE^2) \) | Rovamo and Virsu (1979) | Nonlinearity by an added small 3rd-order term |
| \( M^{-1} - M_0^{-1}/(1 + \alpha E) \) | Van Essen et al. (1984), \(\alpha = 1.1\) | Power function with constant term. Exponent \(\alpha\) is close to 1. Problematic. |
| \( M^{-1} = aE^\alpha \) | Duncan and Boynton (2003), \(\alpha = 0.83\) | Pure power function w/o constant term (see Fig. 6). Problematic. |
| \( M^{-1} = a + \text{sin}(E) \) | Virsu and Hari (1996), Näsänen and O’Leary (1998) | Only 1/8 of the sine period is used |
starting at the fovea centre: \( d(E) = \int M(E) \, dE \). If we insert eq. (1) – i.e. the equation using \( E_2 \) – into that integral equation, we have

\[
d(E) = \int_0^E \frac{M_e}{1 + E/E_2} \, dE = M_e E_2 \ln(1 + E/E_2) \quad (\text{with } E \geq 0)
\]

where \( \ln \) denotes the natural logarithm. It is shown in Fig. 3B. The inverse function, \( E(d) \), shown in Fig. 3A, is derived by inverting eq. (3),

\[
E = E_2(\exp(d/E_2) - 1) \quad (\text{with } d \geq 0)
\]

It states how the eccentricity \( E \) in the visual field depends on the distance \( d \) of the corresponding location in a retinotopic area from the retinotopic centre. With slight variations, discussed below, it is the formulation often referenced in fMRI papers on the cortical mapping. Note that, by its nature, it is only meaningful for positive values of cortical distance \( d \). The significance of this point will become apparent later. Note also that the function passes through the origin (i.e., \( E = 0 \) when \( d = 0 \)), so any empirical fit to the function must be constrained thus to be meaningful.

We can simplify that function further by introducing an analogue to \( E_2 \) in the cortex. Observe that like any point in the visual field the location at \( E_2 \) has a representation (on the meridian in question), whose distance from the retinotopic centre we denote as \( d_2 \). Thus, \( d_2 \) represents \( E_2 \) in the cortex.

To express eq. (4) using \( d_2 \) instead of \( M_0 \), we first apply eq. (4) to that location \( d_2 \) and solve for \( M_0 \) which gives

\[
d_2 = M_0 E_2 \ln 2
\]

Inserted into eq. (4) in turn gives

\[
E = E_2(2^{d_2/E_2} - 1)
\]

Eq. (6) is the most concise way of stating the cortical location function. However, since the exponential to the base \( e \) is often more convenient to use, we can also restate it as

\[
E = E_2(\exp(d_2/E_2) - 1)
\]

This equation (eq. (7)) is particularly nice and simple provided that \( d_2 \), the cortical equivalent of \( E_2 \), is known. That value, \( d_2 \) could thus play a key role in characterizing the cortical map, similar to the role of \( E_2 \) in visual psychophysics (cf. Table 4–Table 6 in Strasburger et al., 2011, or earlier the tables in Levi et al., 1984, Levi et al., 1985, or Klein & Levi, 1987). Estimates for \( d_2 \) derived from literature data are summarized in Section 3.4 below (Table 3), as an aid for concisely formulating the cortical location function. The new cortical parameter \( d_2 \) can be calculated from eq. (5).

### Table 2

Summary of symbols used in the paper.

| Visual Field | Cortical Map |
|--------------|--------------|
| \( M \) | \( M \) |
| \( S \) | \( d \) |
| \( E \) | \( E \) |
| \( E_2 \) | \( E_2 \) |
| \( E_0 \) | \( E_0 \) |
| \( d(E) \) | \( M(E)dE \) |

**Symbols in the paper.** To keep the overview, symbols used in the paper are summarized in Table 2. Some of those are in standard use and some are newly introduced in the remainder.

### 3. The cortical location function

#### 3.1. Cortical location measured from the retinotopic centre

The ratio \( S/S_0 \) in eq. (2) is readily estimated in psychophysical experiments as the size of a stimulus relative to its foveal value for achieving equal perceptual performance. However, its physiological counterpart \( M^{-1}/M_0^{-1} \) in eq. (1) appears difficult to assess directly. Instead, it is typically derived by extrapolation from peripheral values, e.g. from the cortical-location function \( d = d(E) \) (Fig. 3). That function links a cortical distance \( d \) in a retinotopic area to the corresponding distance in the visual field that it represents. More specifically, \( d \) is the distance (in mm) on the cortical surface between the representation of a visual-field point at eccentricity \( E \), and that of the fovea centre. Under the assumption of linearity of the cortical magnification function \( M^{-1}(E) \), this function is logarithmic (Fig. 3B) and its inverse \( E = E(d) \) is exponential (Fig. 3A), as shown by Fischer (1973), Schwartz (1977), Schwartz (1980). Since the \( E_2 \) parameter allows a simple formulation of the linear eccentricity functions (Fig. 2), as e.g. in eq. (1), it will be useful to state the location function with those notations. First steps have been derived in Strasburger et al. (2011, eqns. (10)–(13); corresponding here roughly to eqs. (3) and (4)). The present derivations go further. The location function allows a concise quantitative characterization of the early retinotopic maps.

For its derivation, notice first that, locally, the cortical distance of the respective representations \( d(E) \) and \( d(E + \Delta E) \) of two nearby points along a radius at the eccentricities \( E \) and \( E + \Delta E \) is given by \( M(E)dE \). This follows from \( M \)'s definition and the fact that \( M \) refers to \( 1 \). The cortical magnification factor \( M \) is thus the first derivative of \( d(E) \). Conversely, the location \( d \) on the cortical surface (i.e., the global aspect) is the integral over \( M \),
3.2. Cortical location measured from a reference location

Implicit in the definition of \( d \) or \( d_2 \) is the knowledge about the location of the fovea centre’s cortical representation, i.e. of the retinotopic centre. Since that locus seems hard to determine precisely, it has become customary to use some fixed eccentricity \( E_{\text{ref}} \) as a reference instead. Engel et al. (1997, Fig. 9; 1994, Fig. 2), for example, use \( E_{\text{ref}} = 10^\circ \). Larsson and Heeger (2006, Fig. 5) use \( E_{\text{ref}} = 3^\circ \).

It will thus be useful to restate the cortical location function with some reference eccentricity as parameter. We can derive that from eq. (7) with a few simple steps (applying eq. (7) to the reference eccentricity, solving for \( d_2 \) and eliminating \( d_2 \) from the equation). We arrive at

\[
E = E_2(e^{\beta (d/d_{\text{ref}})} - 1), \quad \text{with } \beta = \ln\left(\frac{E_{\text{ref}}}{E_2} - 1\right) (ad d \geq 0) \tag{8}
\]

It represents the location function with the reference eccentricity \( E_{\text{ref}} \) and its equivalent in the cortical map, \( d_{\text{ref}} \), as parameters. Parameter \( \beta \) is introduced for readability. \( E_2 \) can be considered as a special case of a reference eccentricity. Note further that, unlike the location equations often used in the retinotopy literature (Van Essen et al., 1984, in the introduction; Duncan & Boynton, 2003; Larsson & Heeger, 2006), the equations are well defined in the fovea centre: for \( d = 0 \), the eccentricity \( E \) is zero, as it should be.

What reference to choose is up to the experimenter. However, the fovea centre itself cannot be used as a reference – the equation is undefined for \( d_{\text{ref}} = 0 \) (since the exponent is then infinite). Thus, the desired independence of knowing the retinotopic centre’s location has not been achieved – that knowledge is still needed, since \( d \) and \( d_{\text{ref}} \) in these equations are defined as the respective distances from that point.

Equation (8) has the ratio \( d/d_{\text{ref}} \) in the exponent. It is a proportionality factor for cortical distance. From the intercept theorem in geometry we know that this factor cannot be re-expressed by any other expression that leaves the zero point undefined. True independence from knowing the retinotopic centre, though desirable, thus cannot be achieved.

We can nevertheless shift the coordinate system such that locations are specified relative to the reference location, \( d_{\text{ref}} \). For this, we define a new variable \( \tilde{d} \) as the cortical distance (in mm) from the reference \( d_{\text{ref}} \) instead of from the retinotopic centre (i.e., \( \tilde{d} = d - d_{\text{ref}} \); see Fig. A1 in the appendix for an illustration).

In the shifted system – i.e., with \( \tilde{d} \) instead of \( d \) – eq. (8) becomes

\[
E = E_2(e^{\beta \tilde{d}/E_{\text{ref}}} - 1), \quad \text{with } \beta = \ln\left(\frac{E_{\text{ref}}}{E_2} - 1\right) (ad \tilde{d} + d_{\text{ref}} \geq 0) \tag{9}
\]

This is now the cortical location function with a reference eccentricity as parameter, and distance from that as the independent variable.

Note how the foveal magnification factor \( M_0 \) – still a part of eq. (4) – has dropped from the equation. Similar to eq. (5) it can be calculated from \( d_{\text{ref}} \) and \( E_2 \) as

\[
M_0 = \frac{d_{\text{ref}}}{\beta E_2} \tag{10}
\]

where \( \beta \) is defined as in the previous equation. With an approximate location of the retinotopic centre (needed for calculating \( d_{\text{ref}} \)) and an estimate of \( E_2 \), that latter equation leads to an estimate of the foveal magnification factor, \( M_0 \) (see Section 3.4 and Supplement for examples).

Equations (9) and (10) are crucial to determine the retinotopic map in early areas. They should work well for areas V1 to V4 as discussed below. The connection between the linear and log or exponential-function based estimations provided by these equations allows cross-validating the empirically found parameters and thus leads to more reliable results. Duncan and Boynton (2003), for example, review the linear law and also determine the cortical location function empirically but do not draw the connection. Their’s and others’ approaches are discussed as practical examples in the section after next (Section 3.4).

3.3. Simpler fitting with the simplified function?

Schwartz (1980) had offered a simplified location function where the constant term is omitted, which works at sufficiently large eccentricities. Frequently that was the preferred one by other authors as seemingly being more practical (Engel et al., 1997; Duncan & Boynton, 2003; Larsson & Heeger, 2006). The present section briefly highlights how this approach leads astray if pursued rigorously.

The simplified version of the location function \( E(\tilde{d}) \) omits the constant term in eq. (4) and those that follow from it (i.e., the “−1” in the preceding equations). Instead, the equation

\[
E = e^{a(\tilde{d} + b)} \tag{11}
\]

is fit to the empirical data, with free parameters \( a \) and \( b \). The distance variable is \( \tilde{d} \) as before, i.e., the cortical distance from a reference \( d_{\text{ref}} \) representing some eccentricity \( E_{\text{ref}} \) in the visual field. Engel et al. (1997, Fig. 9; 1994, Fig. 2), for example, use \( E_{\text{ref}} = 10^\circ \) for such a reference, and for that condition report the equation \( E = \exp \left(0.063 (\tilde{d} + 36.54)\right) \). Larsson and Heeger (2006, Fig. 5), as another example, use \( E_{\text{ref}} = 3^\circ \), and for area V1 in that figure give the function \( E = \exp \left(0.0577 (\tilde{d} + 18.0)\right) \). Note that neither of these equations contains the required constant term (cf. Fig. 3), since the constants (36.54 and 18.0) are inside, not outside, the exponential’s argument.

We can try to attach meaning to the parameters \( a \) and \( b \) in eq. (11) by constraining the function appropriately (see ffffff for the derivation). By that we arrive at an equation

\[
E = E_{\text{ref}}(1 - E_{\text{ref}}/d_{\text{ref}}^2) \tag{12}
\]

where \( d_1 \) is the distance of the 1° line from the reference eccentricity’s representation; it is around ~36.5 mm for \( E_{\text{ref}} = 10^\circ \) as used by Engel et al. (1994, 1997).
distance, which is physically meaningless. The pink and green line both show
go through the origin. With respect to their shape, the equations are under
linear law (eq. (1)). Note that, by definition, the fitted curves are constrained to
graphs of the preferable eq. (9) that was derived from integrating the inverse
cortical location function. Symbols show the retinotopic data for
the CMF, and the new structural parameter $d_2$ — are given in the

3.4. Practical use of the equations: examples

The following examples from the literature illustrate how the new
equations are used. The focus in each case is on the mathematics and in
particular the constant term. Details of how structural parameters can be
obtained for the reviewed studies — the CMF in the retinotopic centre, $E_2$
for the CMF, and the new structural parameter $d_2$ — are given in the

Comparison of Laws, ref. Larsson & Heeger Fig. 5, V1

Fig. 4. Comparison of conventional and improved analytic functions for
describing the cortical location function. Symbols show the retinotopic data for
area V1 from Larsson and Heeger (2006, Fig. 5) with reference location $d_{ref} = 3^\circ$
(symbols for nine subjects). Superimposed is the original fit (thick black line),
according to eq. (11), i.e. a fit without a constant term. The blue dotted line
continues that fit to lower eccentricities; it goes to (negative) infinite cortical
area V1 from Larsson and Heeger (2006, Fig. 5) with reference location

3.4.1. Larsson and Heeger (2006)

No constant term. The first example illustrates what happens when
the constant term is omitted, with data from Larsson and Heeger (2006,
Fig. 5) for area V1. As a reminder, this in essence is about $E = a(d + 1)$
versus $E = a e^{b\hat{d}}$.

The retinotopic centre is left undefined in the study, and a reference
eccentricity of $E_{ref} = 3^\circ$ is used instead. The fitted equation in the original
graph is $E = \exp(0.0577(\hat{d}+18.0))$, which corresponds to eq. (11),
i.e. the version without a constant term. Its graph is shown in Fig. 4 as
the thick black line copied from the original graph. It is continued to the
left as a dotted blue line to show the behaviour toward the retinotopic
centre. At a distance of $-18.0$ mm from the $3^\circ$ representation (as seen
from eq. (12)), the line crosses the $1^\circ$ point. To the left of that point the
curve deviates upward and so the retinotopic centre ($E = 0$) cannot be
reached.

Importantly, the data can be re-fit with the constant term included (i.
e. eq. (9)), with a more realistic result. Since the exponential equation is
underconstrained unless either the location of the retinotopic centre or
the central CMF $M_0$ are known (eq. (5) or (10)), we tried out two
parameter pairs (pink and the green curve in Fig. 4). It turns out that
smaller $E_2$ values go together with larger $d_{ref}$ values for a similar shape.
Within the range of the data set, the two curves fit about equally well.
Below about $1^\circ$ eccentricity the two curves deviate markedly from the
original fit. The new curves fit the data better there than the original
and, in particular, reach a retinotopic centre. Of the two, the pink curve
reaches the centre at 38 mm from the $3^\circ$ point, and the green curve at 35
mm. These values are summarised later for a literature comparison
(Table 3).

3.4.2. Engel et al. (1994, 1997)

No constant term. Fig. 5 shows the same curves again without the
data symbols, for visibility of the curves’ shape; it also includes an
additional graph depicting the exponential function reported by Engel

Comparison of Laws, ref. Larsson & Heeger Fig. 5, V1

Fig. 5. Same as Fig. 4 but without the data symbols, for better visibility of the
curves. The curves for the new law go through the origin, i.e. $E = 0$ when $d = 0$
(note that the origin is not seen in the graph). The additional dash-dotted line
next to that of Larsson & Heeger’s depicts the equation by Engel et al. (1997).
et al. (1994, 1997), \( E = \exp(0.063(\hat{d} + 36.54)) \). Note that their equation has no constant term (parameter ‘36.54’ is part of the argument). \( \hat{d} \) is here measured from the 10° representation; for comparison with the other curves, the curve is therefore shifted by 19.1 mm on the abscissa. The curve runs closely with that of Larsson and Heeger (2006) and shares its difficulties.

3.4.3. Duncan and Boynton (2003)

**No constant term.** Fig 4 and Fig 5 show two further \( E(\hat{d}) \) functions (black and brown) that we based on results of Duncan and Boynton (2003, Fig. 8). These functions pass through the retinotopic centre (since based on eq. (9)) but differ somewhat from the others and we might ask how these parameters were derived. The paper takes a slightly different approach than those discussed before; details are given in the Supplement. In short, Duncan and Boynton (2003) estimate lines of equal eccentricity in the V1 map for the central visual field, using the equation with a constant term (eq. (4)). The authors then graphically estimate the CMFs at those locations from their anatomical data (this is where they differ from other approaches); the CMFs are then plotted vs. eccentricity in their Fig. 4 and Fig. 8.

Things get confusing then since their results figure – on which \( M_0 \) is said to be based – shows a pure power function (9.81 \( E^{-0.83} \); see Fig. 6). Since that omits the constant term it is invalid in the retinotopic centre and does not allow estimating \( M_0 \) (see Supplement). Only later in the paper it turns out that the same data were also fitted with the inverse-linear equation, eq. (1) \( M^{-1} = 0.065 E + 0.054 \). From that, both \( M_0 \) and \( E_2 \) are readily derived and they were used in Figs. 4 and 5. Furthermore, our eq. (10) is useful for the paper in that it allows deriving how these parameters were derived. The paper takes a slightly different approach than those discussed before; details are given in the Supplement.

3.4.4. Mareschal, Morgan and Solomon (2010)

Fig S1 in the Supplement shows an additional curve from a paper by Mareschal et al. (2010) on cortical distance who base their cortical location function partly on the equation of Duncan and Boynton (2003). Mareschal et al. (2010) state their location function as

\[
M(E) = \begin{cases} 
(0.065E + 0.054)^{-1} & E < 4^\circ \\
5.72 - \log_{10}(E) & E > 4^\circ 
\end{cases}
\]  

(13)

The upper part of the equation is that of Duncan and Boynton (pink curve) and is used for eccentricities below 4°. The green continuous line shows Mareschal’s log equation above 4°, and the dashed line shows how the log function would continue below 4°. As before, the latter is not meaningful which is why Mareschal et al. switched to the inverse-linear function (the pink curve) at that point. For their conclusions the switch is not relevant; the example is added here to illustrate that the case distinction in eq. (13) can be avoided with the new equations.

3.4.5. An added exponent: Sereno et al. (1995)

Failure of the equations with exponent. To accommodate for a slight curvature in the inverse CMF function (Fig. 2A), several authors suggested using a modestly nonlinear function for its modelling (Rovamo & Virsu, 1979; Van Essen et al., 1984; see Table 1). One way to achieve this is using a power function, i.e., adding an exponent to the linear function:

\[
M^{-1} = M_0^{-1} + (1 + aE)^n
\]  

(14)

We will see why this is a bad idea. Van Essen et al. (1984) used a power function with an exponent of 1.1 (Table 1 and Fig. 2A). Following their lead, Sereno et al. (1995), equivalently, posit \( M(r) = A/(r + B)^2 \) for the CMF and treat \( A, B, C \), as free parameters \( r \) denotes eccentricity \( E \) along a radius; the equations are in the paper’s footnotes 24–26. For the case \( C = 1 \), the equation is reduced to the standard inverse-linear function (eq. (1)). For \( C \neq 1 \) they derive, by integration, the cortical location function (mapping function): \( D(r) = A(r + B)^{1-C}/(1-C) \). If \( C \neq 1 \). In their fits to the anatomical data, \( C \) comes out with values very close to 1 – which is tricky since exactly 1 is not allowed. So, even though the location function is well-defined in the centre \( r = 0 \), the important case \( C = 1 \) is excluded, i.e. the location function is undefined for the inverse-linear CMF function. That latter is discussed in their Footnote 26, where, for \( C = 1 \), the cortical location function is said to converge to \( D(r) = A \log(r + B) \).

In that equation, however, lies the fatal error that led to the avoidance of the, much simpler, logarithmic location function. By comparison to eq. (3), one can see that the scaling factor for the independent variable \( r \) (eccentricity) is missing. The equation should be \( D(r) = A \log(Cr + B) \). Therefore, \( B \) is effectively constrained to 1 (because only then is \( D(r = 0) = 0 \), i.e., \( B \) is not a free parameter.

Notably, Sereno et al. (1995) were aware of the shortcomings of their equations. They write, “The combinations of parameters given here still give unrealistically large estimates of cortical magnification at the exact center of the fovea […], indicating that the standard equation for \( M \) is inadequate to accurately describe cortical magnification in the very center.” A simple derivation error has thus led to the rejection of the best equation in part of the literature.

3.4.6. Near the retinotopic centre: Schira et al.

Predictions on the properties at the retinotopic centre depend critically on its precise location and thus require data at small eccentricities. Schira, Tyler and coworkers addressed that problem in a series of papers (Schira et al., 2007; Schira, Tyler, Breakspear, & Spehar, 2009; Schira et al., 2010) and provide detailed maps of the centres of the early visual areas, down to 4.5 arcmin eccentricity! They also develop parametric, closed analytical equations for the 2D maps. In the horizontal direction, these equations correspond to those discussed above (eq. (1) and eq. (9)/(10)). The equations differ near the vertical meridian. \( M_0 \) and \( E_2 \) are not specified in their papers but can be obtained by applying eq. (1) (see Fig. S2A in the Supplement).

3.4.7. \( d_2 \) – A structural parameter to describe the cortical map and a comparison of central CMFs

The cortical location function takes on a particularly concise form with the newly defined structural parameter \( d_2 \) (Section 3.1, eq. (6) or (7)). Parameter \( d_2 \) is the cortical representation of Levi and Klein’s \( E_2 \) (Fig. 2): \( d_2 \) is the distance from the retinotopic centre, measured in mm, where the central CMF is halved. Eq. (5) can serve as a means to obtain an estimate for \( d_2 \). Essentially, \( d_2 \) is the product of \( M_0 \) and \( E_2 \) with a scaling factor. Table 3 gives a summary of \( d_2 \) estimates thus derived. Values vary widely and this is a problem that needs to be addressed in
the mapping literature. Which one is correct? The value of \( \delta_2 \approx 8 \) mm with \( E_2 = 0.33^\circ \) obtained from Schira et al.'s (2009) data – which go down to extremely low eccentricities – might currently be the most accurate estimate.

Similar to what \( E_2 \) does for the linear or inverse-linear function, \( \delta_2 \) concisely captures the properties of the map in a single number. It is given in physical units (mm) and can thus be drawn directly into a retinotopic map. \( E_2 \) is not as well-suited because its units are in deg visual angle which need to be translated to spatial, cortical units. Currently, typical characterizations of the cortical map are done by \( E_2 \) or by drawing iso-eccentricity lines at several eccentricities. In a similar way, a single \( \delta_2 \) line can be drawn on the cortical map (Fig. 7) or marked as a point on a radius.

As a characteristic measure, \( \delta_2 \) can be used in many ways, for comparison of the anisotropy in the cortical maps, between species, individuals, gender, etc. Or indeed it can describe any other retinotopic map, like those for V2 – V4 or that for the LGN, the pulvinar, the reticular nucleus of the thalamus, once data are available. Differences between \( \delta_2 \) show a difference in the architecture.

\( \delta_2 \) shares certain limitations of \( E_2 \) (Fig. 11 and Table 3 in Strasburger et al., 2011). Like the latter it relies on data in and near the retinotopic centre and is thus likely most meaningful at small to medium eccentricities. Its validity for describing the curve at larger eccentricities further depends on the premise that location in the map results from integrating the local magnification function, i.e., that local magnification factors “add up”. For the CMF, that appears to be the case, as evidenced by the good fit of location data shown in Fig. 4 and other log location functions in the literature. However, for local properties that are likely based on differences in neural wiring, like the colour channels studies in D’Souza et al. (2016), that might not be the case. \( \delta_2 \), in those cases, will characterize the function, but not its map.

4. Crowding and Bouma’s Law in the cortex

The preceding was about the cortical location function; in the final section that function will be applied to an important property of cortical organization: visual crowding. Whereas, in the former, cortical location was the target of interest, we are now concerned with cortical distances.

4.1. Crowding properties relevant for the cortical map

MAR-like functions like acuity generally change in peripheral vision in that critical size scales with eccentricity, so deficits can mostly be compensated for by \( M \)-scaling (Rovamo & Virsu, 1979). For crowding, in contrast, target size plays little role (Tripathy & Cavanagh, 2002) and, instead, the critical distance between target and flankers scales with eccentricity, though at a different rate than MAR (Rosenholtz, 2016; Strasburger, 2020). This scaling characteristic of crowding is known as Bouma’s law (Bouma, 1970; Strasburger et al., 1991; Pelli et al., 2004; Pelli & Tillman, 2008; Strasburger, 2020). The corresponding distances in the primary cortical map are thus governed by differences of the cortical location function as derived here in Section 3. Crowding’s critical distance, or indeed any distance, is thus, in a sense, a spatial derivative of location. Pattern recognition, at even slight eccentricities, is governed by the crowding phenomenon and is largely unrelated to visual acuity or to cortical magnification (e.g. Pelli & Tillman, 2008).

For understanding crowding, we thus need to look at its cortical basis, since we know that crowding is of cortical origin (Flom, Weymouth, & Kahnemann, 1963).

A question that arises naturally then (Pelli, 2008) is how the cortical equivalent of critical crowding distance varies across the visual field. Klein and Levi (1987) were the first to ask a similar question, how visual distance (in a vernier task) maps onto cortical distance. Their empirically determined position thresholds, when mapped by an inverse-linear CMF function (with \( E_2 = 0.6 \)), turned out mostly constant across a wide range of eccentricities Klein and Levi (1987, Fig. 5). Later, Duncan and Boynton (2003), after estimating the CMF based on Schwartz’s (1980) log mapping and applying that to obtain cortical distances (discussed above), showed that, for scaled vernier tasks and scaled gratings, the cortical equivalents are again mostly constant (above 1.5° eccentricity; Duncan & Boynton, 2003, Fig. 4). Similarly, with respect to the cortical distance for crowding’s critical distance, it has been proposed that it is likely constant, with the same reasoning Motter & Simoni, 2007; Pelli, 2008; Mareschal, Morgan, & Solomon, 2010).

4.2. Critical crowding distance in the cortical map

Elegant as it seems, however, the constancy assumption is most likely incorrect as a general rule; it rests on the same shortcut of equating linearity and proportionality that gave rise to those cortical location functions that miss the retinotopic centre (Section 3.3). Using the new cortical location function derived in Section 3, it will turn out that the critical cortical crowding distance is far from constant, increasing steeply within the fovea and reaching an asymptote only beyond ~5° eccentricity. Remarkably, after I had completed the derivations it turned out that the analytic equation exposed below nicely agrees with those presented by Motter and Simoni (2007). In their Fig. 7, reproduced here in Fig. 8B, only the peripheral data show the presumed constancy.

Let us turn to the equations. Bouma (1970) stated what is now known as Bouma’s law for crowding (Strasburger, 2020): \( \delta_{\text{pacc}} = b\delta \), where \( \delta_{\text{pacc}} \) is the free space between the patterns at the critical distance and \( b \) is a proportionality factor. Bouma (1970) proposed an approximate value of \( b = 0.5 = 50\% \) (which is now widely cited) but \( b \) can take quite different values, depending on the visual task and criterion. Yet even
though the factors may differ, the implied linearity of eq. (15) almost always holds up. The law can thus be restated as saying that free space for critical spacing is proportional to eccentricity.

In today’s literature it has become customary to state flanker distance differently, as measured from the respective centres of target and flankers. Bouma’s law then becomes \( \delta = bE + S \), where \( S \) is target size in the radial direction. This equation no longer represents proportionality yet is still linear in \( E \). Importantly however, adding the constant “\( S \)” reflects adding the constant term that was talked about in the preceding sections. And formally, that equation is analogous to size scaling as in eq. (2). Analogously to eq. (2) we therefore introduce a parameter \( \hat{E} \) for crowding, as the eccentricity where the foveal value of critical distance doubles. Denoting the foveal value by \( \delta_0 \), we get

\[
\delta = \delta_0 (E/\hat{E} + 1)
\]  

(15)

This is how we will use Bouma’s law in the remainder. Obviously, that equation is analogous to eq. (1) and (2) that we started out with; it describes how critical distance in crowding is linearly dependent on (but is not proportional to) eccentricity in the visual field. In this respect, it thus behaves like acuity or many other spatial visual performance measures, just with a different slope and axis intercept.

With the equations derived in the preceding sections, we can derive the critical crowding distance in the cortical map, i.e. the cortical representation of critical distance in the visual field. We denote that distance by \( \kappa \) (kappa); by definition, it is the difference between the map locations for the target and a flanker at the critical distance in the crowding task: \( \kappa = \delta_f - \delta_t \). The two cortical locations \( \delta_f \) and \( \delta_t \) are, in turn, obtained from the mapping function, which is given by inverting eq. (4) above:

\[
d = M_0 E_2 \ln (1 + E_2/E_0) \quad \text{(with } E \geq 0)\]

(16)

where \( d \), as before, is the distance from the retinotopic centre. We thus calculate the respective \( d \) values for target and flanker from eq. (16), take their difference, and further note that the eccentricity of a radially positioned flanker’s location is given by that of the target plus or minus flanker distance, the latter given by eq. (15). After simplifying for the peripheral flanker this becomes

\[
\kappa = M_0 E_2 \ln \left( 1 + \frac{\delta_0}{E_2} \frac{1 + E_2/E_0}{1 + E_0/E_2} \right)
\]  

(17)

(the explicit derivation is in the Supplement). Note that we stated that equation before (Strasburger & Malania, 2013, eq. (13), and Strasburger et al., 2011, eq. 28), but, alas, incorrectly: a factor was missing.

To explore this function, its graph is shown in Fig. 8A and we look at two special cases: In the retinotopic centre, equation (17) predicts a critical distance \( \kappa_0 \) in the cortical map of

\[
\kappa_0 = M_0 E_2 \ln \left( 1 + \frac{\delta_0}{E_2} \right)
\]  

(18)

With increasing eccentricity, \( \kappa \) departs from that foveal value and increases, depending on the ratio \( E_f/E_2 \) (since \( E_f > E_2 \) Latham & Whittaker, 1996; Strasburger, 2020). Numerator and denominator are the \( E_2 \) values for the location function and the crowding function, respectively (eq. (1) vs. eq. (15)).

With sufficiently large eccentricity, the equation converges to

\[
\lim_{E \to \infty} \kappa = M_0 E_2 \ln \left( 1 + \frac{\delta_0}{E_2} \right)
\]  

(19)

the expression is shown as the dashed asymptote in Fig. 8A. The expression is identical to that for the foveal value in eq. (19) except that \( E_2 \) is now replaced by the corresponding value for crowding, \( \hat{E}_2 \) (which has “taken over”).

\( \kappa \) varies substantially around the centre, by around two-fold between the centre and \( \hat{S} \) eccentricity with realistic values of \( E_2 \) and \( \hat{E}_2 \). This is at odds with the conjecture that the cortical critical crowding distance is basically a constant (Motter & Simoni, 2007; Pelli, 2008; Mareschal et al., 2010). Pelli (2008) presented a mathematical derivation for the constancy, very similar to the one presented above, like ours based on Bouma’s law and Schwartz’s (1980) logarithmic mapping function. The discrepancy arises from the underlying assumptions: Pelli used Bouma’s law as proportionality, i.e., in its simplified form without a constant, its graph passing through the origin. That was done on the grounds that the error is small outside the retinotopic centre and plays little role at sufficiently large eccentricities; Pelli appropriately warns that additional provisions must be made at small eccentricities. Schwartz’s (1980) mapping function was consequently also used in its simplified form, for the same reason. With both constant terms removed, the critical distance in the cortex indeed turns out as simply a constant.

As should be expected, at sufficiently high eccentricities \( \kappa \) is close to constant in the derivations given above (Fig. 8). These equations (eq. (17)–(19)) can thus be seen as a generalization of Pelli’s result that now also covers the case of central vision.

For comparison, Fig. 8B shows critical crowding spacing on the cortical map from a paper by Motter and Simoni (2007), based on Bouma’s law and Duncan and Boynton’s (2003) inverse-linear equation.

Pelli and Tillman (2008, Online Supplement) derive a value of 6 mm for the asymptote. It is based on eq. (11) above, as reported by Larsson and Heeger (2006), and a Bouma factor of 0.4.

The equations have \( M_0 \) as a scaling factor whose empirical estimates vary widely. It can be replaced by the more stable \( d_2 \) (eq. (5)). The resulting equations for the critical cortical crowding distance are given in the appendix. Values for \( d_2 \) that could be plugged in were provided in Table 3 above. The equations could lend themselves for empirically
determining critical crowding distance in the cortex.

In summary for the cortical crowding distance, the two well-established linear eccentricity laws – for cortical magnification in neuroscience and critical crowding distance in psychophysics – together with the logarithmic mapping rule, predict a highly systematic behaviour of crowding’s critical distance in the cortical map. Given the very similar mappings in areas V2, V3, V4 (Larsson et al., 2006; Schira et al., 2009), that relationship can be expected to be similar in those areas. Since the equations for crowding follow mathematically, they should work well there with suitable $E_2$ or $d_2$ values inserted. Thus, direct confirmations of their behaviour can cross-validate mapping models and might shed light on the cortical mechanisms underlying crowding.

5. Outlook

Where does this leave us? The early cortical visual areas are very regularly organized and their spatial maps appear to be pretty similar. However, empirical $E_2$ estimates for the CMF, and particularly the latter’s value in the retinotopic centre, differ vastly. The present equations might help to draw comparisons and uncover reasons for these variations.

For low-level psychophysical tasks that are somehow connected to stimulus size there is a remarkable similarity between their $E_2$ and that of the CMF. In contrast, $E_2$ for critical crowding distance is decidedly not related to stimulus size; it rather reflects location differences. The underlying cortical architecture that brings about psychophysical $E_2$ values differing from that of the CMF (like $E_2$) are likely neural wiring differences in early visual areas, underneath a similar topography.

The link between the (local) CMF function and the (global) cortical location function derived here rests on the assumption of spatial additivity – that local distances add-up to global distances and the location function is thus the integral of the CMF function. $E_2$ values different from that of the CMF thus do not translate to a location function. When two different $E_2$ values interact, as in crowding, nonlinear functions as those in Fig. 8 arise.

The aim of the present paper is to point out that a common spatial location function underlies the early cortical architecture that can be described by a unified equation. This equation includes the retinotopic centre, and has parameters that are common in psychophysics and physiology.

CRediT authorship contribution statement

Hans Strasburger: Conceptualization, Methodology, Validation, Formal analysis, Writing – original draft, Writing – review & editing.

Acknowledgements

I thank Dany d’Souza for the original question and first calculations, Barry Lee for critical comments on the manuscript and meticulous language corrections, Zhaoping Li, Josh Solomon, and Christopher W. Tyler for critical reading. Thanks also to an anonymous reviewer for pointing out Klein & Levi’s (1987) paper and to two reviewers for very thorough reading and pointing out misleading phrasings.

Appendix

The appendix contains a few further details and the equation for critical crowding distance in the cortical map expressed with $d_2$. Further details are given in the Supplement.

Further concepts

Anisotropy. The visual field is not isotropic: Performance declines differently between radii. Slopes differ between vertical and horizontal direction, and upper vs lower field. Accordingly, iso-performance lines (for the binocular field) are distorted ellipses rather than circular outside the central visual field, which is isotropic (e.g. Wertheim, 1894, Harvey & Pöppel, 1972, Rovamo & Virsu (1979, p. 498), e.g., computed separate $M$ estimates for each meridian. There is further a nonlinearity at the transition from the isotropic to the anisotropic field (Pöppel & Harvey, 1973, Fig. 6). Correspondingly, early visual areas are also anisotropic (e.g. Horton & Hoyt, 1991). The effect of anisotropy on the cortical magnification factor is quantitatively treated by Schira et al. (2007, 2010); their $M_0$ estimate is the geometric mean of the isopolar and isoeccentric $M$ estimates. In the equations presented below, the horizontal/vertical anisotropy can be accommodated by letting the parameters depend on the radius in question. There are further anisotropies that are not accounted for by varying slopes along the radii (Schira et al., 2007, 2010). These authors, for preserving area constancy across meridians, extend modelling by a shear function (using the hyperbolic secans; Schira et al., 2010, eq. (6) and Fig. 2). Mappings then differ between meridians, with deviations from linearity most noticeable on, and close to, the vertical meridian at around 1° eccentricity (Schira et al., 2010, Fig. 2). The derivations presented here, for simplicity, do not include these refinements.

Cortical distance measures and symbols used in the equations

Cortical distance is either measured from the retinotopic centre or from some reference location (1D case) or reference contour line (2D case). Fig. A1 illustrates the various distance measures and how they are related.

Fig. A1. Illustration of the cortical distance measures used in the equations. $d$ – Cortical distance of a location from the retinotopic centre, in mm; $d_{ref}$ – Cortical distance (from the centre) of the reference that corresponds to $E_{ref}$; $d_r$ – Cortical distance of the location that corresponds to $E = 1$; $\hat{d}$ – Cortical distance of a location $d$ from the reference $d_{ref}$.
Critical crowding distance in the cortical map, expressed with $d_2$

The equations for critical crowding distance in the cortical map (eq. (17)–(19)) have $M_0$ (the central CMF) as a scaling factor in it. Its empirical estimates vary widely and it makes sense to replace it by the more stable $d_2$ (eq. (5)). The equation for the critical cortical crowding distance (eq. (17)) then becomes

$$
\kappa = \frac{d_2}{\ln 2} \left(1 + \frac{\delta_0}{E_2} \right) \left(1 + \frac{E_2}{E_1}\right) \left(E_1 + E_2\right)
$$

(A1)

Similarly, the two special cases for the foveal and peripheral critical distance (eq. (18) and (19)) are then

$$
\kappa_0 = \frac{d_2}{\ln 2} \left(1 + \frac{\delta_0}{E_2} \right) \text{ and } \lim_{E_1 \to \infty} \kappa = \frac{d_2}{\ln 2} \ln \left(1 + \frac{\delta_0}{E_2}\right)
$$

(A2)

Values for $d_2$ derived from the literature that could be plugged in are provided in Table 3 or can be obtained by eq. (5). The two special cases could lend themselves for empirically determining critical crowding distance in the cortex.

Parameters assumed for the graph of cortical crowding distance (Fig. 8)

Fig. 8 shows an example graph for eq. (17) – critical crowding distance in the cortex – with realistic values for $M_0$, $E_2$, $E_3$, and $\delta_0$ assumed. The assumptions are a best guess from the literature. The value of $E_2$ for $M^{-1}$ was chosen as $E_2 = 0.8'$ from Dover, Snyder, Vautin, and Biederman-Thorson (1981) (as cited in Levi et al., 1985, or Strasburger et al., 2011). $M_0 = 29.1$ mm was chosen to give a good fit with this $E_2$ in Fig. 4. Foveal critical distance was set to $\delta_0 = 0.1$ from Siderov, Waugh, and Bedell (2013, 2014). An $E_2 = 0.36'$ would obtain with this $\delta_0$ and the value of $\delta_0 = 1.2$ in Strasburger et al. (1991); it is markedly different from $E_2$ for the CMF, showing the $E_2/E_3$ ratio’s influence on the graph.

Supplementary data

The supplement provides further details on four examples from the literature (Larsson & Heeger, 2006; Duncan & Boynton, 2003; Schira et al., 2007, 2009, 2010; and Motter & Simon, 2007), furthermore help on how to derive critical distance in the cortical map, and finally details on the derivation of the deprecated location function without a constant term (eq. (12)). The Supplement can be found online at https://doi.org/10.1016/j.visres.2021.107972.

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