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

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The surface area of human primary visual cortex (V1) varies substantially between individuals for unknown reasons. We found that this variability was strongly and negatively correlated with the magnitude of two common visual illusions, where two physically identical objects appear different in size as a result of 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 that our more basic sensory perception of the world is very similar from person to person. However, the neural apparatus that is 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 volume1. 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. 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 in which perceptual judgments of participants were dissociated from physical stimulation. Contextual visual illusions afford such dissociations by creating situations in which two test objects appear to be different in size, despite being physically identical, as a result of their spatial context2. 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 as a result of 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 (Supplementary Fig. 1) with functional magnetic resonance imaging3. Measurement of the size illusions and retinotopic mapping were separate procedures carried out days to weeks apart.

For both size illusions, we found substantial variation between individuals in the magnitude of the illusory perceptual effect. However, at the level of individual participants, measures were very reliable on repeated testing (Supplementary Results). Thus, the subjective experience of how big something looks differed substantially across individuals, independently from differences in physical stimulation. Notably, 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 in V1 (refs. 4,5), whereas the Ponzo illusion (Fig. 1b) must be mediated by feedback projections from areas that extract the three-dimensional context of the background6,7.

Across our participants, we found substantial variability in the surface area of retinotopically mapped regions, consistent with previous reports1, but in a much larger sample. We found significant negative correlations (Ebbinghaus, R = −0.38, P = 0.037; Ponzo, R = −0.48, P = 0.008) between the magnitude of both size illusions and the surface area of V1 (Fig. 1c). These were specific to V1, as the correlations between size perception and area of visual regions V2 and V3 were weak and not significant (Ebbinghaus: V2, R = 0.02, P = 0.906; V3, R = −0.28, P = 0.127; Ponzo: V2, R = −0.06, P = 0.742; V3, R = −0.01, P = 0.947). Thus, participants with a small functionally defined V1 tended to have a stronger perceptual illusion than those individuals with a large V1 (Fig. 2).

Notably, the magnitude of each illusion showed a strong 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 be a result of the overall weakness of the Ponzo compared with the Ebbinghaus illusion (mean magnitude for Ebbinghaus at 3°, 0.264; Ebbinghaus at 4.5°, 0.269; Ponzo, 0.072). Although the two behavioral measures may utilize (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 (Supplementary Fig. 2), we observed a hemispheric asymmetry of the relationship between V1 surface area and visual perception for the Ebbinghaus, but not for the Ponzo illusion. This may be related to previously reported differences in the size of the foveal confluence in left and right visual cortex1. 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 were also distributed between the upper and lower visual field in the Ponzo illusion (Fig. 1).

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When expressing the surface area of V1 as a proportion of the overall cortical area, we observed a similar pattern of results (Supplementary Results). 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. Although this suggests that the factors determining these two measures may be related, it also indicates 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 found that inter-individual variability in functionally defined V1 surface area did not arise as a result of our use of an attention task during retinotopic mapping (Supplementary Fig. 3), that it reflected variability in both the length and width of V1 (Supplementary Table 1) and that it was not related to the surface area of the peri-calcarine cortex, a purely anatomical measure (Supplementary Results).

Our findings are consistent with observations that activity of neuronal populations in human V1 represents the apparent size of objects, but go substantially beyond these earlier studies. Instead of showing a neural correlate of the strength of the illusions themselves, our results indicate 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. However, 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. Instead, we found a relationship between subjective conscious experience and cortical organization, independent of physical differences in sensory processing.

What anatomical or functional mechanisms might account for such a relationship? The cross-sectional nature of our study means that we cannot determine whether it arises during development or as a consequence of plasticity in adult life. One possibility is that the anatomical structures mediating the illusions that we studied (that is, either feedback or lateral connections) might have a fixed size that is 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.

A question for future work will be to determine whether the individual differences that we found are related to other differences in the properties of human V1, such as the concentration of the inhibitory neurotransmitter GABA. 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. Moreover, the magnitude of the

**Figure 1** Size illusions and variability in V1 surface area. (a) Ebbinghaus illusion. The two central circles are physically identical, but appear to be different in size because of the presence of the surrounding circles. (b) A variant of the Ponzo illusion. The two checkerboard circles are physically identical, but appear to be different in size as a result of the three-dimensional context. (c) The smaller the V1, the stronger the illusion. Representative maps showing cortical regions V1-V3 on a reconstructed three-dimensional mesh of the left hemisphere gray-white matter surface of three participants (denoted by initials MK, PS and AS). The surface area of the left V1 and Ebbinghaus illusion strength are given for each participant. Red indicates V1, green indicates V2 and blue indicates V3.

**Figure 2** Surface area of V1 predicts illusion strength. (a,b) 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 Ponzo (b) illusions (Supplementary Methods). Each data point represents a measurement from one participant. The solid black lines indicate 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.
Ebbinghaus illusion differs in populations with autism\textsuperscript{11} and in different cultures\textsuperscript{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 suggest 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. However, our finding of substantial 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.

Note: Supplementary information is available on the Nature Neuroscience website.

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AUTHOR CONTRIBUTIONS

D.S.S. conducted the functional magnetic resonance imaging experiment and analyzed the data. C.S. conducted the behavioral experiment. D.S.S., C.S. and G.R. wrote the paper.

COMPETING FINANCIAL INTERESTS

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