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Two common psychophysical measures of surround suppression reflect independent neuronal mechanisms

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Psychophysical surround suppression is believed to reflect inhibitory neuronal mechanisms in visual cortex. In recent years, two psychophysical measures of surround suppression have been much studied: (i) duration thresholds on a motion-discrimination task (which are worse for larger than for smaller stimuli) and (ii) contrast thresholds on a contrast-detection task (which are worse when grating stimuli are surrounded by a stimulus of the same orientation than when they are presented in isolation or surrounded by a stimulus of orthogonal orientation). Changes in both metrics have been linked to several different human conditions, including aging, differences in intelligence, and clinical disorders such as schizophrenia, depression, and autism. However, the exact nature of the neuronal correlate underlying these phenomena remains unclear. Here, we use an individual-differences approach to test the hypothesis that both measures reflect the same property of the visual system, e.g., the strength of GABA-ergic inhibition across visual cortex. Under this hypothesis we would expect the two measures to be significantly positively correlated across individuals. In fact, they are not significantly correlated. In addition, we replicate the previously reported correlation between age and motion-discrimination surround suppression, but find no correlation between age and contrast-detection surround suppression. We conclude that the two forms of psychophysical surround suppression arise independently from different cortical mechanisms.

Introduction

In visual neuroscience, the term *surround suppression* was originally introduced by physiologists studying the responses of individual neurons, to describe a reduction in firing produced by stimuli placed outside the classical receptive field (Allman, Meizin, & McGuiness, 1985; Benevento, Creutzfeldt, & Kuhnt, 1972; Jones, Grieve, Wang, & Sillito, 2001; Maffei & Fiorentini, 1976; Sceniak, Ringach, Hawken, & Shapley, 1999; Sengpiel, Sen, & Blakemore, 1997) that is thought to be mediated by GABA-ergic inhibitory connections (Alitto & Dan, 2010; Angelucci & Bressloff, 2006; Gieselmann & Thiele, 2008; Nurminen & Angelucci, 2014; Smith, 2006). Surround suppression is found in many visual areas—including primary visual cortex V1 (Allman et al., 1985), secondary visual cortex V2 (Shushruth, Ichida, Levitt, & Angelucci, 2009), V4 (Sundberg, Mitchell, & Reynolds, 2009), middle temporal area MT (Allman et al., 1985; Huang, Albright, & Stoner, 2007, 2008; Tsui & Pack, 2011), lateral intraparietal area LIP (Falkner, Krishna, & Goldberg, 2010), and the frontal eye fields FEF (Cavanaugh, Joiner, & Wurtz, 2012)—

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leading many to speculate that it is a fundamental feature of visual computation.

At a perceptual level, surround suppression may contribute to visual attention (Falkner et al., 2010; Reynolds & Heeger, 2009; Sanayei, Herrero, Distler, & Thiele, 2015) and scene segmentation (Hupe et al., 1998; Park & Tadin, 2014). It is also believed to underlie two counterintuitive properties of human visual perception. First, the apparent contrast of a visual stimulus can be reduced by stimuli in the surrounding visual field (Andriessen & Bouma, 1976; Cannon & Fullenkamp, 1991; Petrov, Carandini, & McKee, 2005; Snowden & Hammett, 1998). This and related effects are attributed to surround suppression processing in V1 (Zenger-Landolt & Heeger, 2003). Second, discriminating the direction of motion of a moving pattern becomes more difficult with increasing stimulus size (Tadin, Lappin, Gilroy, & Blake, 2003), which has been attributed to surround suppression in area MT. These perceptual phenomena are often referred to collectively as psychophysical surround suppression.

In recent years, several studies have used these two perceptual phenomena to reveal differences between healthy control participants and several clinical groups, including people with schizophrenia (Chen, Norton, & Ongur, 2008; Golomb et al., 2009; Robol et al., 2013; Serrano-Pedraza et al., 2014; Tibber et al., 2013; E. Yang et al., 2013b; Yoon et al., 2009; Yoon et al., 2010), depression (Golomb et al., 2009), autism (Flevaris & Murray, 2014; Foss-Feig, Tadin, Schauder, & Cascio, 2013; Koldewyn, Whitney, & Rivera, 2010), and migraine (Battista, Badcock, & McKendrick, 2010, 2011), as well as differences between younger versus older adults (Betts, Sekuler, & Bennett, 2009, 2012; Betts, Taylor, Sekuler, & Bennett, 2005). Such results suggest that these simple and noninvasive psychophysical tests have the potential to cast light on the underlying pathology in these conditions and could provide clinically useful information about individual patients.

A key question to resolve, however, is whether different psychophysical metrics of surround suppression really probe different aspects of pathology. The clinical changes have been attributed to changes in GABA-ergic inhibition—e.g., lower cortical concentrations of GABA in patients with depression (Sanacora et al., 1999) or schizophrenia (Yoon et al., 2010). If these changes could selectively affect different areas of visual cortex, the various metrics of psychophysical surround suppression could be differentially impacted. On the other hand, if cortical surround suppression reflects whole-organism properties such as genetics, age (Betts et al., 2005; Betts et al., 2009, 2012) or IQ (Melnick, Harrison, Park, Bennetto, & Tadin, 2013), or if surround suppression in higher visual areas is "inherited" from processing in V1 (Tsui, Hunter, Born, & Pack, 2010), then the various metrics would reflect a single fundamental neuronal property.

To examine the relationship between these two surround suppression phenomena, we made use of the fact that both metrics show wide variation between individuals even in healthy populations (Read et al., 2015). This allows for a powerful test of the hypothesis that contrast detection and motion-direction discrimination both reflect a common underlying property, because it would predict that the two metrics would show a strong positive correlation across the population. Here, for the first time, we report both metrics in the same group of neurologically healthy individuals, and find that they are not correlated. We conclude that the two forms of psychophysical surround suppression reflect independent aspects of cortical networks.

Methods

Participants

Thirty-six healthy volunteers (10 male; mean age: 42.3 years; range: 19.4–69.1) were recruited. All had normal or corrected-to-normal visual acuity. Experimental procedures were approved by the Newcastle and North Tyneside 1 Research Ethics Committee (reference number 09/H0906/90). Participants gave written informed consent and were paid a nominal fee for their participation. Participants completed the two tasks described later. All participants were given instructions and were assessed briefly during practice runs to ensure that they understood the procedure, prior to any data collection. Participants could ask for a break within each trial and also in between the two tasks. The overall time to complete both tasks was around 30 min.

Apparatus

Stimuli were created in MATLAB (www.mathworks.com) with the Psychophysics Toolbox (Brainard, 1997; Pelli, 1997). A DATAPixx Lite visual stimulator from VPixx Technologies (http://www.vpixx.com/products/visual-stimulators/datapixx-lite.html) was used to generate the visual stimuli with 12-bit pixel depth. A RESPONSEPixx tabletop (http://www.vpixx.com/products/response-boxes/tabletop.html) was used to record subject responses. The Procedural Gabor functionality of the Psychophysics Toolbox was used to display the drifting Gabor patch. Experiments were shown on a 22-in. P1210 Compaq CRT monitor with 800 × 600 pixels of resolution and frame rate of 160 Hz. A Minolta photometer, model Luminance

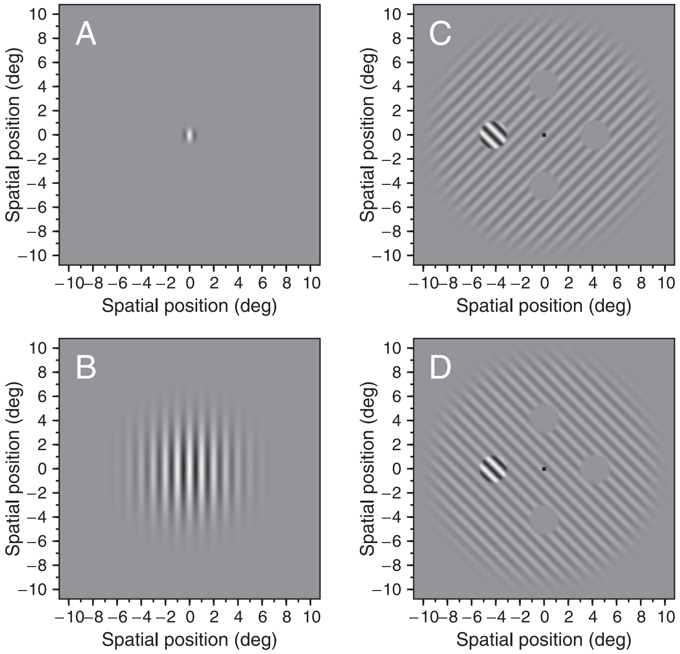

Figure 1. Schematic illustration of the two example stimuli. Left: Tadin stimulus (A: small; B: large) is a standard Gabor patch, a drifting vertical sine grating windowed by a Gaussian spatial envelope. Right: Annulus stimulus (C: stimulus with an orthogonal surround; D: stimulus with a parallel surround) is a contrast-detection threshold of a grating located in the periphery. On each trial, a grating was placed in one of four possible positions in parallel or orthogonal orientation to the surround.

Meter LS-100, was used to measure the gamma correction ($\gamma = 2.3$). All code was programmed in MATLAB using the Psychophysics Toolbox (Kleiner, Brainard, & Pelli, 2007). Viewing was binocular at 100 cm in a dimly lit room (the luminance reflected by a white sheet of paper was about 0.8 cd/m^2).

Task 1: Motion-direction discrimination

We followed the protocol described by Tadin and colleagues (Tadin et al., 2003; Tadin et al., 2006). Prior to each trial, observers were guided to fixate at the center of the monitor by the appearance (500 ms) of a small cross within a Gaussian temporal window with a standard deviation of 80 ms. The stimulus was a standard drifting Gabor patch, i.e., a vertical sine-wave grating windowed by a Gaussian envelope (Figure 1A, B). We used two different stimulus sizes, defined as twice the spatial standard deviation of the Gaussian envelope (2σ). Small stimuli had $2\sigma = 0.7^\circ$ and large stimuli had $2\sigma = 5^\circ$. The envelope was stationary on the screen, but the carrier sine wave moved horizontally at constant speed. The carrier spatial and temporal frequencies were 1 c/° and 2 c/s (Hz), respectively, resulting in a speed of 2°/s. Stimuli appeared within a temporal Gaussian envelope, so the stimulus contrast ramped up from zero to a peak value and then down again. When we refer to the contrast of the stimulus, we mean the value of this peak. We used two different stimulus contrasts: high (peak contrast = 92%) and low (peak contrast = 2.8%). We defined the duration of the stimulus as twice the temporal standard deviation (2τ).

Participants' task was to report the direction of motion of the Gabor by pressing the left or right button on the ResponsePixx box. Task difficulty was modulated by altering stimulus duration. Duration threshold was measured as described by Read et al. (2015). Briefly, a Bayesian adaptive staircase was used to choose the stimulus duration on each trial. For each participant, either two or three staircases, each containing 50 trials, were randomly interleaved. We then fitted a psychometric function to all trials collected for that participant in order to arrive at an estimate of duration threshold, defined as the value where performance reached 82% correct. As described by Read et al. (2015), bootstrap resampling was used to extract 95% confidence intervals for the fitted thresholds.

The total time taken for each trial was slightly different from that described by Read et al. (2015). There, each trial lasted 700 ms, independent of the temporal standard deviation τ of the stimulus. Here, each trial was set to last 10τ, with the peak contrast occurring halfway through. This means that the total time taken by each trial depends on the value of τ. The benefit is that the temporal Gaussian was never truncated; stimuli always began with zero contrast at the beginning of a trial rather than appearing abruptly, as could otherwise occur when τ exceeded $\sim$300 ms. We constrained τ to lie in the range 10–1000 ms; it was clipped to this range if the staircase tried to choose values outside this. As the Results and discussion show (Figure 2), duration thresholds for almost all subjects were well below 1000 ms, so in practice this clipping had little effect.

Task 2: Contrast detection

This stimulus was adapted directly from Serrano-Pedraza, Grady, & Read (2012); it is closely related to those used by previous authors including Cannon & Fullenkamp (1991), Petrov et al. (2005), and Yoon et al. (2010). The stimulus is shown in Figure 1C and D. It consisted of a large static sinusoidal luminance grating, of spatial frequency 1.1 c/°, contrast 25%, and diameter 18°, oriented at ±45° to the vertical, with four circular holes cut out of it. The holes had a diameter of 2.3°, were centered on an eccentricity of 4.2°, and lay on the four cardinal directions. On each trial, one of the holes

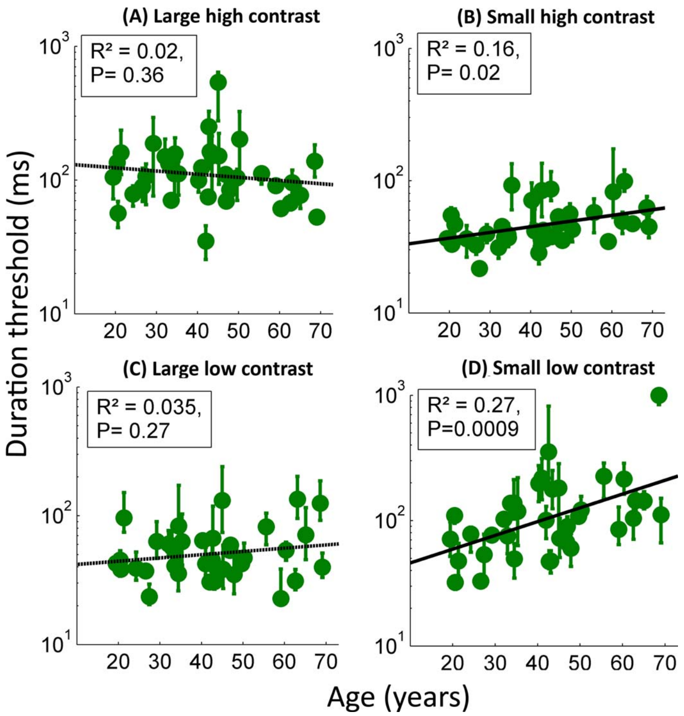

Figure 2. Duration thresholds plotted as a function of age on log axes for 36 participants for the motion-discrimination task. Four stimulus conditions are shown: (A) large high-contrast (92%); (B) small high-contrast (92%); (C) large low-contrast (2.8%); (D) small low-contrast (2.8%). Error bars show 95% confidence intervals. Lines show regression with age; solid lines are those where the regression with age was significant, dashed lines are where it was nonsignificant. R^2 and *p* values are marked in each panel.

was filled with a small sinusoidal luminance grating of the same diameter as the hole. This target grating had the same spatial frequency as the large background grating and was also oriented at ±45° to the vertical. All gratings and holes were presented within a 10th-order Butterworth window so that edges were smooth. The stimulus was presented within a temporal Gaussian window with standard deviation 50 ms. As before, by stimulus contrast we mean the peak contrast reached during this Gaussian. Before each trial, a rotating fixation cross was displayed at the center of the screen for 1 s. This was intended to help capture the participant's attention to the center of the screen. Trials consisted of brief presentations of a four-alternative spatial forced-choice paradigm. Participants were asked to detect the position of the target by choosing one of four buttons on the ResponsePixx box.

The location of the target and the orientation of the background were chosen randomly on each trial. The target orientation had two possible conditions: parallel or orthogonal to the surround. Task difficulty was modulated by altering target contrast. A 30-trial Bayesian staircase procedure was used to choose target contrast on each trial. Separate, interleaved staircases were used for the parallel and orthogonal conditions; the computer chose the condition randomly on each trial. The experiment was repeated such that all participants completed at least two (several completed three) 30-trial staircases per condition. The contrast threshold was defined as a performance of 62.5% correct. As before, the threshold was measured by fitting a psychometric function to all data collected for that participant.

Suppression index (SI)

We use the surround suppression index introduced by Tadin et al. (2006), defined as the logarithm of the ratio of the duration thresholds *T* for large and small stimuli:

$$\begin{aligned} S_{\mathrm{M}} &= \log_{10}(T_{\mathrm{large}}/T_{\mathrm{small}}) \\ &= \log_{10}(T_{\mathrm{large}}) - \log_{10}(T_{\mathrm{small}}) \end{aligned} \quad (1)$$

A positive index is taken as a measure of surround suppression (i.e., shorter thresholds for small stimuli), whereas a negative index is indicative of spatial summation (i.e., shorter thresholds for larger stimuli; Anderson & Burr, 1991). Accordingly, we shall use the term motion suppression index when Equation 1 is used with the thresholds for high-contrast stimuli (and is thus usually positive), and motion summation index when it is used with thresholds for low-contrast stimuli (and is thus usually negative).

In the contrast-detection task, contrast thresholds *C* are generally higher when the eccentric target is surrounded by a parallel grating (same orientation) than by an orthogonal grating (Ejima & Takahashi, 1985; Lev & Polat, 2011; Petrov et al., 2005; Polat & Sagi, 1993; Serrano-Pedraza et al., 2012; Snowden & Hammett, 1998; Xing & Heeger, 2000; Yu & Levi, 2000). Accordingly, we define an analogous contrast suppression index as

$$\begin{aligned} S_{\mathrm{c}} &= \log_{10}(C_{\mathrm{para}}/C_{\mathrm{ortho}}) \\ &= \log_{10}(C_{\mathrm{para}}) - \log_{10}(C_{\mathrm{ortho}}) \end{aligned} \quad (2)$$

Results and discussion

Task 1: Motion-direction discrimination

Figure 2 shows duration thresholds on the motion-discrimination task for 36 subjects plotted as a function of age. The upper panels (A, B) show thresholds for the high-contrast stimulus; lower panels (C, D) show thresholds for low-contrast stimulus. The left panels

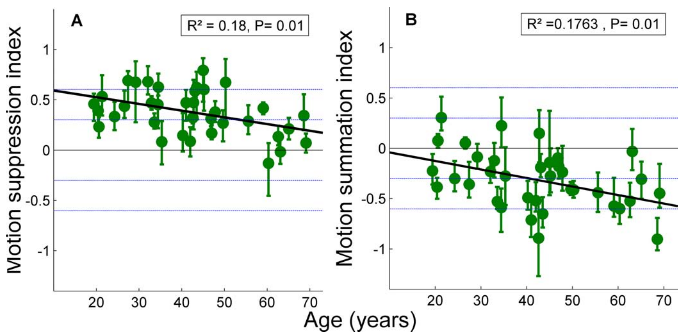

Figure 3. Motion-discrimination task. Index is log ratio of large/small duration thresholds, shown for 36 subjects as a function of age. (A) Suppression index for high-contrast stimuli; (B) summation index for low-contrast stimuli. As before, error bars show 95% confidence intervals, and the black line is the regression line. The solid horizontal line shows index = 0—i.e., thresholds are the same for large and small stimuli. The inner and outer dashed lines mark values of the index where thresholds differ by a factor of 2 and 4, respectively. The fitted regression lines are (A) index = −0.006 × (age in years) + 0.65 and (B) index = −0.0085 × (age in years) + 0.04. R^2 and p values are marked in each panel.

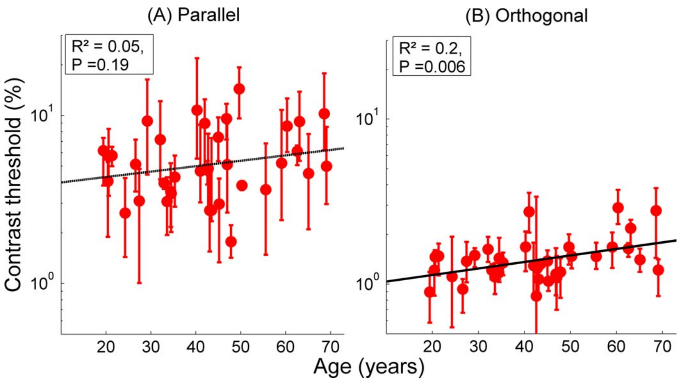

Figure 5. Contrast thresholds for contrast-detection task, plotted against age, when the background grating was (A) parallel or (B) orthogonal to the target. Error bars show 95% confidence interval. Solid line is where the regression with age was significant, dashed line is where it was nonsignificant. R^2 and p values are marked in each panel. The fitted regression lines are (A) $\log_{10}$(threshold) = 0.003 × (age in years) + 0.57 and (B) $\log_{10}$(threshold) = 0.004 × (age in years) − 0.02.

(A, C) show thresholds for large stimuli, the right (B, D) for small stimuli. In line with previous reports (Aaen-Stockdale, Thompson, Huang, & Hess, 2009; Betts et al., 2005; Betts et al., 2009, 2012), we found that for high-contrast stimuli, duration thresholds were longer for large than for small stimuli, whereas for low-contrast stimuli, thresholds were shorter for large stimuli. Duration thresholds tended to increase with age, but this effect was significant only for the small stimuli ($p = 0.02$ for small high-contrast: Figure 2B; $p = 0.0009$ for small low-contrast: Figure 2D). This is in agreement with Betts et al. (2005). They divided their subjects into "younger" (mean age: 23 years) and "older" (mean age: 68), reporting that duration thresholds were higher for the older observers for the small stimuli ($2\sigma = 0.7°$) at all contrasts but did not differ between age-groups for the large stimuli ($2\sigma = 2.7°$).

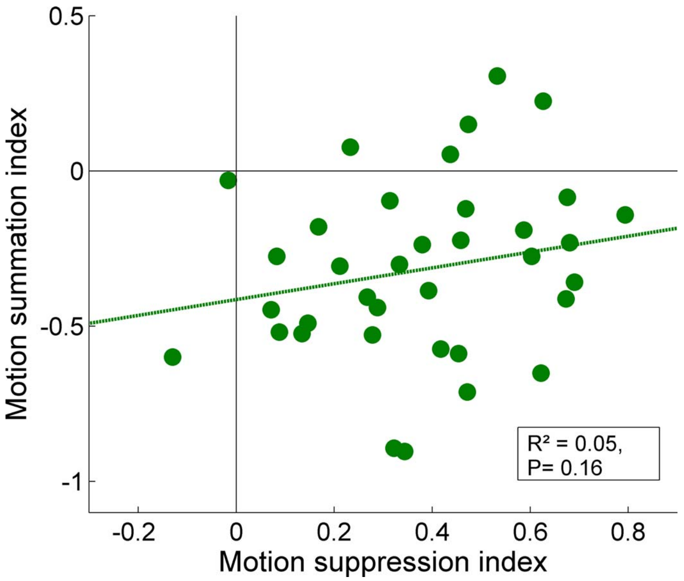

Figure 4. Scatterplot of motion summation index against suppression index for 36 subjects. R^2 and p values for the Pearson correlation coefficient are marked in the box. The green line shows the regression line, fitted assuming that both variables are subject to the same amount of error (Draper & Smith, 1998). The slope of this regression also did not differ significantly from zero. The solid black lines show index = 0.

In Figure 3, we plot the motion suppression index (A) and motion summation index (B; Equation 1) as a function of age. Both metrics showed a significant decline with age (we defined the summation index such that more negative values indicate stronger summation). This is again in close agreement with Betts et al. (2005). For comparable stimulus parameters, they reported a mean suppression index of around 0.2 at 23 years and 0 at 68 years, or an average decline of 0.004 per year. The suppression index was fractionally higher in our population, at around 0.5 at 25 years, but the rate of decline was similar (0.006 per year). We found that the summation index also declines with age at a similar rate (0.008 year; Figure 3B). We found that spatial summation was nearly absent in younger adults, in that duration thresholds were very similar for both large and small low-contrast stimuli. However, with increases of age, spatial summation appeared to increase, until by age 70, thresholds for large low-contrast stimuli were almost a factor of 4 shorter than those for small ones. This decline is rather steeper than

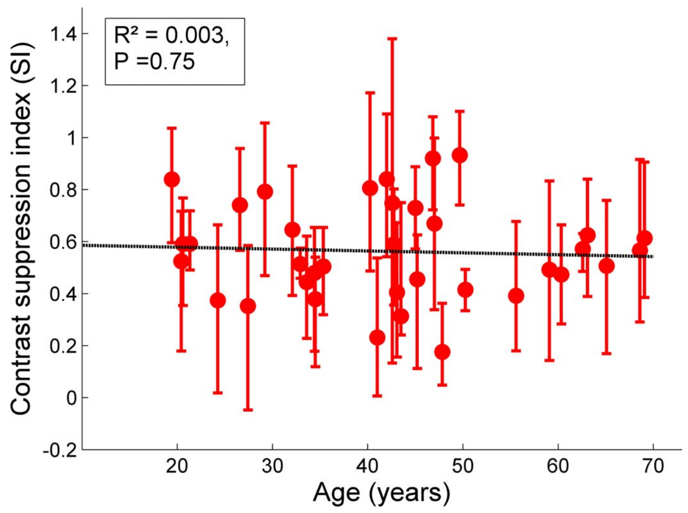

Figure 6. Contrast suppression index on the contrast-detection task for 36 subjects as a function of age. Error bars show 95% confidence intervals, and the dashed line is the regression between contrast suppression index and age. There is no significant relationship between age and index ($p = 0.75$).

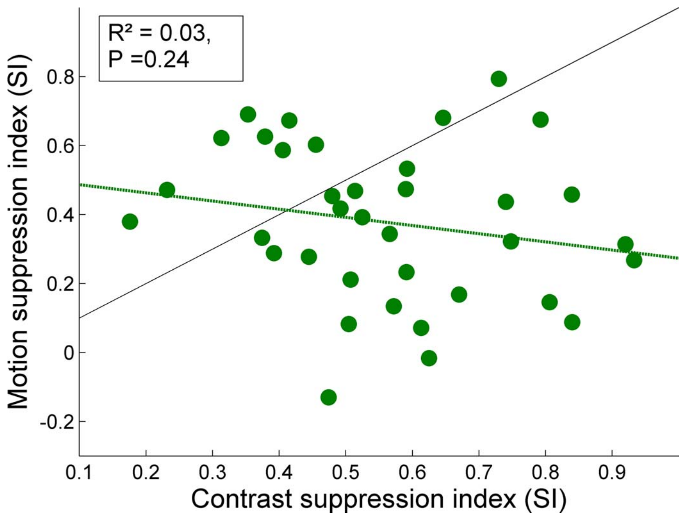

Figure 7. Scatterplot of surround suppression index on the motion-discrimination task compared to the contrast-detection task for 36 participants. The dashed line is the regression line ($p = 0.24$), and the solid black line indicates the line of equality. There is no significant correlation between motion-discrimination suppression index and contrast-detection suppression index (correlation coefficient $\rho = -0.1978$, $p = 0.24$).

that implied by the difference between the younger and older groups of Betts et al. Because our stimuli were presented at fixed contrast, as opposed to a fixed multiple of contrast threshold, the decline in summation index with age may reflect an increase in contrast threshold with age (Figure 5). The decline in suppression index with age is unlikely to reflect this, since suppression index is much less sensitive to contrast (Tadin et al., 2006).

Figure 4 shows the motion summation index plotted against the suppression index. Given that both decline with age, one might expect them to be positively correlated. However, although the slope of the regression line is positive, it is not significant.

Task 2: Contrast detection

Figure 5 shows contrast thresholds measured with the surround parallel (A) and orthogonal (B) to the target, as a function of participant age. Contrast thresholds increase with age in both cases, although due to the greater variability in the parallel-surround case, the increase is significant only for the orthogonal-surround case ($p = 0.006$). The same result was found by Serrano-Pedraza et al. (2014) in an independent sample of 24 controls. According to the fitted regression line, the mean orthogonal contrast threshold rises from 1.1% at age 20 to 1.3% at age 69. This is in broad agreement with the literature on aging and vision. Many studies have reported a tendency for contrast thresholds to increase with age, especially at high spatial and temporal frequencies (reviewed in Owsley, 2011), although our increase of a factor of 1.6 is high compared with studies using grating stimuli. Our stimuli had a low spatial frequency (1.1 c/°) and had most power at low temporal frequencies (they were presented within a temporal Gaussian window with standard deviation of 50 ms, so their amplitude spectrum is a Gaussian function with a temporal frequency of 3.2 Hz). For comparison, Elliott, Whitaker, & MacVeigh (1990) found no difference in contrast sensitivity between young (mean age: 23 years) and old (mean age: 69 years) observers at low temporal frequencies (0 and 4 Hz) but found that younger observers were a factor of ~1.1 more sensitive at 16 Hz.

Figure 6 shows the contrast suppression index (Equation 2) against age. In this task, there was no correlation between age and surround suppression ($R^2 = 0.003$, $p = 0.75$). The contrast suppression index was 0.56 ± 0.2 (mean ± population *SD*), independent of age, again in agreement with Serrano-Pedraza et al. (2014). Contrast thresholds become slightly worse with age, but they increase roughly equally in both the parallel- and orthogonal-surround conditions, meaning that the threshold ratio remains constant.

Serrano-Pedraza et al. (2014) also found no effect of age when they examined the ratio of contrast threshold for a grating patch with a parallel surround to the threshold for an isolated patch (no-surround condition). However, Karas & McKendrick (2009, 2011, 2012, 2015) have shown that there is an effect of age for stimuli above threshold. Suprathreshold patches ap-

	Motion suppression index	Contrast suppression index
Estimated between-subjects standard deviation s in the absence of measurement error	$s_M = 0.21$	$s_C = 0.14$
Mean within-subject standard deviation of measurement error ω	$\omega_M = 0.075$	$\omega_C = 0.12$
Ratio ω/s	0.36	0.86

Table 1. Estimated standard deviations between and within subjects.

pear lower contrast when presented with a parallel surround than when presented in isolation, and this surround suppression is greater for older adults (65–70 years) than for younger ones.

Relationship between motion and contrast suppression indices

Figure 7 is a scatterplot of the suppression index on the motion-discrimination task plotted against that on the contrast-detection task. The black solid line represents the line of equality, and the green dashed line shows a nonsignificant regression line ($p = 0.24$). If surround suppression indices produced on both tasks were the same, the data points should be scattered around the line of equality. The population means and standard deviations were quite similar for the two suppression indices, at 0.40 ($SD = 0.22$) for the motion-discrimination task and 0.56 ($SD = 0.19$) for the contrast-detection task, but critically, the two suppression indices were not correlated with one another.

Before accepting this, it is important to ask whether errors in measuring the individual suppression indices could obscure a real correlation. Estimates of suppression index were fairly unreliable (compare the error bars in Figures 3 and 6), since they are the log ratios of two thresholds which are themselves each subject to noise. Experimental error affecting the measurements of the two variables will systematically reduce the value of the measured correlation below the true value. How badly the measurement error degrades the observed correlation depends on the size of the measurement error relative to the variability present in the population. In the Appendix, we show that if the sample correlation coefficient between the two suppression indices, measured in the presence of noise, has the value R, the true correlation coefficient ρ between the two indices could be as high as

$$\rho = R\sqrt{\left[1+\left(\frac{\omega_M}{s_M}\right)^2\right]\left[1+\left(\frac{\omega_C}{s_C}\right)^2\right]} \quad (3)$$

where ω_M and ω_C are the standard deviation of measurement noise affecting the motion and contrast suppression indices, and s_M and s_C are the standard deviations of the (noise-free) between-subjects variation. The between-subjects and within-subject standard deviations for both suppression indices are given in Table 1 (see Appendix for details of calculation).

The observed correlation coefficient was $R = -0.20$, but Equation 3 implies that, given the reliability of our estimates of surround indices in Table 1, the true correlation coefficient could be as large as $\rho = -0.27$. Thus it would be hard to rule out a negative correlation between the two indices. However, it is highly unlikely that they are positively correlated.

General discussion

In this article, we have considered two visual-psychophysics measures which have both been considered to represent perceptual consequences of cortical surround suppression (Alitto & Dan, 2010). The first is the longer time required to discriminate motion direction for large high-contrast moving stimuli compared to small ones, quantified by the motion suppression index. The second is the lower contrast threshold obtained for oriented stimuli presented on a background of orthogonal orientation compared to backgrounds of the same orientation. This was quantified by the contrast suppression index.

Differences in both these indices have been found between control groups and clinical groups. For example, Tadin et al. (2006) examined motion suppression index and found that patients with schizophrenia had significantly higher thresholds than did members of a control group for the small high-contrast stimulus but were similar for the large stimulus, resulting in a lower suppression index for the patients with schizophrenia. The researchers attributed this to an abnormality of cortical area MT in schizophrenia, probably reflecting a deficit in GABA-ergic inhibition (Wassef, Baker, & Kochan, 2003). Interestingly, Chen et al. (2008) found the opposite result: Using random-dot motion stimuli, they found that surround suppression was abnormally increased in patients with schizophrenia when compared with members of a matched control group. In spatial vision, Yoon et al. (2009) and Serrano-Pedraza et al. (2014) showed reduced contrast suppression in patients with schizophrenia. Both of those studies found that patients with schizophrenia had significantly higher thresholds than members of a control group on the easier conditions (no surround and a surround grating orthogonal to the signal) but similar thresholds for the harder condition (surround parallel to the signal), again resulting in a lower suppression index. In a subsequent study, Yoon et al. (2010) used magnetic resonance spectroscopy to show that patients with schizophrenia had lower concentrations of the inhibitory neurotransmitter GABA in visual cortex, and that GABA concentration was positively correlated with suppression index across patients and controls. Thus, the lower-than-usual suppression indices on both tasks may reflect reduced levels of GABA in people with schizophrenia. Golomb et al. (2009) also reported lower suppression indices on the motion-discrimination task in patients with major depressive disorder, and suggested that this too was linked to dysfunction of GABA-ergic inhibition in these patients. Given the wide range of indices studied in the literature and the relative paucity of replications, it is possible that some of the reported correlations represent type I error, but changes in suppression are increasingly being linked to pathology.

In all these studies, the suppression indices have been interpreted as being a psychophysical measure of cortical inhibition, which is taken to be disrupted in the clinical groups. As we have seen (Table 1), the two indices of surround suppression show considerable variation even among healthy members of a control group. Yoon et al. (2010) found a positive correlation between GABA concentration and the contrast-discrimination suppression index in seven control participants ($r = 0.71$), although unsurprisingly, given the low numbers, this just failed to reach significance ($p = 0.077$). It is reasonable to speculate, therefore, that individual variation in suppression index reflects individual variation in some aspect of GABA-ergic inhibition. If so, and if both indices reflect the same aspect of inhibition, we would expect them to be positively correlated across individuals.

In this article, we examined this proposition and found that individual variations in the two different suppression indices were not positively correlated. E. Yang et al. (2013a, 2013b) have also found no correlation between performance, in either control or clinical groups, on several different tasks all chosen to assess the effect of visual context. Their tasks did not include any used here but did include a motion-direction discrimination task and a contrast-discrimination task. Only the contrast-discrimination task showed a difference in patients with schizophrenia. The researchers concluded that the lack of intertask correlation indicates that their tasks "reflect largely distinct neural mechanisms"(E. Yang et al., 2013b, p. 11). We now extend this conclusion to our two surround indices, even though both are altered in schizophrenia (Serrano-Pedraza et al., 2014; Tadin et al. 2006).

The separate nature of these two indices is further corroborated by differences in their relationship to age. The motion suppression index decreases with age, as does the motion-discrimination summation index measured at low contrast. On the other hand, the contrast suppression index shows no change with age between the ages of 20 and 70 with our prethreshold measures, while with suprathreshold contrasts, contrast suppression actually increases with age (Karas & McKendrick, 2009, 2011, 2012, 2015).

The contrast suppression index depends on differences in contrast sensitivity depending on the orientation of the surround, suggesting an early cortical locus (Yoon et al., 2010; Zenger-Landolt & Heeger, 2003). Its spatial-frequency tuning (Serrano-Pedraza et al., 2012) also agrees with the properties of V1 neurons (Blakemore & Tobin, 1972; Cavanaugh, Bair, & Movshon, 2002; DeAngelis, Robson, & Freeman, 1992). This antagonism is believed to be implemented by feedback projections from extrastriate cortex, mediated by inhibitory projections from nearby interneurons (Alitto & Dan, 2010). In contrast, the motion suppression index has been advanced as a perceptual correlate of center–surround antagonism in cortical area MT (Betts et al., 2012; Churan, Khawaja, Tsui, & Pack, 2008; Tadin et al., 2003). Thus, one possible explanation of our results is that, while previous authors have been correct in postulating that the contrast and motion suppression indices reflect the strength of inhibition in cortical areas V1 and MT respectively, the strengths of inhibition in these two areas are not correlated with one another across individuals. It may be that both indices reflect the concentration of GABA in a particular cortical area but that these different areal GABA concentrations change independent of each other. This is not necessarily at odds with the fact that both indices have been shown to be reduced in patients with schizophrenia. For example, it could be that the two indices are affected both by some global parameter G controlling the strength of inhibition all over visual cortex, but also by some local parameter L which varies between cortical areas as well as between individuals. Under this model, our results imply that the variance of L, across cortical areas V1/MT and healthy individuals, is large compared to the variance of G across healthy individuals, resulting in no correlation between the two suppression indices. The results from the clinical studies imply that the variance of G between patients with schizophrenia and healthy individuals is large. We would then expect to observe a positive correlation between our two suppression indices across a population containing a large enough variance in *G*—e.g., containing both healthy individuals and patients with severe schizophrenia. This prediction has not yet been tested.

However, the dependence on age does not fit well with the interpretation that the contrast and motion indices provide psychophysical estimates of the strength of GABA-ergic inhibition in V1 and MT, respectively. Several studies have suggested that the effective strength of GABA-ergic inhibition declines with age, but this appears to affect both V1 (Fu, Yu, Ma, Wang, & Zhou, 2013; Hua, Kao, Sun, Li, & Zhou, 2008; Hua et al., 2006; Leventhal, Wang, Pu, Zhou, & Ma, 2003; Pinto, Hornby, Jones, & Murphy, 2010) and MT (Liang et al., 2010; Y. Yang et al., 2009). Thus, it is not clear on this account why the contrast suppression index shows no dependence on age, whereas motion tasks have been shown by several different authors to show a decline in suppression and/or an increase in summation with age (Aaen-Stockdale et al., 2009; Betts et al., 2005; Betts et al., 2009, 2012).

An alternative explanation is that at least one index does not, in fact, provide a psychophysical measure of any aspect of cortical inhibition. Churan et al. (2008) pointed out that there are many visual cortical neurons which do not show surround suppression, raising the question of why the brain does not simply use the outputs of these neurons to perform the task. Those researchers went on to show that brief stimuli ($<$40 ms) preferentially activate surround-suppressed MT neurons, providing an explanation of why psychophysical surround suppression is observed in duration thresholds, which by definition relate to the shortest detectable stimuli. However, this cannot be the whole story, since psychophysical surround suppression is also observed in several long-duration stimuli (Aaen-Stockdale et al., 2009; Tadin, Paffen, Blake, & Lappin, 2009). Based on this and other arguments, Aaen-Stockdale et al. (2009) argue that the paradoxical effect of stimulus size ("psychophysical surround suppression") may not be a perceptual correlate of surround-suppressed neurons in MT. They argue that the effect represents a weakening of spatial summation at high contrast rather than the onset of surround suppression. However, a weakening of spatial summation could only reduce the advantage of large stimuli relative to small; it cannot make the task actually harder for the large stimulus than the small one. Glasser and Tadin (2010) showed that the increase in duration thresholds with stimulus size is still observed even after correcting for the increase in contrast sensitivity. Thus, we think the motion task does reflect both surround suppression and spatial summation, but it is not clear how this relates to the properties of neurons in MT.

It is perhaps not surprising that the contrast and motion suppression indices are independent. Several studies have already argued that there are physiologically distinct forms of surround suppression even within V1—e.g., surround suppression inherited from the lateral geniculate nucleus versus that contributed by horizontal connections within V1 or feedback connections from other cortical areas (Angelucci & Bressloff, 2006; Ichida, Schwabe, Bressloff, & Angelucci, 2007; Tailby, Solomon, Peirce, & Metha, 2007; Webb, Dhruv, Solomon, Tailby, & Lennie, 2005). Webb et al. (2005) distinguished between two different forms of surround suppression in primate V1: "one that is prominent when high-contrast stimuli drive the CRF [classical receptive field], is orientation selective, has relatively sharp spatiotemporal tuning, is binocularly driven, and can be substantially desensitized by adaptation; the other is relatively more prominent when low-contrast stimuli drive the CRF, has very broad spatiotemporal tuning, is monocularly driven, and is insusceptible to adaptation" (p. 11666, abstract). Furthermore, the contrast-based surround suppression considered here is psychophysically and physiologically distinct from the phenomenon known as cross-orientation or overlay suppression, where a neuron's response to its preferred orientation is reduced when the orthogonal orientation is presented at the same location, which is mediated by different mechanisms from the surround suppression (DeAngelis et al., 1992; Durand, Freeman, & Carandini, 2007; Petrov et al., 2005; Walker, Ohzawa, & Freeman, 1998). Clearly the convenient shorthand "surround suppression" covers a multitude of distinct neuronal mechanisms.

Conclusion

Motion and contrast suppression indices are increasingly widely used in clinical studies, but it remains unclear exactly what aspect of neuronal function these two suppression indices measure. Our results on the interrelationships between age, contrast suppression index, motion suppression index, and motion summation index provide some constraints. We find that the magnitude of motion suppression declines with age, while the magnitude of motion summation increases. Although contrast thresholds themselves increase with age, orientation-dependent contrast suppression does not change with age. Motion suppression and contrast suppression indices are not correlated between individuals. We conclude that these two indices are measuring different aspects of cortical function, which can vary independently between individuals.

Keywords: visual surround suppression, psychophysics, motion perception, vision, GABA

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Appendix: Effect of measurement error on measured correlation

The population Pearson correlation coefficient ρ is a normalized measurement of the dependence between two variables X and Y:

$$\rho = \frac{\mathrm{cov}(X, Y)}{\sigma_X \sigma_Y}.$$

This can be estimated from a finite sample of N variables drawn from the bivariate distribution:

$$r = \frac{\sum_{j=1}^{N} (X_j - \bar{X})(Y_j - \bar{Y})}{(N-1) s_X s_Y},$$

where $\bar{X}$ and $\bar{Y}$ are the sample means, and s_X and s_Y the corrected sample standard deviations:

$$\bar{X} = \frac{1}{N} \sum_{j=1}^{N} X_j$$

$$s_X = \frac{1}{\sqrt{N-1}} \sqrt{\sum_{j=1}^{N} (X_j - \bar{X})^2}.$$

In practice, our sample is not only finite but subject to noise—measurement error. We write R for the noisy sample Pearson correlation coefficient, as distinct from r, which is the sample correlation coefficient we would obtain in the absence of measurement error. We denote the errors on individual measurements by ϵ, so that the noisy estimates are $X'_j = X_j + \epsilon_{Xj}$ and $Y'_j = Y_j + \epsilon_{Yj}$. Substituting these noisy estimates into the definition of r, we obtain the following expression for R:

$$R = \frac{\sum_{j=1}^{N} (X'_j - \bar{X}')(Y'_j - \bar{Y}')}{\sqrt{\sum_{j=1}^{N} (X'_j - \bar{X}')^2} \sqrt{\sum_{j=1}^{N} (Y'_j - \bar{Y}')^2}}$$

where $\bar{X}'$ and $\bar{Y}'$ represent the sample means of the noisy data. Evidently, $\bar{X}' = \bar{X} + \overline{\epsilon_X}$—i.e., the sample mean of the ideal noise-free data plus the sample mean of the noise—and similarly for $\bar{Y}'$. Substituting for X' and Y' and expanding, we obtain:

$$R = \left[\sum_{j=1}^{N} \Big((X_j - \bar{X})(Y_j - \bar{Y}) + (X_j - \bar{X})(\epsilon_{Y_j} - \overline{\epsilon_Y}) + (Y_j - \bar{Y})(\epsilon_{X_j} - \overline{\epsilon_X}) + (\epsilon_{X_j} - \overline{\epsilon_X})(\epsilon_{Y_j} - \overline{\epsilon_Y}) \Big)\right] \div \left\{ \left[\sum_{j=1}^{N} \Big((X_j - \bar{X})^2 + 2(X_j - \bar{X})(\epsilon_{X_j} - \overline{\epsilon_X}) + (\epsilon_{X_j} - \overline{\epsilon_X})^2 \Big)\right]^{-2} \times \left[\sum_{j=1}^{N} \Big((Y_j - \bar{Y})^2 + 2(Y_j - \bar{Y})(\epsilon_{Y_j} - \overline{\epsilon_Y}) + (\epsilon_{Y_j} - \overline{\epsilon_Y})^2 \Big)\right]^{-2} \right\}.$$

Equation 3

We assume that the measurement errors on each variable are uncorrelated with each other and with the size of the other variable relative to the mean. That is, we neglect the sums over $(\epsilon_{X_j} - \overline{\epsilon_X})(\epsilon_{Y_j} - \overline{\epsilon_Y})$, $(Y_j - \bar{Y})(\epsilon_{X_j} - \overline{\epsilon_X})$, $(X_j - \bar{X})(\epsilon_{X_j} - \overline{\epsilon_X})$, $(Y_j - \bar{Y})(\epsilon_{Y_j} - \overline{\epsilon_Y})$ and $(X_j - \bar{X})(\epsilon_{Y_j} - \overline{\epsilon_Y})$. We write ω_X and ω_Y for the standard deviations of the measurement error and assume that these are approximately equal to the corrected sample standard deviation, so that

$$\sum_{j=1}^{N} (\epsilon_{X_j} - \overline{\epsilon_X})^2 \approx (N-1)\omega_X^2.$$

With these assumptions, Equation 3 reduces to

$$R \approx \frac{\sum_{j=1}^{N} (X_j - \bar{X})(Y_j - \bar{Y})}{(N-1)\sqrt{(\omega_X^2 + s_X^2)(\omega_Y^2 + s_Y^2)}}$$

or, equivalently,

$$r \approx R\sqrt{(1 + \omega_X^2/s_X^2)(1 + \omega_Y^2/s_Y^2)}.$$

Equation 4

In other words, if we observe a sample correlation coefficient of R between two variables in the presence of noise, the underlying population correlation coefficient could be as high as

$$\rho = R\sqrt{(1 + \omega_X^2/s_X^2)(1 + \omega_Y^2/s_Y^2)}.$$

The between-subjects and within-subject standard deviations for our two suppression indices are given in Table 1. We estimate the within-subject measurement error ω from the 95% confidence intervals for the index measured for each individual participant, produced by bootstrap resampling (Read et al., 2015). We assume that the error is normally distributed, so that the measurement error for each participant is one quarter of the 95% confidence interval. We then average this value across all participants to produce the estimate of ω given in Table 1.

To obtain estimates of the noise-free between-subjects standard deviation s, we assume that the measured standard deviation reflects both within-subject and between-subjects error—i.e., that it is $\sqrt{(s^2+\omega^2)}$. We therefore correct this with our estimate of ω to obtain s (Read et al., 2015).