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Report

Interhemispheric Connections Shape Subjective Experience of Bistable Motion

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Summary

The right and left visual hemifields are represented in different cerebral hemispheres and are bound together by connections through the corpus callosum. Much has been learned on the functions of these connections from split-brain patients [1–4], but little is known about their contribution to conscious visual perception in healthy humans. We used diffusion tensor imaging and functional magnetic resonance imaging to investigate which callosal connections contribute to the subjective experience of a visual motion stimulus that requires interhemispheric integration. The "motion quartet" is an ambiguous version of apparent motion that leads to perceptions of either horizontal or vertical motion [5]. Interestingly, observers are more likely to perceive vertical than horizontal motion when the stimulus is presented centrally in the visual field [6]. This asymmetry has been attributed to the fact that, with central fixation, perception of horizontal motion requires integration across hemispheres whereas perception of vertical motion requires only intrahemispheric processing [7]. We are able to show that the microstructure of individually tracked callosal segments connecting motion-sensitive areas of the human MT/V5 complex (hMT/V5+; [8]) can predict the conscious perception of observers. Neither connections between primary visual cortex (V1) nor other surrounding callosal regions exhibit a similar relationship.

Results

For most observers, the perception of the "motion quartet" (Figure 1A; see also Movie S1 and Movie S2 available online) is biased toward vertical motion, presumably due to the cost of interhemispheric transfer. If so, the optimal ratio between horizontal and vertical distance, called "parity ratio" (PR), that leads to equal durations of horizontal and vertical motion perception can be used as a behavioral measure of interhemispheric communication between areas responsible for apparent-motion processing. We determined the PR in 28 participants with a retest after 16 weeks to ensure stability of our behavioral measure (Figure 1B; Figure S1). Analyses showed a large interindividual variability of the PR but a high test-retest reliability [$r(26) = 0.80$, $p < 0.001$], suggesting that the quality of interhemispheric motion integration is a stable trait in participants (Figure 1C). The mean PRs for time point 1 (geometric mean = 0.80) and time point 2 (geometric mean = 0.78) were not significantly different [$t(27) = 1.23$, $p = 0.23$]. Values below one indicate that the vertical distance of motion quartets must be larger than the horizontal distance for optimal bistability, in accordance with previous results [6, 7, 9].

One candidate area for the processing of apparent motion is the human motion complex (hMT/V5+), a region in the lateral occipitotemporal cortex that has been related to motion processing in general [8] and to processing of bistable apparent motion [9, 10]. We acquired brain-activation data with functional magnetic resonance imaging (fMRI) to identify hMT/V5+ and V1 employing standard localizer and retinotopic-mapping techniques (Figures 2A and 2B; Table S2; see Supplemental Experimental Procedures). From these functionally defined regions, we determined corpus callosum segments in individual participants connecting hMT/V5+ as well as V1 of the two hemispheres using fiber tracking with diffusion tensor imaging (DTI) data (Figure 2C; Figure 3A; Figure S1). For comparison, we also defined a segment comprising the posterior fifth of the corpus callosum, excluding hMT/V5+ and V1 segments (splenium remainder; Figure 2C; Figure 3A). Finally, different measures of white-matter microstructure in the corpus callosum segments were correlated with PR to identify pathway properties predicting subjective experience of the motion quartet. The measures were fractional anisotropy (FA), which reflects the degree of directed water diffusion; axial diffusivity (AD), representing water diffusion along the main axon direction, which is the left-right axis in the case of the corpus callosum; and radial diffusivity (RD), representing water diffusion perpendicular to the main axon direction (Figure 3B; see Supplemental Results and Supplemental Experimental Procedures). We found significant correlations between PR and microstructural integrity of those corpus callosum segments that interconnect left and right hMT/V5+ [$r(26) = -0.44$, $p = 0.02$ for FA]. In accordance with a previous report [11], we found that AD did not contribute to PR prediction [$r(26) = 0.17$, $p = 0.38$], but there was a strong correlation with RD [$r(26) = 0.56$, $p = 0.002$; Figure 4]. Therefore, further analyses focused on RD as a measure of callosal microstructure.

To examine the extent to which these structure-function relations reflected interindividual differences in the global layout of the corpus callosum, we compared correlations between PR and anatomical measures not only for the segment linking hMT/V5+ but also for the segment linking V1 and the splenium remainder. In a combined multiple-regression analysis with segment RDs as independent variables and PR as dependent variable, RD of the hMT/V5+ segment was the only variable providing a unique contribution to PR

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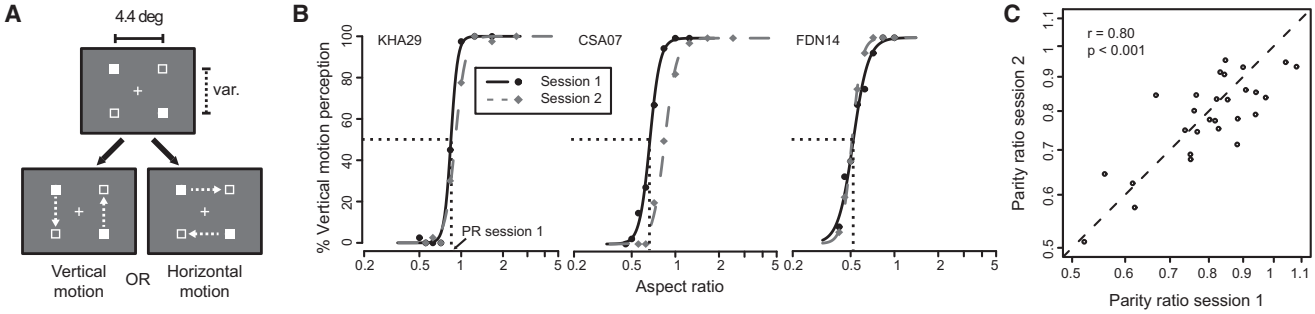

Figure 1. Stimuli and Psychometric Fits of Behavioral Data

(A) Configuration of the "motion quartet" used in this study. The diagonally opposing pairs of squares (filled and open) were presented in alternation, leading to a percept of either vertical or horizontal motion.

(B) Presenting the motion quartet at several different aspect ratios (horizontal distance divided by vertical distance) generates a sigmoid distribution of data points (black dots for test, gray diamonds for retest) that includes the "parity ratio" (PR) for a given observer, where motion along the two axes is perceived with equal probability. Fits of a logistic function (see Supplemental Experimental Procedures) in test (solid black lines) and retest sessions (dashed gray lines) of three representative participants with high, medium, and low PR are shown. PR is determined by taking the aspect ratio where the logistic function has a value of 50% vertical motion perception.

(C) High test-retest reliability demonstrates that PR is a stable feature in humans. The dashed line indicates slope = 1, where data points would be identical for test and retest.

Aspect ratios are $\log_{10}$ scaled in (B) and (C).

prediction [beta = 0.65, t(24) = 3.23, p = 0.004; other predictors, p > 0.40]. Also, separate correlation analyses for the two control segments did not reveal significant effects [V1 segment, r(26) = 0.18, p = 0.36; splenium remainder, r(26) = 0.15, p = 0.45; Figure 4].

Because the hMT/V5+ and V1 segments showed some degree of overlap, we created two corpus callosum segments of hMT/V5+ and V1 separating the intersection of both segments and performed correlation analyses for the three new segments (Figure 3A). Only RD in the unique hMT/V5+ segment showed a significant correlation with PR [r(26) = 0.58, p = 0.001]. There was no effect in the intersection segment [r(24) = 0.26, p = 0.20; note that there was no overlap in two participants] or in the unique V1 segment [r(26) = 0.24, p = 0.22]. Defining the hMT/V5+ corpus callosum segment by a more liberal tract threshold (see Supplemental Experimental Procedures for more details) also did not affect the outcome. A separate correlation analysis with the RD of the liberal hMT/V5+ corpus callosum segments and PR showed that the relationship between microstructure and behavior remained significant [r(26) = 0.45, p = 0.02]. One reason for the weakening of correlations could be the expanding size of the hMT/V5+ segments (size for 0.01 threshold in voxels, M = 72, standard deviation [SD] = 34; size for 0.005 threshold in voxels, M = 97, SD = 38), which might reduce the accuracy of representing hMT/V5+ projections in the corpus callosum. Further control analyses included changes in sample composition, as well as consideration of confounding and control variables. None of the controls changed the pattern of results (see Supplemental Results and Table S1).

We focused our analyses on RD because, in accordance with a previous study [11], we found that RD was stronger as a predictor than FA. Nevertheless, because FA is widely used as a main marker of microstructural integrity, we repeated the main analyses with FA values. With regard to the anatomical specificity of results, we performed multiple regression of PR on FA values of the hMT/V5+, V1, and splenium remainder segments. Again, only FA of the hMT/V5+ segment provided a unique contribution to PR prediction [beta = −0.61, t(24) = −2.95, p = 0.007; other predictors, p > 0.14]. Also, separate correlation analyses for the two control segments did not reveal significant effects [V1 segment, r(26) = −0.04, p = 0.83; splenium remainder, r(26) = −0.10, p = 0.61].

Discussion

To the best of our knowledge, we have demonstrated for the first time that PR is a stable characteristic of visual motion processing and is related to the microstructure of specific corpus callosum segments connecting motion-selective cortical areas in healthy humans. Particularly, the high correlation between conscious motion perception and the microstructure of the corpus callosum segment connecting hMT/V5+ of the two hemispheres was topographically specific. No significant correlations were found for neighboring corpus callosum segments in the splenium.

Physiological interpretations of diffusion parameters are challenging because diffusion anisotropy can be influenced by a number of factors, including myelination, axon diameter, and fiber density [12]. The myelin hypothesis would predict a negative correlation between PR and RD, because increased myelin thickness hinders radial diffusion [12] and is associated with faster nerve conduction velocity. The increased conduction velocity, in turn, would result in a better interhemispheric connectivity and thereby a higher PR. However, the PR-RD correlations we found were positive. An alternative explanation for a highly coherent tissue like the corpus callosum would be the axon diameter hypothesis [12, 13], which would predict a positive correlation between PR and RD because increased axonal diameter has been related to increased RD [14, 15] and faster nerve conduction velocity [16], which would result in a higher PR. A straightforward interpretation of our results would then be that individuals differ in the speed of callosal transfer, suggesting that the hMT/V5+ segments of observers with a high PR, who showed a higher prevalence of perceiving interhemispheric motion, are characterized by larger-diameter axons and thus faster conduction velocities.

Evidence suggests that axonal membranes are the primary source of diffusion anisotropy in fiber tracts of the nervous

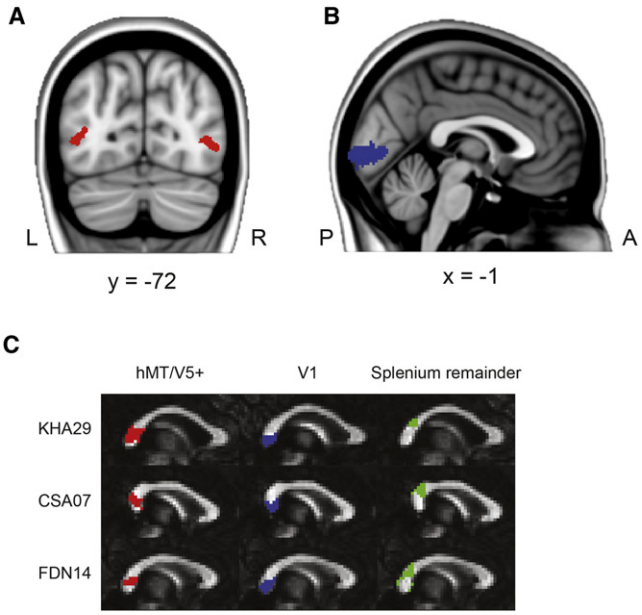

Figure 2. Group Display of the Regions of Interest and Tractography Results

(A) Random-effects group map of the bilateral hMT/V5+ for 28 participants (red), thresholded at z = 5.0. Group centroid coordinates in Montreal Neurological Institute (MNI) space for left hMT/V5+ were x = −44, y = −75, z = 4 and for right hMT/V5+ were x = 44, y = −70, z = −1.

(B) Group display of V1 for 28 participants (blue). Individual V1 areas were determined by standard retinotopic-mapping techniques (see Supplemental Experimental Procedures) and nonlinearly transformed into MNI space. Only voxels that were part of V1 in at least 21 out of 28 participants are displayed.

(C) Midsagittal tracking results of three representative participants overlaid on each individual's corpus callosum. The red area indicates transcallosal fiber projections of motion-sensitive visual areas (hMT/V5+), whereas the blue area indicates projections of early visual areas (V1). The green area represents the splenium, geometrically defined, excluding the projections from hMT/V5+ and V1 (splenium remainder).

The following abbreviations are used: L, left; R, right; P, posterior; A, anterior.

system and that myelination, although it can modulate the degree of anisotropy, is not necessary for significant anisotropy [12, 15]. Further support for the diameter hypothesis stems from a substantial fraction of other studies demonstrating correlation signs between behavioral measures and microstructure that are consistent with our results [11, 17–19]. The results of other studies are interpreted as being supportive of the myelin hypothesis [20–23], and a few studies describe microstructure changes in both directions for different relevant structures [13, 24]. For the visual system, DTI parameters of interhemispheric connections have been related to behavioral and electroencephalography (EEG) measures of interhemispheric integration, but the results of the studies are contradictory and therefore do not conclusively support any one of the physiological interpretations [19, 25, 26].

A more subtle mechanism of interhemispheric integration that might be affected by the microstructural properties of transcallosal connections is the coordination of neuronal assemblies in both hemispheres by neuronal synchrony and coherent oscillations. In animals, sectioning of the corpus callosum leads to a loss of interhemispheric coherence on the single-cell [27, 28] as well as the population level [29]. In humans, interhemispheric functional connectivity measured with fMRI breaks down after callosal sectioning [30], and interhemispheric EEG coherence is sensitive to the configuration of visual stimuli across the midline [31]. For the motion quartet, it has been demonstrated that interhemispheric EEG coherence in the gamma band is increased when observers perceive horizontal compared to vertical motion [32]. Our findings provide strong evidence that, in healthy humans, those effects are mediated by specific callosal connections.

In humans, evidence for the function of callosal connections in conscious visual perception mainly stems from investigations in split-brain patients, who have a partly or completely severed corpus callosum in order to curtail globally spreading epileptic seizures [1]. After surgery, the patients show a deficit in interhemispheric integration for different tasks requiring the transfer of information between hemispheres [33]. In the case of apparent motion, some patient studies suggest that motion perception is abolished or impaired across hemispheres [3, 4], whereas another study found preserved perception of apparent motion—also for the motion quartet—across the midline [2]. However, the interpretation of findings in split-brain patients is complicated by the fact that initial deficits have been found to fade over time [1]. It is possible that alternative routes through subcortical structures are strengthened after the loss of callosal connections, enabling interhemispheric transfer at least for a limited set of functions.

The neural correlates of apparent-motion processing have been extensively studied using fMRI. Activity in hMT/V5+ is most consistently modulated by perceptual switches in bistable motion displays [10, 34]. In addition, switch-related activations have been described in the right inferior parietal cortex and bilateral frontoparietal networks [34, 35]. The different roles of those areas have not been studied in detail yet, but the right inferior frontal cortex has been related to the initiation of perceptual switches ([35], but see [36]), and anatomy and function of superior parietal cortices seem to determine the duration of perceptual states [22, 37]. In particular, the connections between frontal and parietal networks have been implicated in other forms of bistable perception [38]. Our results underscore the role of hMT/V5+ for apparent-motion processing. Interindividual variations in interhemispheric connection strength determine the binding of motion cues across the left and right visual field and thereby bias conscious experience of the motion quartet.

Although the splenial topography of our tracking results for hMT/V5+ and V1 are in good agreement with previously published results [39–42], we do not claim that the identified callosal segments exclusively connect the seed regions that were the basis for our analysis. From anatomical tracer studies, it is known that human MT receives massive callosal afferents concentrating near the representation of the vertical meridian, but also terminating in other parts of MT [43]. But as a result of the lateral position of hMT/V5+ and crossing fibers from the inferior longitudinal fascicle, connections between the corpus callosum and hMT/V5+ are hard to track using diffusion tractography [39, 44]. In general, several DTI studies have shown that different areas from parietal, temporal, and occipital cortices send transcallosal connections through the middle part of the splenium [40, 42, 45, 46]. In V1, callosal connections seem to connect only neurons near the border to V2 [43] and are also hard to detect using DTI in humans [45]. The logic of our approach was to differentiate callosal segments most likely connecting early visual areas and segments connecting motion-selective areas in

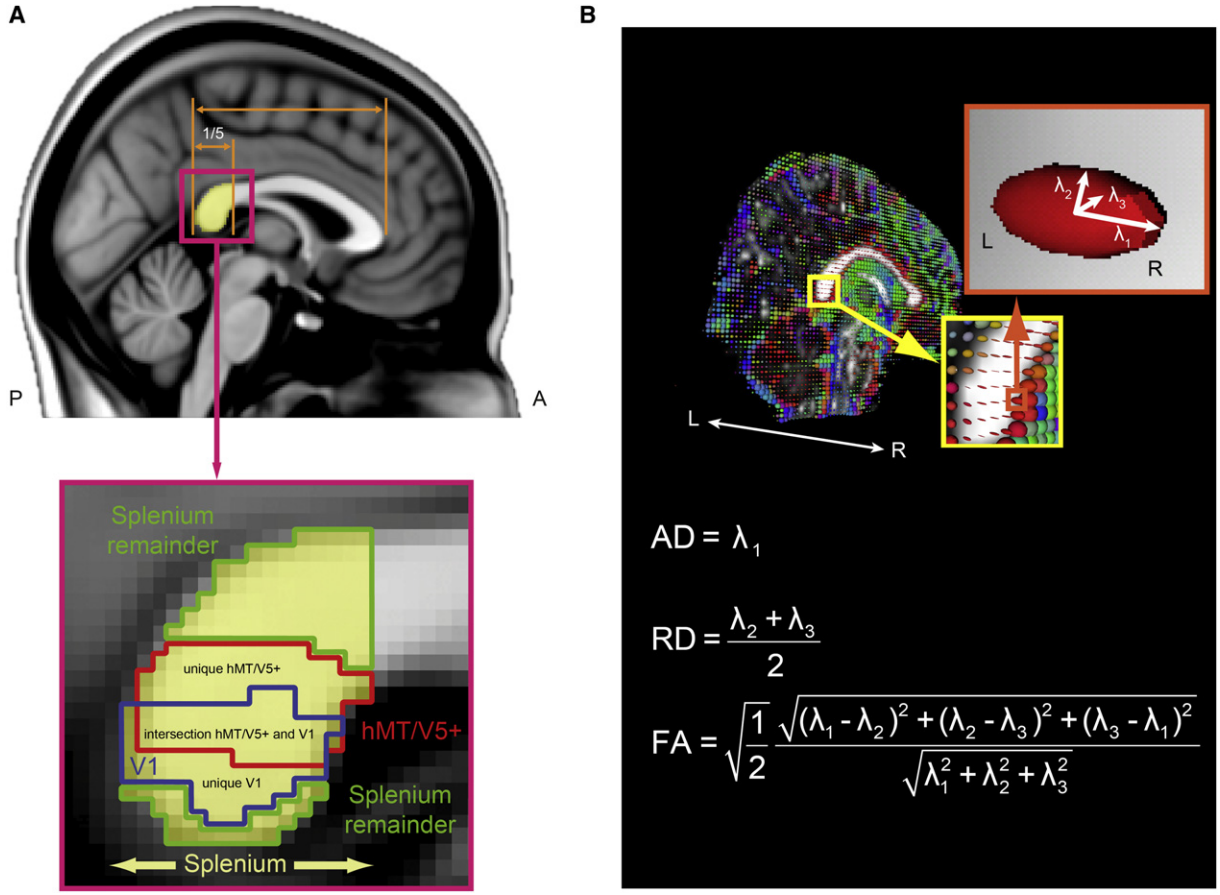

Figure 3. Schematic Description of the Parcellation Logic for the Transcallosal Fibers and Ellipsoid Representation of Diffusion Tensors in the Corpus Callosum

(A) Schematic description of subregions in the splenium, which is geometrically defined as the posterior fifth of the corpus callosum (top; see Supplemental Experimental Procedures). The subregions for hMT/V5+ (red) and V1 (blue) were defined according to the fiber-tracking results (bottom; see Figure 2C). The parts of the splenium excluding hMT/V5+ and V1 (splenium remainder, green) were used for control analyses. Because the hMT/V5+ and V1 subregions overlapped in most participants, an additional regression was performed with the intersection and unique segments of hMT/V5+ and V1.

(B) Midsagittal slice of diffusion ellipsoids viewed from behind and right at a slight angle. Colors indicate main diffusion direction. Selecting one diffusion ellipsoid in the corpus callosum, it can be seen that diffusion is strongest along the left-right direction, parallel to the main fiber orientation. The diffusion ellipsoids can be characterized by three eigenvalues, λ_1, λ_2, and λ_3, representing the three main orthogonal diffusion directions (see Supplemental Experimental Procedures). Axial diffusivity (AD) is identical to λ_1 and represents the main direction of water diffusion, which is the left-right axis in the corpus callosum (see Supplemental Results), whereas radial diffusivity (RD) is the average of λ_2 and λ_3 and represents water diffusion perpendicular to the main direction. In the corpus callosum, λ_2 and λ_3 are highly correlated (see Supplemental Results) so that it is warranted to merge the two parameters. Fractional anisotropy (FA) combines all three eigenvalues in a nonlinear fashion and indicates how much a diffusion ellipsoid deviates from a spherical shape (FA = 0; maximum FA = 1). Estimation and illustration of the diffusion ellipsoids were performed using MEDINRIA v1.8.0 (http://www-sop.inria.fr/asclepios/software/MedINRIA/).

The following abbreviations are used: L, left; R, right; P, posterior; A, anterior.

lateral occipitotemporal cortex. It was expected that the callosal routes connecting early and motion-selective areas would be in close proximity (see Figure 2C; Figure S1), thereby providing a stringent test for the anatomical specificity of the hypothesized relationship.

The results of our study are based on correlations between variables representing structural brain features and features of participants' subjective experience and therefore do not directly support causal inferences. Nevertheless, it is implausible that perception would per se causally determine white-matter structure rather than the other way around. The concurrent determination of both our structural and behavioral variable by a third factor cannot be excluded, but we demonstrated the specificity of our effects by comparison to neighboring callosal segments, and we also considered a large number of third variables (age, sex, brain volume, volume of hMT/V5+ callosal segments, distance between left and right hMT/V5+; see Supplemental Results) that might mediate or generate such a relationship. The correlation that we found is high and therefore explains a substantial amount of variance, but there might be other factors that could contribute to the remaining variance in subjective experience. In particular, observers may also vary in the intra-hemispheric component, i.e., how motion is processed within a hemisphere.

In conclusion, we have shown that the interindividual variability in interhemispheric integration during perception of the motion quartet is partly predicted by the microstructural properties of fibers in a highly specific segment of the posterior corpus callosum. This provides strong evidence in

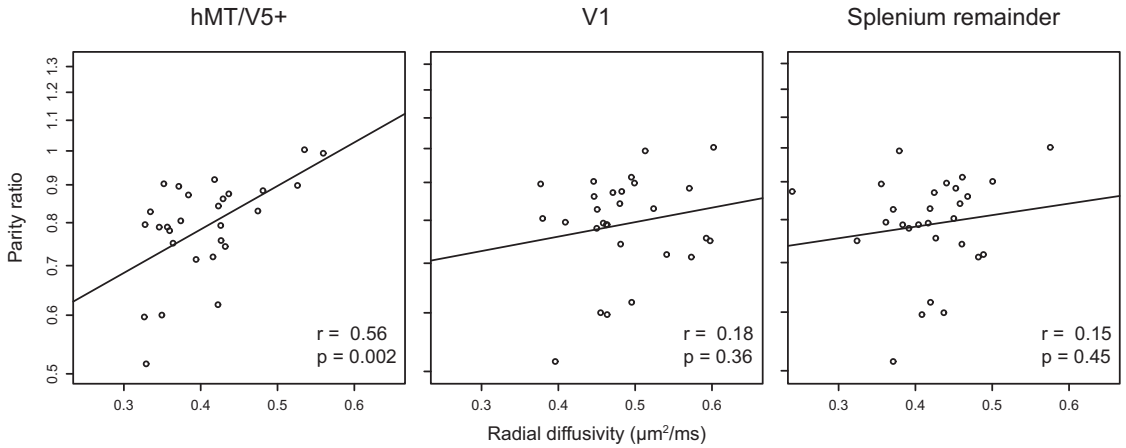

Figure 4. Correlations between Behavior and Fiber Properties of Different Callosal Projections

Only radial diffusivity of hMT/V5+ callosal projections predicted behavioral variance of the parity ratios. No relations were found between parity ratios and radial diffusivity in callosal V1 projections and in the splenium remainder.

healthy humans for the importance of callosal connections in interhemispheric integration of visual functions. In addition, we have established a robust behavioral measure of interhemispheric communication in the visual domain. This measure revealed substantial interindividual variability in interhemispheric communication in healthy humans that is largely unexplored and might be relevant for other functions. Linking properties of fiber pathways to subjective visual experience opens up new possibilities for understanding the neural correlates of conscious perception.

Experimental Procedures

Details of the participants, stimuli, procedure, acquisition of imaging data, and data analysis can be found in the Supplemental Experimental Procedures.

Supplemental Information

Supplemental Information includes one figure, two tables, Supplemental Results, Supplemental Discussion, Supplemental Experimental Procedures, and two movies and can be found with this article online at doi:10.1016/j.cub.2011.08.003.

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