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**Supporting Online Material**  
[www.sciencemag.org/cgi/content/full/309/5744/2222/DC1](http://www.sciencemag.org/cgi/content/full/309/5744/2222/DC1)  
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## Direct Evidence for a Parietal-Frontal Pathway Subservicing Spatial Awareness in Humans

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Intraoperative electrical stimulation, which temporarily inactivates restricted regions during brain surgery, can map cognitive functions in humans with spatiotemporal resolution unmatched by other methods. Using this technique, we found that stimulation of the right inferior parietal lobule or the caudal superior temporal gyrus, but not of its rostral portion, determined rightward deviations on line bisection. However, the strongest shifts occurred with subcortical stimulation. Fiber tracking identified the stimulated site as a section of the superior occipitofrontal fasciculus, a poorly known parietal-frontal pathway. These findings suggest that parietal-frontal communication is necessary for the symmetrical processing of the visual scene.

Left unilateral neglect is a neurological condition resulting from right hemisphere damage (1, 2). Neglect patients ignore left-sided events in everyday life (3) and have a poor functional outcome. They typically bisect horizontal lines to the right of the true center (2, 4), perhaps because they perceive the left half of the line as being shorter or less salient than the right half (5, 6). The study of unilateral neglect is important if we are to understand the mechanisms of spatial cognition, but its anatomical correlates are controversial. Most studies implicate the inferior parietal lobule (IPL) (7, 8), consistent with the known role of posterior parietal cortex in spatial attention (9, 10) and perceptual salience (11). Others implicate the rostral superior temporal gyrus (rSTG) (12), suggesting a segregation of spatial awareness in the ventral cortical visual stream (13, 14). The underlying subcortical association circuits have received less attention (15).

We used intraoperative direct electrical stimulation (16) to study line bisection performance. During brain surgery for tumor resection, it is common clinical practice to awaken patients in order to assess the functional role of

restricted brain regions (the brain has no receptors for pain), so that the surgeon can maximize the extent of the exeresis without provoking cognitive impairment. Patients perform cognitive tasks, such as counting or figure naming, while the surgeon temporarily inactivates restricted regions (~5 mm) around the tumor by means of electrical stimuli (16). If the patient stops talking or produces incorrect responses, the surgeon avoids removing the stimulated region.

CAL, a 27-year-old woman, and SB, a 28-year-old man, both left-handed, underwent surgical resection of a low-grade glioma (WHO II). In CAL, the glioma was centered on the caudal part of the right temporal lobe (17). CAL showed a rightward deviation upon stimulation of two cortical sites: the supramarginal gyrus (SMG, the rostral subdivision of the IPL) and the caudal portion of the superior temporal gyrus (cSTG) (Fig. 1) (table S2). There was no deviation during stimulation of the rSTG or of the frontal eye field.

In SB, the glioma was centered on the right inferior parietal lobule (17). SB showed a rightward deviation remarkably identical in amplitude to that shown by CAL (Fig. 2) (table S2) upon stimulation of the SMG. SB also deviated rightward during cSTG stimulation, again consistent with CAL's performance. Stimulation of other neighboring areas ("control 1" in Fig. 2B) did not determine pathological shifts. During tumor resection, subcortical regions on the floor of the surgical cavity were stimulated.

SB showed a large rightward deviation upon stimulation of the restricted region labeled as 42 in Fig. 2A, but not of neighboring cortical or subcortical areas ("control 2" in Fig. 2B). Stimulation of region 42 was repeated after additional excavation of the surgical cavity, causing even greater deviations ("O-FF 2" in Fig. 2B). Again, stimulation of neighboring subcortical sites had no effect on line bisection performance. Still further extension of the resection into the depth of the angular gyrus caused SB to deviate rightward even during stimulation of neighboring regions, or in the absence of any stimulation ("control 3" in Fig. 2B). As a consequence, the neurosurgeon decided to stop the exeresis at this level. Five days after surgery, SB accurately bisected 20-cm lines ("day +5" in Fig. 2B) and showed no signs of neglect (table S1).

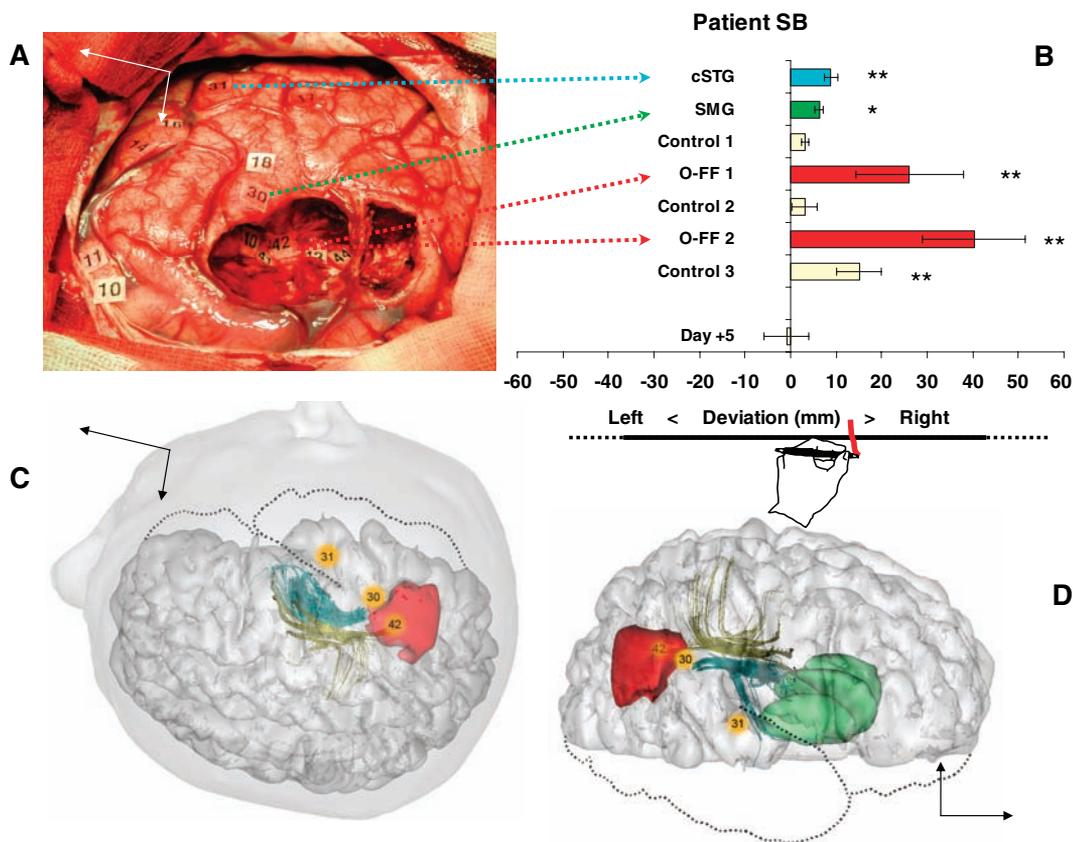
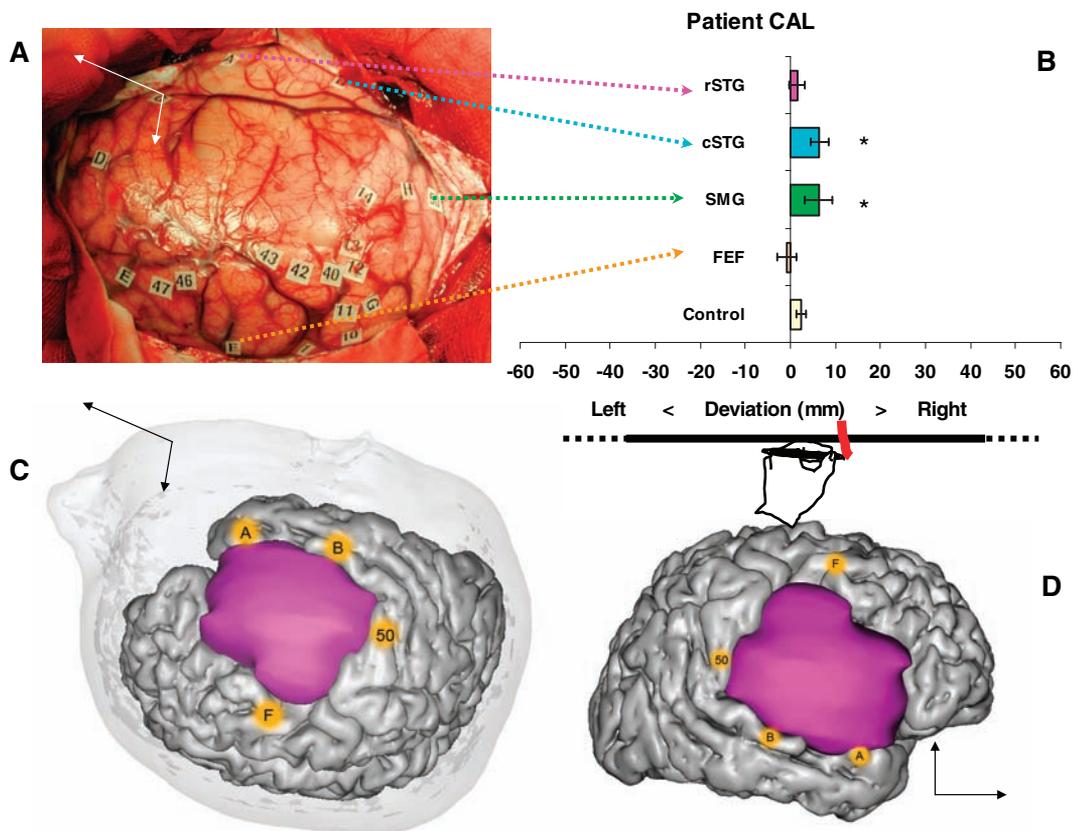
Using diffusion tensor magnetic resonance tractography (18) on postoperative magnetic resonance imaging (MRI) scans and diffusion tensor imaging (DTI) scans, we were able to precisely map the course of long association fibers in the white matter of this patient (19). The region labeled as 42 in Fig. 2A, whose inactivation had produced the maximal rightward shifts on line bisection, corresponded exactly to a portion of the superior occipitofrontal fasciculus (18, 20) that connects the parietal to the frontal lobe (21) (Fig. 2, C and D) (figs. S1 and S2). The stimulated region was both distinct and remote from other corticocortical pathways, such as the optic radiations or the parietal-temporal connections.

Our findings demonstrate that the SMG, the cSTG, and a poorly known parietal-frontal pathway, the superior occipitofrontal fasciculus (18, 20), but not the rSTG, are critical to the symmetrical processing of the visual scene in humans (22). These results provide evidence relevant to the debate about the lesional correlates of neglect, based until now on the relatively imprecise lesion-overlapping method in stroke patients, and support the proposal that damage to the temporal-parietal junction (7, 8, 23) and the underlying white matter (15) is a crucial antecedent of left neglect. As a consequence, there is no need to postulate a segregation of spatial awareness, specific to humans, in the rostral part of the right STG (14).

We observed the maximal deviation upon inactivation of the superior occipitofrontal fasciculus in the depth of the IPL. This result specifies the precise anatomical locus of the parietal-frontal pathway in which neglect

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patients' lesions overlap (15). Our findings are similar to those obtained in nonhuman primates. Monkeys showed persistent signs of neglect after unilateral section of the white matter between the fundus of the intraparietal sulcus and the lateral ventricle (24). The greater effect of subcortical inactivation, as compared to cortical inactivation, is consistent with the idea that symmetrical space processing requires the integrity of a parietal-frontal network (1, 15). Damage to restricted regions of the white matter can cause the dysfunction of large-scale neurocognitive networks. According to an influential model (1), signs of left neglect result from impairment of a right-hemisphere network, including prefrontal, parietal, and cingulate components. The parietal component of the network could be especially important for the perceptual salience of extrapersonal objects, whereas the frontal component might be implicated in the production of an appropriate response to behaviorally relevant stimuli (1), in the online retention of spatial information (1, 25), or in the focusing of attention on salient items through reciprocal connections to more posterior regions (20).

Models of line bisection postulate a competition between the relative salience of the two lateral segments (6). The bisection mark is drawn at the point of subjective equality between the two segments (5). Bisection-related tasks activate the IPL in humans (26). Transcranial magnetic stimulation over the right posterior parietal cortex, but not over the STG, was found to bias the comparison of the lengths of the component segments of pretransected lines in a direction coherent with rightward shifts in line bisection (27). In the monkey, regions adjacent to the intraparietal sulcus, such as the lateral intraparietal area, are related to visual perceptual salience (11) and can reinforce the stimulus attentional priority (10). Parietal inactivation may thus bias the perceptual decision by modulating the salience of the line segments (6).

The assessment of spatial cognition during intraoperative stimulation offers the double opportunity of preserving spatial processing functions during brain surgery and of pinpointing the neurocognitive systems devoted to spatial processing in humans. Spatial awareness is dependent not only on the cortical areas of the temporal-parietal junction, but also on a larger parietal-frontal network communicating via the superior occipitofrontal fasciculus.

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17. CAL and SB attended clinical observation because of epileptic seizures. They showed no abnormality on preoperative neurological and neuropsychological examination, consistent with the slowly infiltrative character of low-grade gliomas, whose clinical presentation rarely includes signs of focal brain disease other than epilepsy. In particular, there were no signs of neglect on paper-and-pencil tests (table S1). Intraoperative electrical stimulation was well tolerated, and the patients reported no abnormal visual sensations. They bisected horizontal lines with their left, dominant hand during brain surgery (28). Eight healthy left-handed subjects (mean age, 31 years; SD, 5.3; range, 26 to 38) served as controls. They performed 30 line bisections each, with the same test material and in a body position similar to that of the patients. Our patients' baseline performance was well within the range of the controls' performance (mean  $\pm$  SD,  $0.28 \pm 2.39$  mm) as well as that of 10 strongly left-handed normal individuals tested in another study (29) (mean  $\pm$  SD,  $-1.50 \pm 3.66$  mm). In an unselected population of 204 patients with right brain damage (2), 5 of the 10 patients with the strongest left-handedness deviated rightward on 20-cm lines as compared to controls (29), a frequency of impairment similar to that showed by right-handed patients (2).
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21. The superior occipitofrontal fasciculus is a poorly known long association pathway. It terminates

rostrally in the lateral prefrontal cortex of the inferior and middle frontal gyri (18). Its caudal terminations are less known (18, 30), but despite its name, derived from early descriptions (31), the superior occipitofrontal fasciculus seems to terminate caudally in the superior parietal gyrus (18) and in the intraparietal sulcus [(30), p. 367].

22. We used line bisection because it is an easy task for patients to perform and allows repeated assessments in the time scale required by intraoperative testing. Bisection of centrally presented 20-cm lines correlates positively and significantly with cancellation tests and is a good predictor of clinical neglect as assessed by standardized scales (2, 28).
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Supporting Online Material

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# Breakdown of Cortical Effective Connectivity During Sleep

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When we fall asleep, consciousness fades yet the brain remains active. Why is this so? To investigate whether changes in cortical information transmission play a role, we used transcranial magnetic stimulation together with high-density electroencephalography and asked how the activation of one cortical area (the premotor area) is transmitted to the rest of the brain. During quiet wakefulness, an initial response (~15 milliseconds) at the stimulation site was followed by a sequence of waves that moved to connected cortical areas several centimeters away. During non-rapid eye movement sleep, the initial response was stronger but was rapidly extinguished and did not propagate beyond the stimulation site. Thus, the fading of consciousness during certain stages of sleep may be related to a breakdown in cortical effective connectivity.

When awakened early in the night from non-rapid eye movement (NREM) sleep, people often report little or no conscious experience

(1). It was first thought that this fading of consciousness was due to the brain shutting down. However, although brain metabolism is re-



## Supporting Online Material for

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Tables S1 and S2

Figs. S1 and S2

References

## **Supporting Online Material**

**Participants.** CAL and SB attended clinical observation because of epileptic seizures. They showed no abnormality on pre-operative neurological and neuropsychological examination. In particular, there were no signs of neglect on paper-and-pencil tests (*S1*) (see Table S1). Eight healthy left-handed subjects (mean age, 31 years; SD, 5.3, range 26-38) served as controls. They performed 30 line bisections each, with the same test material and in a similar body position as the patients.

**Surgical procedure.** Patients were placed in a semidecubitus position on their left side and used their left, dominant hand to perform line bisection tasks. Intraoperative cortico-subcortical mapping was performed under local anesthesia using the technique of direct intraoperative electrical stimulation (*S2*). A bipolar electrode with 5-mm spaced tips delivering a biphasic current with parameters non-deleterious for the CNS (pulse frequency of 60 Hz, single pulse phase duration of 1 ms, amplitude from 2 to 8 mA) was applied to the brain of awake patients. In addition to line bisection, sensori-motor and language functions were assessed (counting and naming). In order to perform a successful tumour removal while sparing functional areas, all resections were pursued until functional pathways were encountered around the surgical cavity, then these were followed according to functional boundaries. These procedures allow the surgeon to minimize the residual morbidity while increasing the quality of the resection, and thereby to improve patient survival by minimizing the anaplastic transformation of low-grade gliomas (*S2*).

**Line bisection task.** Twenty-cm long, 1-mm thick black lines were centered on a horizontal A4 sheet (one line per sheet) (*S3*, *S4*), and presented aligned to the subjects' eye-axis, in central position with respect to the patient's sagittal head plane. Subjects were instructed to mark with a pencil the center of each line. Patients and examiners were blind concerning the stimulated sites. One examiner said "go" just before presenting each line, upon which the surgeon immediately started the stimulation. After each bisection, another examiner assessed the accuracy of the

bisection mark by overlapping the test sheet with a transparency indicating 5% and 10% deviations. When a deviation greater than 5% occurred, the examiner said “yes”, and the neurosurgeon put a numbered label on the stimulated area. Patients kept bisecting lines without further stimulation until their performance reverted to normality. During the surgical intervention, CAL performed a total of 31 line bisections; SB performed 106 line bisections.

**Data analysis.** For each trial, we calculated the deviation in mm from the true center of the line, with leftward errors scored as negative deviations and rightward errors scored as positive deviations. Patients’ bisection performance for each stimulated site was compared to controls’ using a significance test for comparing an individual case with small control samples (*S5*).

**Diffusion tensor analysis.** Diffusion tensor imaging (DTI) was performed using echo-planar imaging at 1.5 T (General Electric) with standard head coil for signal reception. DTI axial slices were obtained using the following parameters: repetition time, 10s; echo time, 88ms; flip angle, 90°; matrix, 128 × 128; field of view; 380 × 380mm<sup>2</sup>, slice thickness, 3mm; no gap (3mm isotropic voxels); acquisition time, 320s. Four averages were used with signal averaging in the scanner buffer. Diffusion weighting was performed along six independent directions, with a b-value of 900 s/mm<sup>2</sup>. High-resolution 3-D anatomical images were used for display and anatomical localization (110 axial contiguous inversion recovery three dimensional fast SPGR images, 1.5mm thick; TI, 400ms; FOV, 240 × 240mm<sup>2</sup>; matrix size, 256 × 256). BrainVisa, a software platform for visualization and analysis of multi-modality brain data (<http://brainvisa.info/>), was used to visualize the anisotropy data, define the regions of interest, track fibres and register T1-weighted MRI with DTI.

**Supplementary discussion.** It has been claimed (*S6*) that line bisection is not a specific task for neglect, because neglect patients (as assessed by cancellation tests) would often perform normally on this task. In this study (*S6*), however, the lines were presented with their right extremity aligned with the right margin of the sheet. This procedure likely resulted in an underestimation of pathological performance on line bisection, because it is well known that displacing the lines towards the right side decreases patients' rightward errors (*S7*). Dissociations between line bisection and cancellation tests may occur (*S8*), and suggest that these tasks recruit different processes or strategies, depending perhaps on the different number of objects that compete for attention, e.g. two segments meeting in an imaginary midpoint target for line bisection, or several physical targets for target cancellation. However, in a study (*S3*) with greater statistical power, which employed centrally placed, 20-cm lines, line bisection performance correlated positively and significantly with cancellation tests and clinical scales of neglect. Thus, in conditions similar to those of the present study, line bisection performance did capture significant aspects of neglect behavior.

**Table S1. Patients' demographical details and their performance on the neglect battery.**

Patient	Gender / Age / Education (years of schooling)	Time between test and surgery	Line Bisection <i>% deviation</i>	Line cancellation <i>max 30 / 30</i>	Bells cancellation <i>max 15 / 15</i>	Letter cancellation <i>max 30 / 30</i>	Overlapping figures <i>max 10 / 10</i>	Landscape drawing <i>max 6</i>
CAL	F / 27 / 12	Day  before surgery	0.00	30 / 30	15 / 15	30 / 29	10/10	6
		114  days after surgery	-1.63	30 / 30	14 / 15	29 / 30	10/10	6
SB	M / 29 / 12	Day  before surgery	+0.04	30 / 30	15 / 14	30 / 30	10/10	6
		5 days  after surgery	-1.00	28 / 25	13 / 12	28 / 29	10/10	6
		51 days  after surgery	-0.03	30 / 30	14 / 15	29 / 30	10/10	6

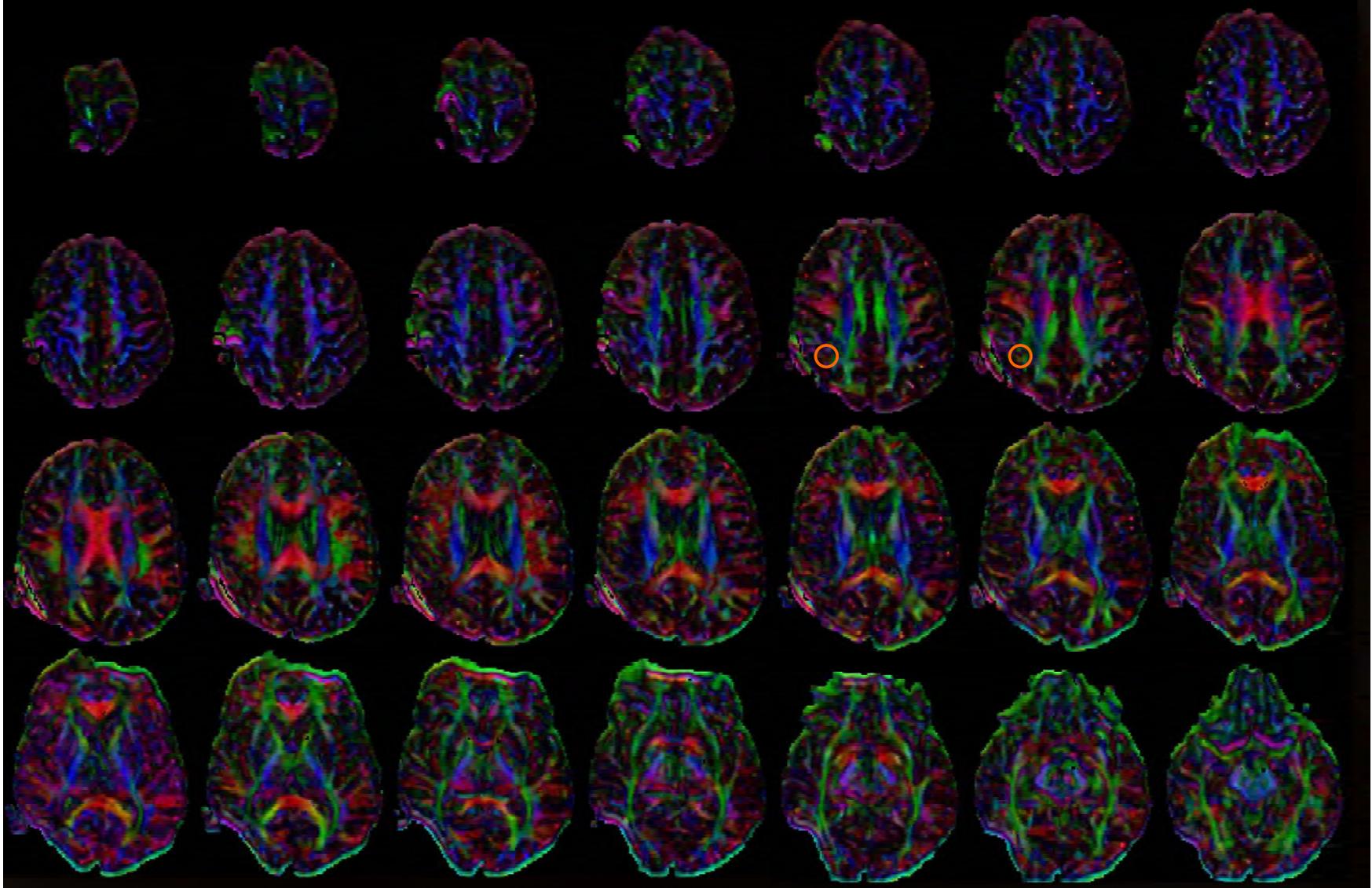
See (SI) for detailed test description. For line bisection, + indicates rightward deviation and - indicates leftward deviation. For the cancellation tests and the overlapping figures test, left / right correct responses are reported. The landscape drawing, consisting of a central house with two trees on each side, was scored by assigning 2 points to the house and 1 point to each tree completely copied.

**Table S2. Intraoperative bisection task: Talairach coordinates (S9) of the stimulated sites and patients' performance**

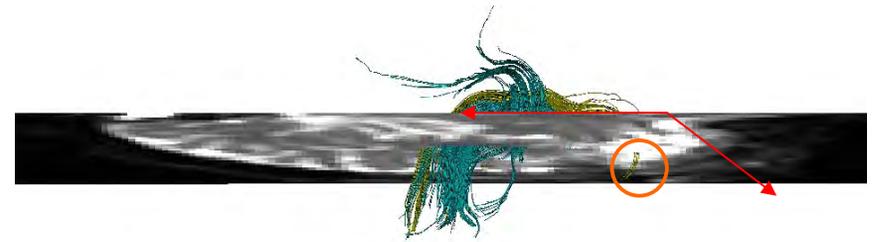
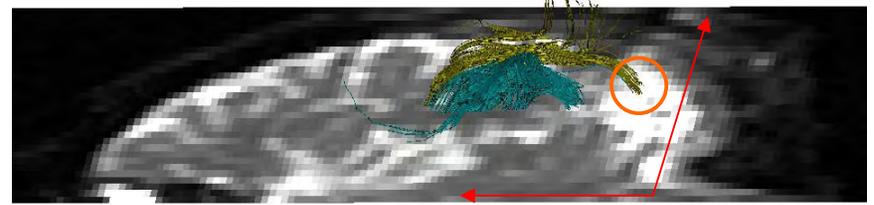
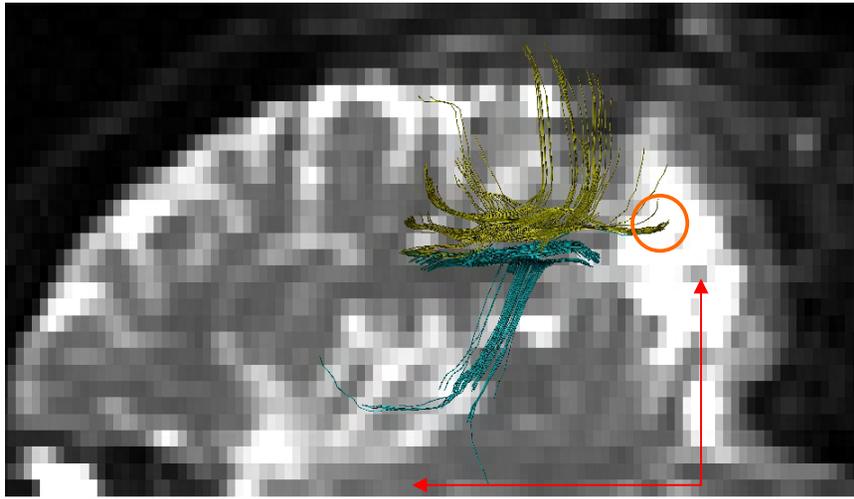
Patient	Talairach coordinates			Anatomical area*	Mean deviation (mm)**	SD (mm)
	X	y	z			
CAL	60	22	-15	rSTG	+1.50	1.29
	71	-21	13	cSTG	+6.50	2.12
	70	-22	32	SMG	+6.25	2.22
	17	2	75	FEF	-0.80	1.92
SB	71	-23	15	cSTG	+8.83	1.86
	67	-40	37	SMG	+6.25	0.96
	39	-52	39	O-FF1	+26.13	1.41
				O-FF2	+40.25	11.62

\*rSTG, rostral superior temporal gyrus; cSTG, caudal superior temporal gyrus; SMG, supra-marginal gyrus; FEF, frontal eye field; O-FF, superior occipito-frontal fasciculus

\*\* + indicates rightward deviation and - indicates leftward deviation.



**Fig. S1.** Orientation colored coding of the post-operative DTI maps for patient SB, illustrated on axial slices. Fiber directions of the right-left, rostral-caudal, and superior-inferior orientations were coded in red, green, and blue, respectively. The orange circle corresponds to region 42 in Fig. 2A.



**Fig. S2.** Additional 3D reconstructions of the superior occipito-frontal fasciculus (in yellow) and of the superior longitudinal fasciculus (in blue) for patient SB. The orange circle corresponds to region 42 in Fig. 2A.

## References and Notes

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Successful plant  
fertilization

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Alternative to  
dark matter

607

“can” happen, Haidt fails to mention that the overwhelming conviction among evolutionary theorists remains that they are most unlikely, since the selection differential between groups would have to exceed the cost differential experienced by self-sacrificial individuals within groups.

By a rhetorical sleight of hand, after describing D. S. Wilson’s group-selection hypothesis for the evolution of religion, Haidt then announces—as though it were fact—that “group selection greatly increased cooperation within the group” (p. 1001). This is pure speculation, not fact, and highly controversial, contrarian speculation at that.

In another case of substituting opinion for reality, Haidt proposes his “Principle 4,” arguing for the biological legitimacy of “patriotism, respect for tradition, and a sense of sacredness” (p. 1001). Perhaps, in the future, these supposed components of morality will be found to have genuine evolutionary underpinnings, but for now they seem closer to a political platform plank for the religious right; psychologists interested in achieving a new synthesis by applying evolutionary biology to human morality should bear in mind that just because these notions appeared in a *Science* Review does not make them genuine science.

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## Response

BARASH IS CORRECT THAT A SURVEY OF ALL evolutionary theorists would show a great deal of skepticism about group selection. That consensus, however, was forged in the 1960s and 1970s on the basis of some simplifying assumptions, most notably that phenotypes are determined solely by genotypes and that culture can be ignored. Models incorporating these assumptions showed that selection pressures operating at the individual level were almost always stronger than selection pressures operating at the group level, leading to the conclusion that genes for apparently altruistic traits can only spread if those genes are in fact “selfish” (1) via one of the two mechanisms of kin selection or reciprocal altruism.

But evolutionary models have become more realistic in recent years. Phenotypes (e.g., cooperator or defector) can now be modeled as joint products of genes, cultural learning, and culturally altered payoff matrices. When culture is included, the old consensus must be reexamined. The time frame shrinks from millennia to years (or less) as groups find culturally innovative ways to police themselves, to increase their phenotypic homogeneity, to lower the costs of prosocial action, and to increase the size of the pie they then share. Just look at eBay: Its genius was to make the prosocial behaviors of gossip and punishment nearly costless through its feedback systems. The eBay community is an emergent group that wiped out many other auction-related groups, without malice or genetic change. If we limit our survey of evolutionary theorists to those who study humans as cultural creatures and who allow for the bidirectional interplay of genetic and cultural evolution, we find the opposite of Barash’s view: Most such theorists believe that cultural group selection has occurred and is occurring, and that such selection might well have shaped human genes whenever culturally altered selection pressures remained constant locally over many centuries. In writing my Review, I ignored the old consensus and drew instead on the new and exciting work of leading theorists such as Richerson and Boyd (2), Boehm (3), Fehr (4), Henrich (5), Maynard Smith (6), and Wilson (7), all of whom believe that natural selection works at multiple levels, including the group level.

As for Barash’s final point about conservative morality, I do not believe that descrip-

tive biology confers normative legitimacy. In my Review, I identified some areas of moral life that are highly elaborated in most cultures, but that are disliked by political liberals and dismissed by moral psychologists. I suggested that evolution may have shaped our intuitions about in-groups, authority, and purity, just as it shaped our intuitions about harm and fairness. If Barash believes that this suggestion is irresponsible because it may strengthen the religious right, then he has demonstrated the danger of moralism in science and has inadvertently illustrated all four of the principles that I proposed as comprising the new synthesis in moral psychology.

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## References

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2. P. J. Richerson, R. Boyd, *Not by Genes Alone: How Culture Transformed Human Evolution* (Univ. of Chicago Press, Chicago, 2005).
3. C. Boehm, *Hierarchy in the Forest: The Evolution of Egalitarian Behavior* (Harvard Univ. Press, Cambridge, MA, 1999).
4. E. Fehr, U. Fischbacher, *Trends Cognit. Sci.* **8**, 185 (2004).
5. J. Henrich, *J. Econ. Behav. Organ.* **53**, 3 (2004).
6. J. Maynard Smith, E. Szathmari, *The Major Transitions in Evolution* (Oxford Univ. Press, Oxford, 1997).
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## CORRECTIONS AND CLARIFICATIONS

**Reports:** “Direct evidence for a parietal-frontal pathway subserving spatial awareness in humans” by M. Thiebaut de Schotten *et al.* (30 September 2005, p. 2226). This study employed a neuroimaging method, diffusion tensor imaging tractography, to identify a fronto-parietal pathway important for spatial awareness. On the basis of the available literature [see, e.g., J. Bossy, *Les hémisphères cérébraux*, Neuroanatomie, Ed. (Springer, Berlin, 1991)], this pathway was labeled as “superior occipito-frontal fasciculus.” However, further evidence from the author’s laboratory (see Supporting Online Material at [www.sciencemag.org/cgi/content/full/317/5838/597/DC1](http://www.sciencemag.org/cgi/content/full/317/5838/597/DC1)) led them to reconsider this labeling. The authors are now convinced that the pathway likely corresponds to the human homologous of the second branch of the superior longitudinal fasciculus (SLF II), described in the monkey brain by Schmahmann and Pandya [J. D. Schmahmann, D. N. Pandya, *Fiber Pathways of the Brain* (Oxford Univ. Press, New York, 2006)]. In the monkey, the SLF II originates in the caudal inferior parietal lobe (corresponding to the human angular gyrus) and the occipito-parietal area and projects to the dorsolateral prefrontal cortex. This modification does not change the main point of the Report, that damage to the fronto-parietal pathways is important to produce neglect. On the contrary, it renders the results even more consistent with the data reported by Doricchi and Tomaiuolo [F. Doricchi, F. Tomaiuolo, *NeuroReport* **14**, 2239 (2003)], which demonstrated that damage to the SLF in human patients with vascular lesions correlates with the presence of spatial neglect. Future studies on the implication of white matter pathways in human cognition would greatly benefit from a stereotaxic atlas of the white matter tracts in the human brain.

## Letters to the Editor

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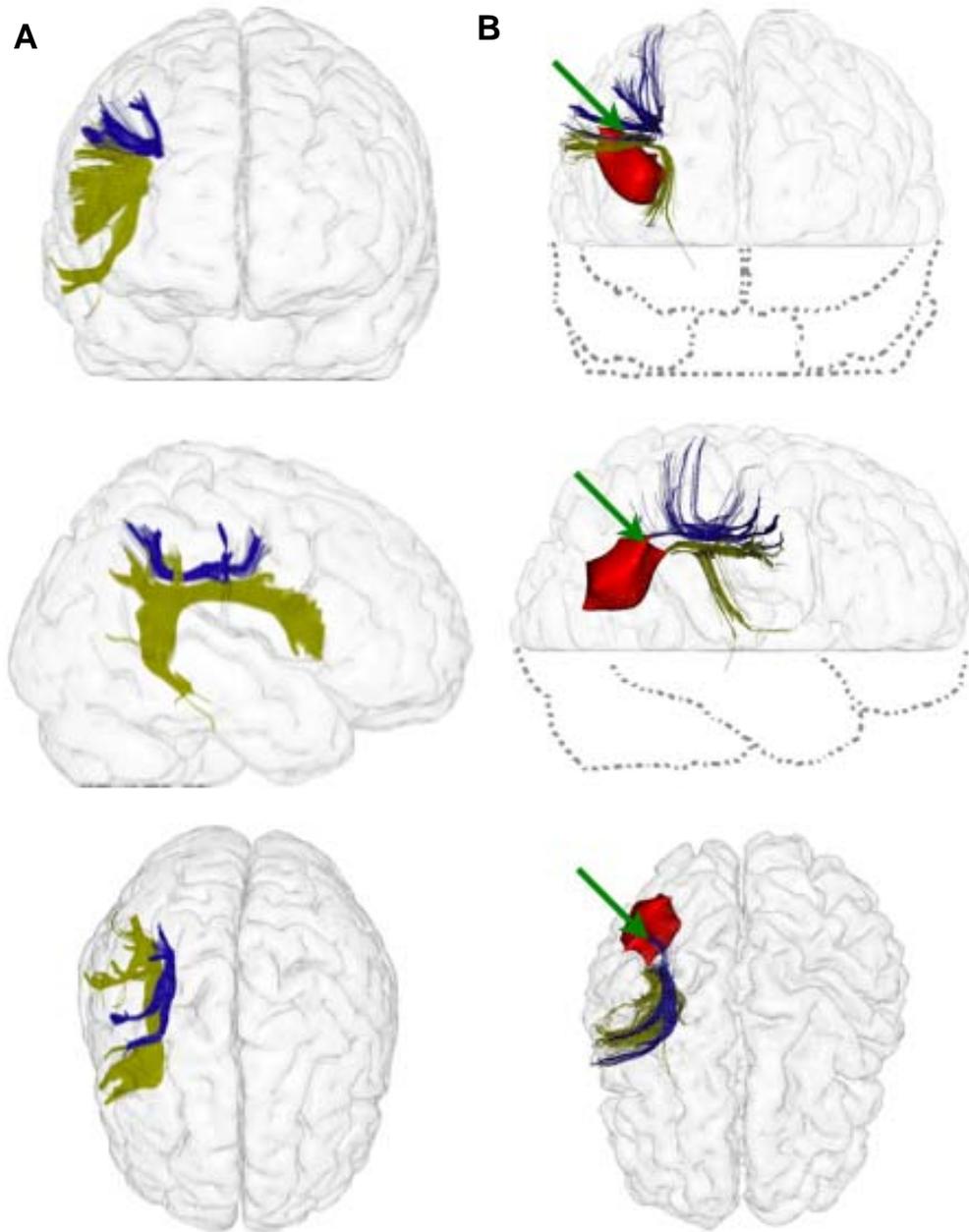
## Supporting Online Material for

Correction to “Direct evidence for a parietal-frontal pathway subserving spatial awareness in humans”

Published 3 August 2007, *Science* **317**, 597 (2007)  
DOI: 10.1126/science.1135832

### **This PDF file includes:**

Fig. S1  
References



**Fig. S1.** (A) Frontal, lateral and top views of a three-dimensional reconstruction of the SLF II (in blue), the arcuate fasciculus [anterior segment (1)/SLF III (2) and long segment (1), in yellow] in the referential space of the Montreal Neurological Institute (<http://www.mni.mcgill.ca>). Reconstructions were performed using BrainVisa 3.0.2 (<http://brainvisa.info/>). (B) Frontal, lateral and top views of the surgical resection (in red) and

of the stimulated region (green arrow) in a neurosurgical patient (3), showing their relationships with the SLF II (in blue) and the arcuate fasciculus (anterior segment/SLF III and long segment, in yellow)

#### References

1. M. Catani, D. K. Jones, D. H. ffytche, *Ann. Neurol.* **57**, 8 (2005).
2. J. D. Schmahmann, D. N. Pandya, *Fiber Pathways of the Brain* (Oxford Univ. Press, New York, 2006).
3. M. Thiebaut de Schotten *et al.*, *Science* **309**, 2226 (2005).