Microstructural properties of the vertical occipital fasciculus explain the variability in human stereovisual performance

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Stereopsis is a fundamental visual function that has been studied extensively. However, it is not clear why depth discrimination (stereovisuality) varies more significantly among people than other modalities. Previous studies have reported the involvement of both dorsal and ventral visual areas in stereopsis, implying that not only neural computations in cortical areas but also the anatomical properties of white matter tracts connecting those areas can impact stereovisuality. Here, we studied how human stereovisuality relates to white matter properties by combining psychophysical, diffusion MRI (dMRI), and quantitative MRI (qMRI). We performed a psychophysical experiment to measure stereovisuality and, in the same participants, we analyzed the microstructural properties of visual white matter tracts on the basis of two independent measurements, dMRI (fractional anisotropy, FA) and qMRI (macromolecular tissue volume; MTV). Microstructural properties along the right vertical occipital fasciculus (VOF), a major tract connecting dorsal and ventral visual areas, were highly correlated with measures of stereovisuality. This result was consistent for both FA and MTV, suggesting that the behavioral-structural relationship reflects differences in neural tissue density, rather than differences in the morphological configuration of fibers. FMRI confirmed that binocular disparity stimuli activated the dorsal and ventral visual regions near VOF endpoints. No other occipital tracts explained the variance in stereovisuality. In addition, the VOF properties were not associated with differences in performance on a different psychophysical task (contrast detection). These series of experiments suggest that stereoscopic depth discrimination performance is, at least in part, constrained by dorso-ventral communication through the VOF.

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Significance

Seeing in the three-dimensional world—stereopsis—is an innate human ability, but it varies substantially across individuals. The neurobiological basis of this variability is not understood. We combined diffusion and quantitative MRI imaging with a psychophysical measurement, and found that variability in stereovisuality is associated with microstructural differences in the right vertical occipital fasciculus, a white matter tract connecting dorsal and ventral visual cortex. This result suggests that the microstructure of the pathways that support information transmission across dorsal and ventral visual areas plays an important role in human stereovisual performance.

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Data deposition: The data for reproducing analyses and codes for replicating psychophysical experiments have been deposited on Open Science Framework (available at https://osf.io/qd8dk).

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Psychophysical experiment measuring stereoacuity. (A) Schematic illustration of the depth discrimination task using RDSs (see SI Appendix, Fig. S1A for details). Each RDS was concentric bipartite. Participants were asked to judge whether the central disk was nearer or farther than the surrounding disk. (B) The psychometric functions of three representative participants with different performances. The horizontal axis depicts binocular disparity (arcmin; logarithmic scale), while the vertical axis depicts the correct rate. The performance on the crossed and uncrossed disparities was averaged. Stereoacuity was estimated as the binocular disparity at which a participant achieved 84% correct rate (Left and Middle). Right shows a participant with a performance of <84% over the tested range of disparities; therefore, we could not quantitatively estimate stereoacuity using the identical criteria. (C) The stereoacuity of all participants (n = 19). The vertical axis shows the disparity threshold at which performance reached 84% correct. The stereoacuity value is arbitrary for the five participants whose stereoacuity could not be quantitatively estimated (performance < 84%; labeled with diamonds). Note, these five participants were not stereoblind (SI Appendix, SI Materials and Methods). We classified participants into good (blue) and poor stereoacuity (green) groups.

Estimated depth discrimination threshold that corresponded to an 84% correct response rate. We succeeded in estimating the stereoacuity of 14 participants; five participants had <84% correct responses over the full range of tested disparities (±7.68 arcmin), and we were unable to determine stereoacuity from their psychometric functions. However, all participants discriminated depth from RDSs with a longer duration (500 ms) and larger disparities (15.36 arcmin) significantly better than chance, indicating that none were stereoblind (SI Appendix, SI Materials and Methods). We pooled trials across all stimulus locations to estimate stereoacuity because there was no notable difference in stereoacuity between left and right visual fields (SI Appendix, Fig. S2A). We confirmed that stereoacuity varied by more than one order of magnitude across participants (Fig. 1C), consistent with previous psychophysical studies (4, 22, 23).

**Microstructural Properties of VOF Explain Individual Variabilities in Stereoacuity.** We collected two independent structural MRI datasets, dMRI and qMRI, from the participants who took part in the psychophysical experiment. We performed tractography on the dMRI dataset to identify the trajectory of major visual white matter tracts (left and right inferior longitudinal fasciculus, ILF; left and right optic radiation, OR; forceps major of the corpus callosum; and left and right VOF) following the anatomical descriptions in previous studies (SI Appendix, SI Materials and Methods). We evaluated the tissue properties along these visual white matter tracts using the widely used dMRI measure, fractional anisotropy (FA) (28), and recently proposed qMRI measure, macromolecular tissue volume (MTV), which quantifies the nonproton neural tissue density (29).

Finally, we examined how the variation of FA or MTV in these visual white matter tracts correlates with the stereoacuity for each participant (see SI Appendix, Fig. S3 for whole-brain comparison between FA and MTV).

First, we examined white matter tracts that explained the variability in stereoacuity by comparing the performance of multiple linear regression models that predict stereoacuity from the tissue properties (MTV or FA) of the examined tracts. This analysis was performed on data from the 14 participants whose stereoacuity was quantitatively estimated (an analysis using the data of all 19 participants is also presented below). Next, we selected the best linear regression model using the Bayesian information criterion (BIC). BIC model selection for the MTV of visual white matter tracts revealed the best regression model using a single tract, the right VOF (Fig. 2A). This was the significant model for predicting the stereoacuity [$R^2 = 0.36, F(1,12) = 6.71, P = 0.024$; Fig. 2B and SI Appendix, Table S1]. In addition, the MTV of the left ILF was a significant predictor of stereoacuity [$R^2 = 0.30, F(1,12) = 5.22, P = 0.041$; SI Appendix, Table S1]. No other models using single, or combinations of, visual tracts were significantly correlated with the stereoacuity (SI Appendix, Table S1). In summary, the microstructural properties of the right VOF best predicted the variability in stereoacuity.

The BIC model selection using FA, a conventional measure of dMRI, provided similar results: The best model to explain variations in human stereoacuity included a single tract, the right VOF [$R^2 = 0.30, F(1,12) = 5.22, P = 0.041$; SI Appendix, Fig. S4A and Table S1; see SI Appendix, Fig. S5A and B for results in axial and radial diffusivity]. No other models, including the model using the FA of the left ILF [$R^2 = 0.12, F(1,12) = 1.57, P = 0.23$], significantly predicted stereoacuity (SI Appendix, Table S1). These results, across two independent measurements using different pulse sequences, suggested that the observed correlation was related to neural tissue volume along the right VOF, rather than the morphological factors specifically affecting FA (e.g., crossing fibers).

We further examined how MTV and FA differed between the good stereoacuity (low disparity-threshold) and poor stereoacuity (high disparity-threshold) groups, by incorporating datasets from all participants (n = 19), including the five participants whose stereoacuity could not be estimated from the psychophysical function analysis (Fig. 1B). First, we classified the participants with quantitative estimates of stereoacuity (n = 14) into different subgroups by applying a two-step clustering algorithm to the stereoacuity data and selecting the best clustering based on BIC (SI Appendix, SI Materials and Methods). The analysis revealed two subgroups, which correspond to good (n = 10) or poor (n = 4) stereoacuity groups. Then the five participants without quantitative estimates of stereoacuity were included in the poor stereoacuity group (n = 9 in total, Fig. 1C). We found that the good stereoacuity group had a significantly higher MTV (Fig. 2C; $d^* = 1.27, t_{17} = 2.77, P = 0.013$) and FA (SI Appendix, Fig. S4B; $d^* = 1.14, t_{17} = 2.48; P = 0.024$) along the direction of the right VOF compared with the poor stereoacuity group.

These differences in MTV and FA between the two groups were consistent with the results of the regression analysis of the microstructural properties of the right VOF and stereoacuity (Fig. 2B for MTV and SI Appendix, Fig. S4A for FA). We also found a significant group difference in axial diffusivity ($d^* = 1.07, t_{17} = 2.33, P = 0.032$) but not radial diffusivity of the right VOF (SI Appendix, Fig. S5 C and D). The spatial profile of the tract properties suggested that the group difference was present along the entire length of the right VOF, from dorsal to ventral (Fig. 2C for MTV and SI Appendix, Fig. S4B for FA), and not restricted to a localized region. Thus, it is unlikely that the group difference can be explained by a partial volume effect with other short-range fibers (such as U-fibers). We did not find any significant differences in MTV and FA between the two groups in any other...
visual white matter tracts, such as the ILF or OR in both hemispheres, forceps major, and left VOF (Fig. 2D). Furthermore, it should be noted that the difference in stereocuity between these two groups was not accompanied by differences in refractive power or pupillary distance of the eyes (SI Appendix, Fig. S1B) nor age ($d' = 0.91, t_{12} = 1.99, P = 0.063; SI Appendix, Fig. S6C). We noted that a significant effect in the right VOF was preserved in the conservative criterion ($d' = 1.20, t_{12} = 2.62, P = 0.018$). These results suggest that a lack of statistical significance in the left VOF may be at least partly explained by the relative difficulty in identifying coherent streamlines.

In the above analysis, we estimated stereocuity by pooling data from the left and right visual fields, which helped to improve the reliability of the estimate by increasing the number of trials. Given that the areas connected by VOF have retinotopic representation (26), we also tested the relationship between stereocuity in left and right visual fields and the MTV of the contralateral VOF. The correlation between the right VOF and left stereocuity was found to be marginally significant ($R^2 = 0.37, F_{1,12} = 4.39, P = 0.058; SI Appendix, Fig. S2B$), whereas the correlation between the left VOF and right stereocuity was not significant ($R^2 = 0.058, F_{1,12} = 0.74, P = 0.41; SI Appendix, Fig. S2B$). Group difference analysis also showed the same tendency ($SI Appendix, Fig. S2 D and E$). The lack of effect in the left VOF can be explained by multiple possible factors, such as a reduced reliability of stereocuity estimates or difficulty in identifying coherent streamlines, as mentioned above.

**VOF Connects Cortical Regions Responding to Visual Stimuli with Binocular Disparity.** To test our hypothesis that the right VOF connects cortical areas that are involved in binocular disparity processing, we performed fMRI experiments to measure the cortical areas activated by the same RDSs as used in the psychophysical experiment (Materials and Methods). We observed significant BOLD responses to the RDSs, compared with uncorrelated RDSs, in both dorsal (V3a/B, IPS0) and ventral (hV4, VO1/2) extrastriate cortices that were consistent with previous fMRI studies in humans (Fig. 3B) (16, 30–32). Importantly, both dorsal and ventral VOF endpoints overlapped with disparity-selective regions (Fig. 3 and SI Appendix, SI Materials and Methods). These results agree with our hypothesis that discriminability of stereoscopic depth involves an interaction between dorsal and ventral cortices through the VOF. We noted that we did not find any significant interhemispheric differences in BOLD responses to RDSs compared with uncorrelated RDSs (uRDSs) in the majority of retinotopic areas (V3, V3a/B, hV4, VO, LO) except for IPS0, which showed a stronger BOLD response in the right hemisphere ($d' = 0.60, t_{5} = 2.58, P = 0.0495, paired t test; SI Appendix, Fig. S7$).

**Psychophysical Experiment on Contrast Detection Sensitivity.** Finally, we addressed whether the tissue properties of the right VOF are also related to another visual performance that does not require binocular integration. We measured the thresholds of participants’ contrast detection using Gabor patch stimuli (Fig. 4I). In contrast to disparity thresholds, contrast detection thresholds did not show a clear bimodal distribution (Fig. 4B), and were not significantly correlated with stereocuity ($r = 0.08, P = 0.82$). A simple linear model that included the tissue properties of the right VOF did not significantly predict the contrast detection threshold [$R^2 = 0.017, F_{1,17} = 0.29, P = 0.59$ for FA; $R^2 = 0.031, F_{1,17} = 0.55, P = 0.47$ for MTV, Fig. 4C]. None of the other models using FA or MTV in the other white matter tracts significantly explained the variations of contrast detection threshold either (SI Appendix, Table S2). Group difference analysis revealed no significant difference in the tissue property of the right VOF between the good (low contrast threshold, $n = 12$) and poor (high contrast threshold, $n = 7$) contrast sensitivity groups (Fig. 4D; $d' = 0.21, t_{17} = 0.44, P = 0.66$ for MTV; $d' = 0.16, t_{17} = 0.34, P = 0.74$ for FA). Taken together, the variability of FA and MTV values did not correlate with the performance of the contrast detection that does not require binocular integration. Relation of the VOF to other visual tasks such as color or motion detection is an open question for future research.

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**Fig. 2.** Tissue property of the right VOF explains varibilities in human stereocuity. (A) VOF in the right hemisphere identified in one representative participant (P9). VOF connects the dorsal and ventral regions of the occipital cortex. (B) Correlation between MTV of the right VOF and stereocuity ($n = 14$; $R^2 = 0.36, F_{1,12} = 6.71, P = 0.024$). The shaded area represents 95% confidence intervals derived from bootstrapping. See SI Appendix, Fig. S4A for the correlation between FA of the right VOF and stereocuity. (C) Tissue properties along the right VOF in good and poor stereocuity groups. The vertical and horizontal axes represent the MTV and spatial position along the right VOF, respectively. The good stereocuity group (blue, $n = 10$) showed significantly higher MTV than the poor stereocuity group (green, $n = 9$) along the entire portion of the right VOF ($d' = 1.27, t_{12} = 2.77, P = 0.013; two-sample t test$). Data are represented as mean (solid line) ± SEM (dotted line). (D) Left depicts the visual white matter tracts estimated by tractography (green, OR; pink, forceps major; dark yellow, ILF; blue, VOF) in one representative participant (P9). Right shows the effect size ($d'$) of the FA and MTV differences in each visual white matter tract between the good and poor stereocuity groups. Positive or negative values represent index values that are larger or smaller in the good or poor stereocuity group, respectively. $*P < 0.05$, two-sample t test. The effect size was largest in the right VOF in the two independent measurements (FA and MTV). There were no significant stereocuity-dependent differences in the FA or MTV of the other visual white matter tracts.
Discussion

In the current study, we examined the neurobiological correlates of the large variability in stereoacuity. Advanced noninvasive neuroimaging methods, such as dMRI and qMRI, are advantageous when investigating the neurobiological origin of individual variance in sensory abilities because neuroanatomical and behavioral measurements collected from the same participants can be compared (33). We have used this advantage to compare human stereoacuity and white matter properties. We found a significant statistical relationship between stereoacuity and the microstructural properties in the right VOF, a specific white matter tract that connects the dorsal and ventral visual cortices (25, 26). These data support classical and recent theories that emphasize the importance of white matter tracts in understanding sensory and cognitive functions (34, 35). The behavior-anatomy correlates were found using the MTV and FA, two independent microstructural measurements, in both regression and group comparison analyses. Furthermore, we confirmed that the VOF had endpoints in disparity responsive regions of the dorsal and ventral cortices, suggesting that the VOF connects cortical regions that are involved in disparity processing. Finally, we found that the tissue properties of the right VOF were not related to contrast sensitivity.

A number of previous studies have used conventional diffusion tensor metrics, such as FA, to examine the tissue properties of white matter tracts relative to behavioral characteristics (33). In contrast, few recent studies have used advanced qMRI metrics, such as MTV (29), to assess the microstructural properties of white matter tracts. FA is a reproducible metric with high sensitivity for detecting the tissue structural differences in white matter tracts (33, 36). However, the microstructural interpretation of differences in FA is challenging because FA measurements can be associated with many biological factors, such as axon diameter, axon density, myelin-sheath thickness, and tightness of fasciculation due to crossing fibers (28, 36). Here, we combined dMRI with qMRI, which can provide additional information for inferring microstructural properties (29, 37). The MTV is a robust qMRI-based metric that quantifies local tissue volume within each voxel via quantification of proton density (29). There is converging evidence indicating that MTV is a reliable approximation of lipid and macromolecular volume fractions (38). While MTV has been used to quantify white matter tissue properties, this study demonstrates the relevance of MTV with behavioral measurements. Taken together, the relationship between the right VOF and stereoacuity, as shown in both FA and MTV analyses, may reflect a difference in lipid or macromolecule volume fractions, such as myelin thickness or axon density, rather than the morphological configuration of axons, such as the degree of fiber crossings.

Duan et al. (39) have investigated the microstructural properties of visual white matter tracts between amblyopia and control groups. They observed a difference in the diffusion property (mean diffusivity) along the right VOF; however, this difference is not supported by qMRI measurements. Additionally, Duan et al. reported a difference in the diffusion property along the optic radiation, which we did not find in this study. Our results and those of Duan et al. (39) suggest that the microstructural basis of stereoacuity is distinct from that of amblyopia.

Some visual neuroscience studies have emphasized the role of the dorsal stream in stereopsis (40–42), which is consistent with

![Fig. 3. Comparison between VOF endpoints and disparity-sensitive regions.](image)

(A) VOF endpoints in the right hemisphere from one representative participant, P8 (Left, dorsal view; Right, ventral view). Color maps on the cortical surface indicate a normalized count of VOF streamlines having endpoints within 3 mm from each gray matter voxel. (B) Disparity selective areas (hot color), which were significantly activated during the “RDS” blocks compared with the “uncorrelated RDS” blocks (P < 0.05, one-sample t test). The borders of estimated VOF endpoints (cyan, identical in A) as well as the borders of visual areas (white) are overlaid. (C) Overlap between VOF endpoints and disparity selective regions in the right hemisphere. The vertical axis indicates the proportion of the gray matter voxels near VOF endpoints, which inter- acted with binocular disparity selective areas. The left and right three bars represent dorsal and ventral VOF endpoints, respectively. Different colored bars show data from varying distance thresholds for selecting the gray matter voxels near VOF endpoints (1.5 mm, blue; 3.0 mm, green; 4.5 mm, red). Disparity-selective regions overlap with similar proportion of VOF endpoints across the dorsal and ventral visual cortex. Data represent mean ± SEM (n = 6).

![Fig. 4. The tissue properties of the right VOF do not explain variabilities in contrast sensitivity.](image)

(A) Gabor patch stimuli were used to measure contrast sensitivity. The white scale bar depicts 1°, which was not visible in the experiment. (B) The contrast sensitivity of all participants (n = 19; four of them were new participants who had not participated in the stereotypy experiment). We classified participants into good (blue) and poor contrast sensitivity groups (green), respectively. This grouping is totally independent of the grouping in the stereoacuity experiment (Fig. 1C). (C) Scatter plot of MTV along the right VOF (horizontal axis) and contrast detection threshold of each participant. The MTV along the right VOF did not significantly predict the contrast detection threshold [R² = 0.031, F(1,17) = 0.55, P = 0.47]. (D) MTV along the right VOF in the good and poor contrast sensitivity groups. We did not find a significant difference in MTV between the groups (d = 0.21, t₁₇ = 0.44, P = 0.66). Data represent mean ± SEM. The conventions are identical to those in Fig. 2C.
Materials and Methods

The code for reproducing psychophysical experiments and analyses is publicly available in OSF.io (https://osf.io/qdb6j/). The full anonymized dataset, which are collected from participants who provided a written informed consent on the data sharing (22 of 23 participants as of September 4, 2018), will be available upon request to the corresponding author (htakemur@niit.go.jp).

Participants. Twenty-three healthy volunteers (19 males, 4 females; mean age, 26.1 ± 0.9 years) participated in the study. None of the participants had a history of eye disease. All participants gave written informed consent to take part in this study, which was conducted in accordance with the ethical standards stated in the Declaration of Helsinki and approved by the local ethics and safety committees at the Center for Information and Neural Networks (CiNet), National Institute of Information and Communications Technology.

Stereocuity Experiment. Nineteen participants (16 males, 3 females; mean age, 25.0 ± 0.9 years) took part in the experiment to determine their stereocuity. The stereocuity experiment employed a haploscope. Each eye viewed one-half of the monitor through an angled mirror and a front triangular prism mirror. Each RDS was composed of a central disk (diameter: 3°) and surrounding ring (width: 0.5°, outer diameter: 4°; see SI Appendix, Fig. 5A) for an example. The surrounding ring always had zero disparity, whereas the binocular disparity in the central disk varied across trials (disparity magnitudes: ±0.12–7.68 arcmin), which were chosen based on a typical range of human stereocuity (22). In each trial, an RDS was presented at one of four different positions (Up-Right, Up-Left, Down-Right, and Down-Left), whose center was 3° away from the fixation point. Participants judged whether the central disk appeared nearer or farther than the surrounding ring while fixating on the central fixation point (SI Appendix, Fig. 5A). We defined stereocuity as the magnitude of binocular disparity that corresponded to the 84% correct rate in the task by fitting a cumulative Gaussian psychometric function. See SI Appendix, SI Materials and Methods for further technical details.

Contrast Threshold Experiment. Nineteen participants (15 males, 4 females; mean age, 26.0 ± 0.9 years) underwent a contrast threshold experiment. Fifteen of these participants also participated in the stereocuity experiment. We presented Gabor patch stimuli whose orientation was tilted 45° to the left or right from vertical (Fig. 4A). Participants were asked to judge whether the stimulus orientation was tilted toward the left or right. The stimulus positions were identical to those used in the stereocuity experiment. The experiment consisted of two stages. An approximate threshold was measured in the first stage, which was used to determine the contrast range that was used at the second stage to estimate a precise threshold. See SI Appendix, SI Materials and Methods for further technical details.

Structural MRI Experiment. All MRI data were acquired using a 3T SIEMENS Trio Tim scanner at CiNet, National Institute of Information and Communications Technology, and Osaka University.

We collected dMRI data (2 mm isotropic) from all participants (n = 23) using a 32-channel head coil. The diffusion weighting was isotropically distributed along the 64 directions (b = 1,000 s/mm²). Non-diffusion-weighted (b = 0) images were acquired at the beginning and end of the dMRI session (two b = 0 acquisitions per image set). Acquisition of the dMRI data took ~20 min for each participant.

We collected qMRI data from all participants (n = 23) using a 32-channel head coil. qMRI measurements (1 mm isotropic) were obtained using protocols described in a previous publication (29). Acquisition of the qMRI data took ~35 min for each participant.

Further details in structural MRI data acquisition and preprocessing methods are described in SI Appendix, SI Materials and Methods.

Diffusion MRI Data Analysis. dMRI data preprocessing was performed using mrDiffusion tools implemented in the vistasoftware distribution (https://github.com/vistalab/vistasoft). We identified visual white matter tracts in each participant, from whole-brain streamline generated by probabilistic tractography implemented in MRtrix3 (www.mrtrix.org) (58) and selected by Linear Fascicle Evaluation (LFE, https://francpetitili.github.io/lfe/) (59). Details are described in SI Appendix, SI Materials and Methods.

Quantitative MRI Data Analysis. qMRI data were processed using the mrQ software package (https://github.com/mezeramrQ) to produce the MTV maps (29). Details are described in SI Appendix, SI Materials and Methods.
Functional MRI Experiment. We collected fMRI data from eight participants who participated in the stereoelectric psychophysical experiment (seven males, one female; ages 18–61 y old). Before the experiment, fMRI scanning of the human occipital lobe was conducted using a 32-channel head coil. The acquisition of T2*-weighted gradient echo sequence included the following: 

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