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# The surface area of human V1 predicts the subjective experience of object size

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## Abstract

The surface area of human primary visual cortex (V1) varies substantially between individuals for unknown reasons. Here, we show that this variability is strongly and negatively correlated with the magnitude of two common visual illusions, where two physically identical objects appear different in size due to their context. Because such illusions dissociate conscious perception from physical stimulation, our findings indicate that the surface area of V1 predicts variability in conscious experience.

We are all familiar with the notion that our thoughts and emotions differ from one person to another, yet often assume our more basic sensory perception of the world is very similar from person to person. But the neural apparatus thought to process such fundamental aspects of sensory perception shows substantial anatomical variability. For example, primary visual cortex (V1) varies between individuals over a threefold range in surface area and volume[1]. Little is known about the reasons for such variability, or whether it has any perceptual consequences. Indeed, studies of the human visual system typically treat such inter-individual variability as a potential confound and deliberately remove it by averaging across small groups of participants. Here, we took a different approach by explicitly examining such morphological variability in a much larger group, and relating it directly to behavioral measures of visual awareness.

We hypothesized that inter-individual differences in the surface area of V1 might predict individual differences in conscious perception, such as how big something looks. To test this, we created situations where perceptual judgments of participants were dissociated from physical stimulation. Contextual visual illusions afford such dissociations, by creating situations where two test objects appear different in size despite being physically identical, due to their spatial context[2]. We measured the magnitude of two different perceptual size illusions (Fig. 1a,b) in a large (n=30) group of healthy humans, using a two-alternative forced choice procedure to ascertain the size ratio at which two physically dissimilar test objects appeared equal in size due to the illusion. We then related such individual differences to measurements of the functionally defined surface area of V1 (plus V2/V3) representing the central visual field, defined on a per-participant basis using standard retinotopic mapping procedures (Suppl. Fig. S1) with functional MRI[3]. Measurement of the

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**Author Contribution Statement**

D.S.S. conducted the fMRI experiment and analysed the data; C.S. conducted the behavioral experiment; D.S.S., C.S., and G.R. wrote the paper.

size illusions and retinotopic mapping were separate procedures carried out days to weeks apart.

For both size illusions, we found substantial individual variation in the magnitude of the illusory perceptual effect. However, at the level of individual participants, measures were very reliable on repeated testing (see Supplementary Information). Thus, the subjective experience of how big something looks differed substantially across individuals, independently from differences in physical stimulation. Interestingly, the inter-individual variability in the magnitude of each illusion was not significantly correlated across participants (R=0.24, p=0.208). This suggests that different factors may contribute to the two illusions. For example, it is conceivable that the Ebbinghaus illusion (Fig. 1a) might be mediated by lateral connections within V1[4,5] while the Ponzo illusion (Fig. 1b) must be mediated by feedback projections from areas that extract the three dimensional context of the background[6,7].

Across our participants we also found substantial variability in the surface area of retinotopically mapped regions, consistent with previous reports[1] but now in a much larger sample. Critically, we found significant negative correlations between the magnitude of both size illusions and the surface area of V1 (Fig. 2). These were specific to V1, as the correlations between size perception and area of visual regions V2 and V3 were weak and not significant (see also Supplementary Information). Thus, participants with a small functionally defined V1 tended to have a stronger perceptual illusion than those individuals with a large V1. Fig. 1c shows maps from three representative individuals illustrating this effect.

Importantly, the magnitude of each illusion showed a strong and significant negative correlation with functionally defined V1 surface area, even though there was no inter-individual correlation between the magnitudes of the two illusions. This may have resulted from the overall weakness of the Ponzo compared to the Ebbinghaus illusion (mean magnitude for Ebbinghaus at 3°: 0.264, Ebbinghaus at 4.5°: 0.269, Ponzo: 0.072). While the two behavioral measures may tap (at least in part) different neuronal mechanisms, they nevertheless converged to a common relationship with the magnitude of the illusion predicted by V1 surface area. Consistent with this difference between the two illusions, in follow-up analyses (see Suppl. Fig. 2), we observed hemispheric asymmetry of the relationship between V1 surface area and visual perception, but only for the Ebbinghaus and not the Ponzo illusion. This may be related to previously reported differences in the size of the foveal confluence in left and right visual cortex[1]. It could also reflect differences in the stimulus configuration for our two illusions: targets in the Ebbinghaus illusion were presented to the left and right of fixation but in the Ponzo illusion they were also distributed between the upper and lower visual field (Fig. 1).

When expressing the surface area of V1 as a proportion of the overall cortical area we observed a similar pattern of results (see Supplementary Information). Moreover, our data hinted at an inverse relationship between V1 surface area and overall cortical area (R=−0.35, p=0.057) such that V1 tended to be physically smaller in larger brains. While this suggests that the factors determining these two measures may be related, it also shows that the surface area of V1 does not simply scale with brain size. Under the assumption that the absolute surface area of V1 indicates the physical cortical territory allotted to cover the visual field, the absolute surface area is the more relevant measure. In control experiments, we further established that inter-individual variability in functionally defined V1 surface area did not arise due to our use of an attention task during retinotopic mapping (Suppl. Fig. 3) and that it was not related to the surface area of the peri-calcarine cortex, a purely anatomical measure (see Supplementary Information for details).

Our findings are consistent with observations that activity of neuronal populations in human V1 represents the apparent size of objects[6],[7], but go substantially beyond this earlier work. Instead of showing a neural correlate of the strength of the illusions themselves[7], our experiments demonstrate that a purely morphological feature of cortical functional architecture - the surface area of V1, which was defined in an unrelated experimental procedure - predicts inter-individual differences in visual awareness of size. The ability to judge fine physical differences in visual stimuli (Vernier acuity) is correlated with the degree of cortical magnification in primary visual cortex[8]. But such a relationship relates an objective resolution limit and cortical organization, and that earlier work did not dissociate changes in physical stimulation from changes in conscious perception, as in the present study. Here, we instead demonstrated a relationship between *subjective* conscious experience and cortical organization, independently from physical differences in sensory processing.

What anatomical or functional mechanisms might account for such a relationship? The cross-sectional nature of our study means we cannot determine whether it arises during development, or as a consequence of plasticity in adult life. One intriguing possibility is that the anatomical structures mediating the illusions we studied (i.e. either feedback or lateral connections) might have a fixed size determined by the anatomical spread of cortico-cortical projections. A larger area of V1 devoted to a particular portion of the visual field would then necessarily be accompanied by a lesser influence of contextual effects mediated by anatomical structures with a fixed spatial scale. Such a hypothesis predicts the negative correlation between perceptual experience of size and V1 surface area that we observed here.

An intriguing question for future work will be to determine whether the individual differences we demonstrated are related to other differences in the properties of human V1, such as the concentration of the inhibitory neurotransmitter GABA[9]. It will also be important to complement retinotopic mapping with anatomical measures of V1 size, either through advances in structural neuroimaging or possibly by combining it with postmortem anatomical analyses[10]. Moreover, the magnitude of the Ebbinghaus illusion differs in populations with autism[11], and apparently in different cultures[12]. Our findings now link the magnitude of this illusion to the surface area of V1, which raises the possibility that such cross-cultural and population differences in size perception might instead be reinterpreted as differences in brain structure between these groups.

Our findings demonstrate that basic aspects of the contents of our consciousness such as perceived size vary substantially between humans, and that they are directly reflected in the area of V1. Much experimental work seeks to eliminate or discount variation between individuals of a species when seeking to uncover neuronal mechanisms. But our demonstration of significant inter-individual variability in awareness directly related to the surface area of focal regions of cortex reminds us of the richness of inter-individual variation in perception and thought that underpins our experiences.

## Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

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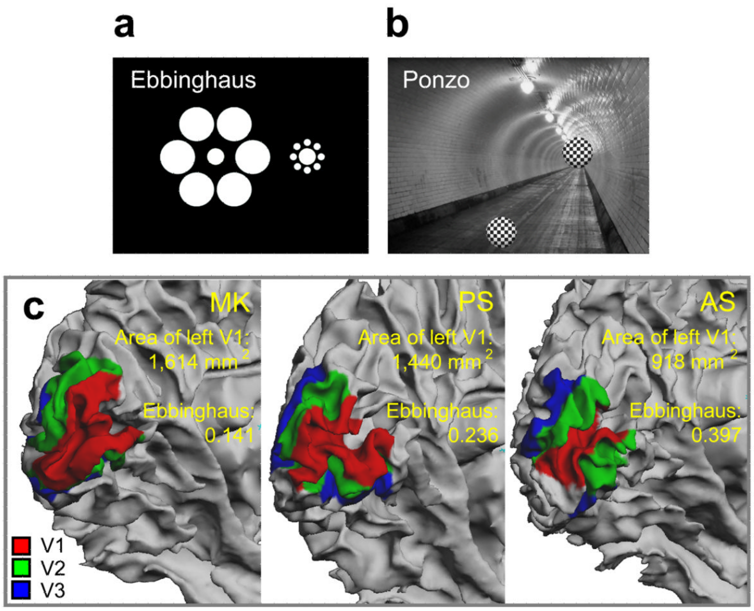

**Figure 1.**

**a**. Ebbinghaus illusion[13]: the two central circles are physically identical but appear different in size due to the presence of the surrounding circles. **b**. A variant of the Ponzo illusion[14]: the two checkerboard circles are physically identical, but appear different in size due to the three dimensional context. **c**. The smaller the V1, the stronger the illusion. Representative maps showing cortical regions V1-V3 on a reconstructed 3D mesh of the left hemisphere gray-white matter surface of three participants. The surface area of the left V1 and Ebbinghaus illusion strength are given for each participant. Red: V1. Green: V2. Blue: V3.

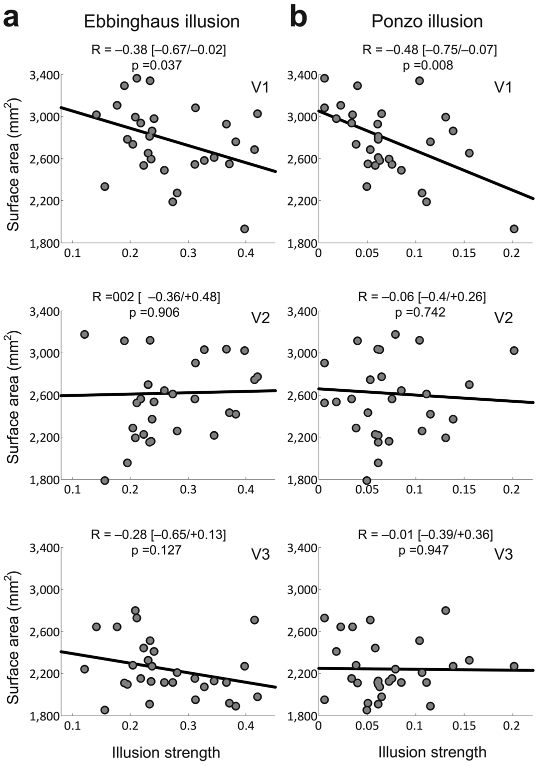

**Figure 2.**

Scatter plots showing the inter-individual variability of the size of the visual regions V1-V3 plotted as a function of the psychophysically measured strength of the Ebbinghaus (**a**) and the Ponzo (**b**) illusions (see Supplementary Material for full details). Each data point represents a measurement from one participant. The solid black lines show the linear regression for each panel. Correlation coefficients and statistical significance are denoted above each panel. The numbers in brackets denote the bootstrapped 95% confidence intervals for the correlation coefficient.