

# Current Biology

## Dorsal and Ventral Pathways for Prosody

### Highlights

- fMRI and categorization of prosody highlight a right-hemispheric neural network
- DWI and fiber tractography reveal dual right fronto-temporal streams for prosody
- TMS suggests a motor contribution to prosody perception in the right dorsal stream

### Authors

Daniela Sammler,  
Marie-Hélène Grosbras,  
Alfred Anwander,  
Patricia E.G. Bestelmeyer, Pascal Belin

### Correspondence

sammler@cbs.mpg.de

### In Brief

Left dorsal and ventral streams are established as the neural core of the language faculty. Sammler et al. show a similar architecture, but with relative rightward asymmetry, for the perception of prosody. The computational roles of the dual streams may complement each other when decoding subtle vocal prosodic cues in interpersonal communication.



# Dorsal and Ventral Pathways for Prosody

Daniela Sammler,<sup>1,2,\*</sup> Marie-Hélène Grosbras,<sup>2,3</sup> Alfred Anwander,<sup>4</sup> Patricia E.G. Bestelmeyer,<sup>5</sup> and Pascal Belin<sup>2,6,7</sup>

<sup>1</sup>Otto Hahn Group Neural Bases of Intonation in Speech, Max Planck Institute for Human Cognitive and Brain Sciences, 04103 Leipzig, Germany

<sup>2</sup>Institute of Neuroscience and Psychology, University of Glasgow, Glasgow G12 8QB, UK

<sup>3</sup>Laboratoire de Neurosciences Cognitives, FR 3C, Aix-Marseille Université, 13331 Marseille, France

<sup>4</sup>Department of Neuropsychology, Max Planck Institute for Human Cognitive and Brain Sciences, 04103 Leipzig, Germany

<sup>5</sup>School of Psychology, Bangor University, Gwynedd LL57 2AS, UK

<sup>6</sup>Institut des Neurosciences de La Timone, UMR 7289, CNRS and Aix-Marseille Université, 13005 Marseille, France

<sup>7</sup>International Laboratory for Brain, Music and Sound Research, University of Montréal and McGill University, Montréal H3C 3J7, Canada

\*Correspondence: [sammler@cbs.mpg.de](mailto:sammler@cbs.mpg.de)

<http://dx.doi.org/10.1016/j.cub.2015.10.009>

## SUMMARY

Our vocal tone—the prosody—contributes a lot to the meaning of speech beyond the actual words. Indeed, the hesitant tone of a “yes” may be more telling than its affirmative lexical meaning [1]. The human brain contains dorsal and ventral processing streams in the left hemisphere that underlie core linguistic abilities such as phonology, syntax, and semantics [2–4]. Whether or not prosody—a reportedly right-hemispheric faculty [5, 6]—involves analogous processing streams is a matter of debate. Functional connectivity studies on prosody leave no doubt about the existence of such streams [7, 8], but opinions diverge on whether information travels along dorsal [9] or ventral [10, 11] pathways. Here we show, with a novel paradigm using audio morphing combined with multimodal neuroimaging and brain stimulation, that prosody perception takes dual routes along dorsal and ventral pathways in the right hemisphere. In experiment 1, categorization of speech stimuli that gradually varied in their prosodic pitch contour (between statement and question) involved (1) an auditory ventral pathway along the superior temporal lobe and (2) auditory-motor dorsal pathways connecting posterior temporal and inferior frontal/premotor areas. In experiment 2, inhibitory stimulation of right premotor cortex as a key node of the dorsal stream decreased participants’ performance in prosody categorization, arguing for a motor involvement in prosody perception. These data draw a dual-stream picture of prosodic processing that parallels the established left-hemispheric multi-stream architecture of language, but with relative rightward asymmetry.

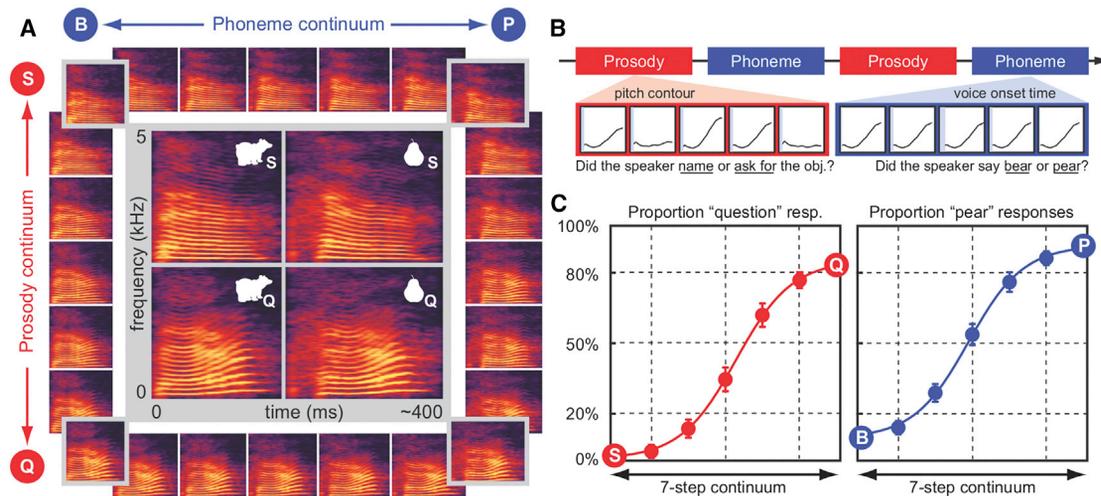
## RESULTS

Language is a uniquely human trait that is supported by parallel but interdependent large-scale neural networks. Currently, the

work of 19<sup>th</sup> century neuroscientists undergoes a revival inasmuch as timely neural language models focus on dorsal and ventral pathways between left frontal and temporal brain areas as the neural backbone of the language faculty [2, 3]. Despite their remarkable appeal and success, these models remain incomplete in one important way: they rarely include prosody [9, 12]. The term prosody subsumes rhythmic and melodic variations in speech that convey conversational and information structure or the speaker’s emotions and intentions—thereby making it an important tool in social interaction. Until today, neurolinguistic research has sought to formalize discrete hierarchical levels of prosody perception from sensory processing via auditory integration toward evaluative judgments of prosody within fronto-temporal cortical and subcortical gray-matter structures [11, 13–15] and to determine the conditions that account for the frequent (but not constant) right-hemispheric dominance of prosody perception [6]. What is still missing, however, is a network approach to prosody that describes how prosodic information passes through these processing stages.

## Experiment 1—Dual Streams for Prosody Perception

Here, we sought to fill this gap by using combined diffusion-weighted imaging (DWI) and fMRI during a prosody categorization task, compared to a non-prosodic control task. To study how the prosodic form of an utterance changes its meaning [1], the prosody task used mono-syllabic words intoned as statements or questions, i.e., conventionalized pitch contours that fulfill distinct communicative functions in everyday life. The use of single words capitalizes on their reduced dependency from left-hemispheric segmental processes (e.g., syntax) that interact with prosody perception at sentence level [16] and may obscure the boundaries of the prosody network. For stimulus construction, four adult Scottish speakers (two females) uttered the words “bear” and “pear” with either falling (statement) or rising pitch contour (question; Figure 1A, central panel). These recordings were fed into an audio morphing algorithm to obtain seven-step prosody continua in which pitch contour gradually changed from statement to question (stepwise increase of offset minus onset F0 by 15.3 Hz; Figure 1A and Audio S1). Orthogonal to that, PRAAT 5.3.01 (<http://www.praat.org>) was used to create seven-step phoneme continua in which pitch contour was fixed but voice onset time (VOT) of the word-initial consonant gradually changed from /b/ to /p/ (stepwise increase of VOT by



### Figure 1. Experimental Design and Stimuli

(A) The words “bear” and “pear” spoken as question (Q) or statement (S) (central panel) were used to construct continua along two dimensions: prosody (vertical; [Audio S1](#)) and word-initial phoneme (horizontal; [Audio S2](#)).

(B) Participants categorized these stimuli in terms of prosody or phoneme, in separate blocks. Tasks alternated across blocks. Each block contained seven repetitions of seven prosody or seven phoneme steps, arranged according to a serially balanced sequence.

(C) Psychophysical identification functions in the prosody (red) and the phoneme (blue) task in the fMRI experiment. The similar slopes indicate that the two tasks were matched in difficulty.

See also [Table S1](#) and [Audio S1](#) and [S2](#).

3 ms; [Audio S2](#)). Step size was chosen such that both tasks were of equal difficulty. Furthermore, continua were centered on each participant’s individual points of subjective equality as assessed in a pre-fMRI test (see the [Supplemental Experimental Procedures](#)).

We first used these stimuli to identify brain areas that are involved in the processing of prosodic pitch contour in speech. We used fMRI to measure neural activity in the brains of 23 healthy native English participants while they completed 16 task blocks in a 3T Siemens TIM TRIO scanner ([Figure 1B](#)). Half of the blocks required a two-alternative forced-choice judgment of prosody (did the speaker *name* or *ask* for the object?; experimental task) or of phoneme (did the speaker say *bear* or *pear*?; non-prosodic control task). Tasks were comparable in difficulty as demonstrated by the similar average regression slopes of the psychophysical identification functions in both prosody (mean slope  $\pm$  SEM:  $0.35 \pm 0.03$ ) and phoneme categorization ( $0.34 \pm 0.03$ ; two-tailed paired-sample *t* test:  $t_{22} = -0.682$ ,  $p > 0.502$ ; [Figure 1C](#)).

fMRI random-effects analyses revealed stronger activations during prosody than phoneme blocks in the right posterior (pSTS) and anterior (aSTS) superior temporal sulcus, the right inferior frontal gyrus (IFG) at the border between pars opercularis and pars triangularis, and the right premotor cortex (PMC) at the level of the “larynx representation” [17] ([Table 1](#); see also [Figure S1](#)). No such activations reached significance in the left hemisphere, and we found a relative right dominance of these clusters when examining their lateralization indices (LIs; one-sample *t* tests against zero; pSTS:  $t_{22} = -5.156$ ,  $p < 0.001$ ; aSTS:  $t_{22} = -2.376$ ,  $p < 0.027$ ; IFG:  $t_{22} = -2.300$ ,  $p < 0.031$ ; PMC:  $t_{22} = -2.102$ ,  $p < 0.047$ ; see [Figure S1](#)). LIs were calculated as  $LI = (L - R) / (L + R)$ , with R and L representing the effect sizes

of the right-hemisphere clusters’ peak voxel and its left-hemisphere homolog (negative *x* coordinate), respectively (see the [Supplemental Experimental Procedures](#)). Apart from these regions, we found prosody-related activations in bilateral supplementary motor area (SMA; LI:  $t_{22} = -1.251$ ,  $p > 0.224$ ) and left intraparietal sulcus (IPS; LI:  $t_{22} = 1.967$ ,  $p > 0.062$ ; see [Figure S1](#)). No area showed stronger activation during phoneme than prosody blocks (but see the [Supplemental Information](#) for a more fine-grained analysis of the phoneme data).

We then used our fMRI activation clusters in right pSTS, aSTS, PMC, and IFG as seed and target regions in multi-fiber probabilistic tractography to estimate the most likely white-matter pathways that connect these prosody-relevant nodes. No tractography was carried out in the left hemisphere given that no left fronto-temporal activation clusters were found in the fMRI experiment. This approach revealed robust ventral and dorsal fiber tracts in the right hemisphere ([Figure 2](#)). Ventrally, the pSTS and aSTS clusters were connected via the middle longitudinal fascicle (MdLF; 23/23 participants). No connections were found between the aSTS and IFG clusters. Dorsally, the pSTS-IFG connection followed the direct branch of the arcuate/superior longitudinal fascicle (AF/SLF; 19/23 participants). The pSTS-PMC connection took a similar but slightly more dorsal and posterior trajectory along the AF/SLF (18/23 participants). Finally, PMC was strongly interconnected with IFG via short U fibers (23/23 participants; see [Figure S2](#) for individual data and [Figure S3](#) for a 3D view of the results).

Dorsal and ventral pathways have been subject to speculation in prosody research for a while [11, 15, 18], but the available data are sparse [9, 10, 19]. They often suggest that prosodic information travels either dorsally [9, 15] or ventrally [11] between superior temporal areas and IFG. Our tractography data argue for a

**Table 1. Overview of Significant Clusters in the Prosody > Phoneme Random-Effects Contrast**

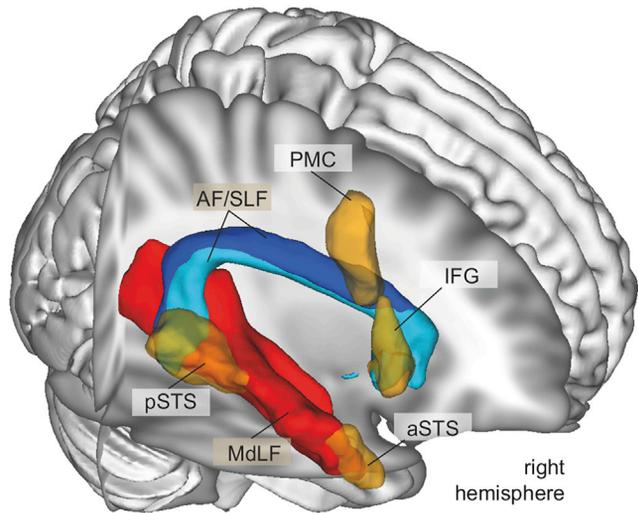
Site	BA	Cluster Size	MNI Coordinate			Z Value
			x	y	z	
L IPS	40	84	-33	-46	34	4.34
			-24	-37	28	3.80
			-36	-40	40	3.67
R pSTS	21/22	156	42	-37	4	4.36
			48	-28	1	4.22
R TP	38	62	57	11	-17	4.06
R aSTS	21/22		57	2	-8	3.75
			45	5	-20	3.51
R PMC	6	120	45	5	40	4.00
R IFG (p. op.)	44		42	8	31	3.50
			33	5	46	3.21
ACC/SMA	32/6	62	9	17	49	3.80
R IFG (p. op.)	44	44	60	20	25	3.71
R IFG (p. tri.)	45		48	20	13	3.46
			60	23	10	3.39

Thresholded at  $p < 0.001$ , cluster extent  $\geq 20$  voxels ( $\sim 540 \text{ mm}^3$ ; equaling whole-brain  $p < 0.01$ ). Specifications refer to peak voxels. BA, Brodmann area; MNI, Montréal Neurological Institute; L, left; R, right; IPS, intraparietal sulcus; pSTS, posterior superior temporal sulcus; TP, temporal pole; aSTS, anterior STS; PMC, premotor cortex; IFG, inferior frontal gyrus; p. op., pars opercularis; p. tri., pars triangularis; ACC, anterior cingulate cortex; SMA, supplementary motor area. See also [Figure S1](#).

more complex connectivity pattern in two respects: First, they show that information travels along both dorsal *and* ventral pathways in the right hemisphere. This invites hypotheses on a computational division of labor between streams as will be outlined in more detail in the [Discussion](#) below. Second, our data show the involvement of an additional dorsal auditory-motor circuit between the right pSTS and PMC. Prevailing neural prosody models [5, 11, 14, 15, 18] typically focus on superior temporal areas and IFG as established prosody processors according to numerous neuroimaging [18, 20], brain stimulation [21], and lesion [5, 13] studies. Only more recently have publications started to report PMC activations during prosody perception [22, 23]. Interestingly, PMC activity is central to an entire research tradition on (non-prosodic) motor theories of speech perception [24]. One recurrent debate in this field pertains to the question whether PMC is essential for tuning-up the processing of speech sounds, e.g., via simulation of articulatory gestures [25, 26]. While our results invite speculations about a similar mechanism in prosody perception, the inclusion of an auditory-motor pathway into a network model of prosody requires more evidence for the *necessity* of PMC in prosody perception in the first instance.

### Experiment 2—Motor-Involvement in Prosody Perception

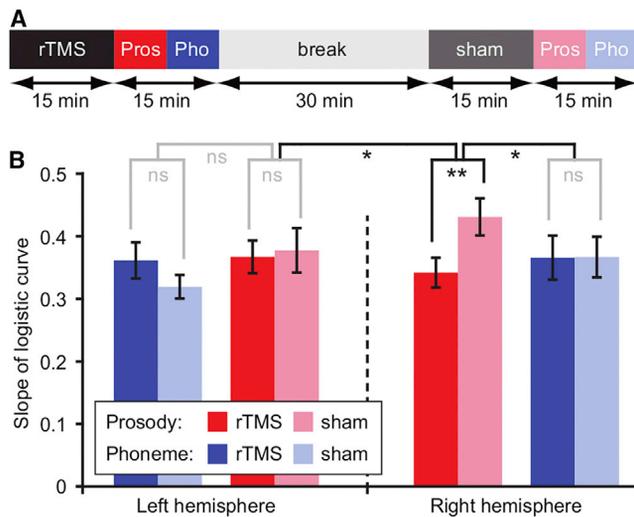
Here, we used repetitive transcranial magnetic stimulation (rTMS) to assess changes in prosody perception after temporary inhibition of PMC in a new group of 32 healthy native English participants. They were invited to do a shortened version of the

**Figure 2. Functional and Diffusion MRI Data**

Brain areas with a stronger blood-oxygen-level-dependent response during prosody than phoneme task (yellow;  $p_{\text{voxel}} < 0.001$ ,  $p_{\text{cluster}} < 0.01$ ) and group overlay of fiber tracts connecting the functional clusters: pSTS with aSTS (red), PMC (blue), and IFG (cyan). U fibers between the PMC and IFG are not depicted. Only voxels with fibers in more than 50% of participants are highlighted. Activation clusters and fiber tracts were slightly smoothed (1 mm full width at half maximum) for visualization. AF, arcuate fascicle; SLF, superior longitudinal fascicle; MdLF, middle longitudinal fascicle. Other abbreviations are as in [Table 1](#). See also [Figures S2](#) and [S3](#).

prosody and phoneme tasks as used in experiment 1, once after 15 min of inhibitory offline 1-Hz rTMS of the PMC, and once after 15 min of sham stimulation of the same area ([Figure 3A](#)). The order of task (prosody/phoneme) and stimulation type (rTMS/sham) was counterbalanced across participants. In half of the participants, rTMS was applied to the right PMC (as identified in experiment 1), and in the other half, the coil was placed over the homolog coordinate in the left hemisphere (negative x coordinate). No rTMS was applied to the pSTS, aSTS, or IFG because their involvement in prosody perception is firmly established [11, 13, 18, 20, 21]. The two participant groups were carefully matched in age, handedness, years of musical training, stimulator output during rTMS, and performance during sham stimulation ( $p_s > 0.107$ ; [Table S3](#)). We ensured that both tasks were challenging and therefore sensitive to possible disruption by rTMS by centering the stimuli on each participant's individual point of subjective equality obtained before the actual TMS session. If the right PMC is functionally relevant for prosody perception, its rTMS (but not sham stimulation) should induce a performance drop that is stronger in the prosody than in the phoneme task, and that might be stronger after rTMS of the right than of the left PMC based on our fMRI results.

Slopes of the psychophysical identification functions served as dependent variable: the shallower the slope the weaker the participant's ability to identify tokens as belonging to one or the other category (statement versus question or /b/ versus /p/). The results showed a clearly reduced performance in the prosody task after rTMS of the right PMC (compared to sham stimulation;  $t_{1,15} = -3.888$ ,  $p < 0.005$ , paired-sample t test, Bonferroni corrected) that was not seen after rTMS of the left PMC



**Figure 3. Repetitive TMS Experiment**

(A) Participants completed one prosody (Pros) and one phoneme (Pho) block after rTMS and sham stimulation of right or left PMC, in counterbalanced order. (B) Performance in the prosody (but not phoneme) task decreased after rTMS of the right (but not left) PMC compared to sham stimulation. Bars depict mean slopes  $\pm$  1 SEM.

See also Tables S2 and S3.

( $t_{1,15} = -0.342$ ,  $p > 0.737$ ; pink and red bars in Figure 3B). Furthermore, rTMS in either hemisphere did not affect performance in the phoneme task ( $t_{1,15} < 2.351$ ,  $ps > 0.132$ ; light and dark blue bars in Figure 3B). This is not surprising given that the stimulation site was chosen to specifically interfere with prosody, not with phoneme perception. Statistically, the interaction between task (prosody/phoneme) and stimulation type (rTMS/sham) was significant in the right hemisphere ( $F_{1,15} = 7.328$ ,  $p < 0.017$ ,  $\eta_p^2 = 0.328$ ; for full statistical details, see Table S2), lending strong evidence for the functional relevance of the right PMC in prosody perception. No such interaction was found in the left hemisphere ( $F_{1,15} = 3.755$ ,  $p > 0.072$ ,  $\eta_p^2 = 0.200$ ). Furthermore, the interaction between stimulation (rTMS/sham) and hemisphere (left/right) was significant in the prosody task ( $F_{1,30} = 4.252$ ,  $p < 0.049$ ,  $\eta_p^2 = 0.124$ ), in line with the relative right dominance observed in experiment 1. No such interaction was found for the phoneme task ( $F_{1,30} = 1.672$ ,  $p > 0.206$ ,  $\eta_p^2 = 0.053$ ). In fact, the stimulation of right (but not left) PMC consistently decreased participants' prosody perception, while phoneme categorization remained unimpaired (see the Supplemental Information for more details on the phoneme data). Finally, this effect cannot be driven by nominal performance differences in the sham conditions, as demonstrated by the absence of a task  $\times$  hemisphere interaction ( $F_{1,30} = 0.02$ ,  $p > 0.901$ ,  $\eta_p^2 = 0.001$ ) in an ANOVA with the factors task (prosody sham versus phoneme sham; within subject) and hemisphere (left versus right; between subjects).

## DISCUSSION

In language research, the notion of dorsal and ventral streams—as the neural core of the language faculty—has become largely

undisputed [2–4, 27]. Functionally, the left dorsal stream has been associated with time-dependent mechanisms of speech processing that afford, among others, the conversion of the auditory speech signal into a motor format to support articulation (“how”) [3, 4, 27] and that allow at the same time a motor influence on perception, i.e., the simulation of articulatory gestures to support comprehension [26, 28]. The ventral stream, in turn, has been proposed to gradually transform complex acoustic feature combinations into abstract time-invariant representations of speech sounds that interface with conceptual systems and, thus, are linked to meaning (“what”) [4, 27, 29]. Whether a similar organization also pertains to prosodic aspects of speech is a matter of debate. Here we provide evidence for a multi-stream architecture of prosodic contour perception and propose a functional division of labor that parallels prevailing language models, but in the right hemisphere.

### Dorsal Pathways—Sound to Articulation and Evaluation

The identification of statements and questions by our participants evoked activity in two dorsal stream regions: right PMC and IFG. The PMC activation was located at the somatotopic level of the dorsal larynx representation [17, 30]. This area controls the pitch of voluntary vocalizations in humans. Our participants did not vocalize (according to self-report) but may have simulated the laryngeal gesture that the speaker used to produce the vocal prosodic contour to sharpen their perception [26]. This proposal is based on the notion of sensorimotor loops that provide auditory feedback control for speech production but that can be reversed to tune up speech perception by recovering the articulatory gesture that generated the speech sound [25, 28, 31, 32]. Although it is arguable whether the motor system is essential for speech perception [25, 26], there is little doubt that passive listening to speech sounds activates (pre)motor areas [26] and that up- or downregulation of lip- or tongue-related motor regions alters performance in phonetic language tasks [31, 32]. The novel implication of our combined fMRI and TMS results is that this motor involvement also applies to prosody: temporary downregulation of the right PMC led to a performance decrease that was specific to prosody categorization, in line with similar findings on emotional prosody perception [33] and vocal pitch discrimination [34]. Importantly, vocal pitch productions are known to rely on sensorimotor loops: self-vocalizations of pitch suppress auditory activity, while transient perturbations of vocal pitch feedback enhance auditory activity and induce instantaneous vocal compensation (for a review, see [35]). It is plausible to assume that these loops can also motor modulate the perception of prosodic contours, similar to how they augment the perception of non-prosodic speech sounds [31, 32]. Note that we do not rule out that motor involvement in prosody perception mainly applies to subtle modulations of vocal tone as those in our ambiguous stimuli [25]. Furthermore, we are not claiming to prove that the PMC is an area of prosodic processing per se. Rather, we favor the view that it is part of a larger action-perception network, including PMC interlinked with temporal auditory areas, the dynamics of which were unbalanced after TMS of the PMC. Crucially, our tractography results highlight the AF/SLF as the most likely anatomical link between the pSTS and PMC to support this mechanism, in keeping with influential models of auditory feedback control [35, 36].

One further node of the dorsal stream was located in the right IFG, at the border between dorsal Brodmann area 44 (BA44) and BA45. Following prevailing models of prosody perception [9, 14, 15, 18], we propose that IFG contributes task-dependent cognitive resources via the dorsal pathways to parse and explicitly label the dynamic prosodic contour. Notably, the anatomical links of IFG with pSTS and PMC via AF/SLF and U fibers, respectively, raise the interesting hypothesis that IFG may evaluate prosodic patterns in both audio and motor formats and eventually supports their integration. More generally, the time-sensitive monitoring and assessment of evolving pitch contours [28] via pSTS-IFG and pSTS-PMC(-IFG) connections may be relevant beyond single words and extend to sentence-level prosody (see below).

Overall, our results show an interesting consistency of the right dorsal tracts in 21 of our 23 participants. Increasing evidence indeed indicates that the prevalence of the right AF is higher than previously believed [37], although its volume is typically lower than in the left hemisphere [38]. Importantly, recent work on aphasia recovery [39] has started to advocate the right AF as a mediator of right-hemispheric language functions, including verbal recall [40] and prosody [39].

### Ventral Pathway—Sound to Auditory Object

Categorizing the prosody of speech sounds further involved two ventral stream regions: the right posterior and anterior STS. Following models of auditory (speech) perception [4], the pSTS is an established processor of non-verbal complex acoustic forms and the aSTS a known seat of invariant sound characteristics that identify auditory objects [41]. Together, they may afford a gradual segregation and abstraction of the prosodic signal from a granular, speaker-dependent representation of speech sounds in pSTS to a speaker-invariant “prosodic Gestalt” in the aSTS [11]. A similar process of abstraction along the ventral auditory stream has been described as the basis for perceptual constancy in speech perception in the left hemisphere [4, 29, 42], as well as for the perception of voice identity [43] in the right hemisphere.

Notably, our data suggest the MdLF [44] as direct anatomical link that would allow prosody to follow these hierarchical processing steps along the axis of the temporal lobe [4]. The left MdLF has been previously described in the context of language comprehension [27, 44, 45], although many authors—when talking about the ventral pathway—refer to the extreme capsule (EmC) or uncinata fascicle (UF) connecting the temporal and inferior frontal lobe [2, 19, 46]. Indeed, a ventral projection to IFG would make IFG the most plausible interface to integrate complementary information provided by ventral and dorsal pathways. In the present study, we did not find the EmC and UF, most likely because their frontal terminations are typically more anterior (BA45/47; see Figures S2 and S3) [38] than our IFG target region (peak in BA44). However, considering the widespread notion that the ventral stream maps sound to meaning [3, 27, 46], the absence of EmC and UF involvement in the present study might reflect an essential difference of how our stimuli were processed: unlike sentences [2, 46] or prototypical emotional vocalizations [19], linguistic prosodic contours of single words may not easily map onto a semantic space, even if they can be processed as a

signal of more general interpersonal significance, to convey a concept of the speaker’s communicative intention or attitude [1]. The mechanisms that link “prosodic Gestalts” and communicative concepts are an interesting topic for future research.

### Right Lateralization

Our fMRI results highlight a relative right dominance of brain activations, in line with prevailing cue-dependent models of prosody [6]. These suggest a processing benefit of the right hemisphere for spectral information [47] that unfolds over extended timescales [48]. As a consequence, this implies that white-matter tracts in the right hemisphere qualify as main (although perhaps not only) routes of prosody perception, despite the frequently reported larger volume of left-hemispheric fiber bundles [38]. Note that we do not exclude the involvement of left-hemispheric pathways per se, but rather favor the view that our experimental design was particularly sensitive to the right-hemispheric core components of a probably more extended bilateral network [19]. In particular, it remains to be specified in which way the present results generalize to sentence-level prosodic functions such as phrasing or accentuation. One conceivable scenario is that time-sensitive prosodic processes of the right dorsal stream interact transcallosally [16] with sentence-level syntactic and semantic operations in the left hemisphere [12]. Interestingly, the rightward asymmetry included the PMC. Although surprising, given a bilateral organization of voice control [17, 30, 49], this finding is in keeping with mounting evidence of a right premotor advantage in auditory-feedback control [35, 36] and might indicate a projection of auditory asymmetries up to premotor areas [48]. Exceptions to the right dominance were (1) a bilateral (but right-trended) activation in the SMA and (2) a left-dominant activation in the IPS, both of which may relate to the cortical sensorimotor control of (simulated) vocalizations [4, 36].

To sum up, our study indicates dual processing streams for prosody in the right hemisphere. The associated computational roles are proposed to parallel those in the left hemisphere, including the time-sensitive evaluation of prosodic contours in audio and/or motor format along the dorsal pathways (“how”) [28] and the gradual formation of time-invariant “prosodic Gestalts” (“what”) along the ventral pathway [4, 29]. While future work is needed to firmly assess these functional hypotheses, the potentially parallel involvement yet flexible weighting and ultimate fusion of both streams could provide a robust basis for prosody perception that is particularly suited to meet the demands of multiple functions and levels of prosody in various listening situations.

### SUPPLEMENTAL INFORMATION

Supplemental Information includes Supplemental Experimental Procedures, three figures, three tables, and two audio files and can be found with this article online at <http://dx.doi.org/10.1016/j.cub.2015.10.009>.

### AUTHOR CONTRIBUTIONS

D.S., M.-H.G., and P.B. designed the study. D.S. performed the research. D.S., A.A., and P.E.G.B. analyzed the data. D.S., M.-H.G., A.A., P.E.G.B., and P.B. co-wrote the manuscript.

## ACKNOWLEDGMENTS

The research protocols were approved by the ethics committee of the College of Science and Engineering at the University of Glasgow (CSE00960; CSE01245). The authors are grateful to Tamara Rathcke, Marianne Latinus, David Fleming, Phil McAleer, Judith L. Stevenson, Rebecca Watson, Frances Crabbe, Merle-Marie Ahrens, Sibylle Mohr, Elizabeth Bucher, Lotta Ranta, and Christoph Scheepers for their help during experiments. Furthermore, the authors are thankful for insightful comments and contributions of the anonymous reviewers. The project was funded by the Otto Hahn award of the Max Planck Society to D.S. and by BBSRC grant BB/1006494/1 and FRM grant AJE201214 to P.B.

Received: December 20, 2014

Revised: September 2, 2015

Accepted: October 5, 2015

Published: November 5, 2015

## REFERENCES

- Bolinger, D. (1986). *Intonation and Its Parts - Melody in Spoken English* (Stanford University Press).
- Friederici, A.D. (2011). The brain basis of language processing: from structure to function. *Physiol. Rev.* *91*, 1357–1392.
- Hickok, G., and Poeppel, D. (2007). The cortical organization of speech processing. *Nat. Rev. Neurosci.* *8*, 393–402.
- Rauschecker, J.P., and Scott, S.K. (2009). Maps and streams in the auditory cortex: nonhuman primates illuminate human speech processing. *Nat. Neurosci.* *12*, 718–724.
- Ross, E.D., and Monnot, M. (2008). Neurology of affective prosody and its functional-anatomic organization in right hemisphere. *Brain Lang.* *104*, 51–74.
- Witteman, J., van Ijzendoorn, M.H., van de Velde, D., van Heuven, V.J., and Schiller, N.O. (2011). The nature of hemispheric specialization for linguistic and emotional prosodic perception: a meta-analysis of the lesion literature. *Neuropsychologia* *49*, 3722–3738.
- Ethofer, T., Anders, S., Erb, M., Herbert, C., Wiethoff, S., Kissler, J., Grodd, W., and Wildgruber, D. (2006). Cerebral pathways in processing of affective prosody: a dynamic causal modeling study. *Neuroimage* *30*, 580–587.
- Frühholz, S., and Grandjean, D. (2012). Towards a fronto-temporal neural network for the decoding of angry vocal expressions. *Neuroimage* *62*, 1658–1666.
- Glasser, M.F., and Rilling, J.K. (2008). DTI tractography of the human brain's language pathways. *Cereb. Cortex* *18*, 2471–2482.
- Ethofer, T., Bretschner, J., Gschwind, M., Kreifelts, B., Wildgruber, D., and Vuilleumier, P. (2012). Emotional voice areas: anatomic location, functional properties, and structural connections revealed by combined fMRI/DTI. *Cereb. Cortex* *22*, 191–200.
- Schirmer, A., and Kotz, S.A. (2006). Beyond the right hemisphere: brain mechanisms mediating vocal emotional processing. *Trends Cogn. Sci.* *10*, 24–30.
- Friederici, A.D., and Alter, K. (2004). Lateralization of auditory language functions: a dynamic dual pathway model. *Brain Lang.* *89*, 267–276.
- Baum, S.R., and Pell, M.D. (1999). The neural bases of prosody: insights from lesion studies and neuroimaging. *Aphasiology* *13*, 581–608.
- Brück, C., Kreifelts, B., and Wildgruber, D. (2011). Emotional voices in context: a neurobiological model of multimodal affective information processing. *Phys. Life Rev.* *8*, 383–403.
- Wildgruber, D., Ackermann, H., Kreifelts, B., and Ethofer, T. (2006). Cerebral processing of linguistic and emotional prosody: fMRI studies. *Prog. Brain Res.* *156*, 249–268.
- Sammler, D., Kotz, S.A., Eckstein, K., Ott, D.V.M., and Friederici, A.D. (2010). Prosody meets syntax: the role of the corpus callosum. *Brain* *133*, 2643–2655.
- Brown, S., Ngan, E., and Liotti, M. (2008). A larynx area in the human motor cortex. *Cereb. Cortex* *18*, 837–845.
- Frühholz, S., and Grandjean, D. (2013). Processing of emotional vocalizations in bilateral inferior frontal cortex. *Neurosci. Biobehav. Rev.* *37*, 2847–2855.
- Frühholz, S., Gschwind, M., and Grandjean, D. (2015). Bilateral dorsal and ventral fiber pathways for the processing of affective prosody identified by probabilistic fiber tracking. *Neuroimage* *109*, 27–34.
- Frühholz, S., and Grandjean, D. (2013). Multiple subregions in superior temporal cortex are differentially sensitive to vocal expressions: a quantitative meta-analysis. *Neurosci. Biobehav. Rev.* *37*, 24–35.
- Alba-Ferrara, L., Ellison, A., and Mitchell, R.L. (2012). Decoding emotional prosody: resolving differences in functional neuroanatomy from fMRI and lesion studies using TMS. *Brain Stimulat.* *5*, 347–353.
- Warren, J.E., Sauter, D.A., Eisner, F., Wiland, J., Dresner, M.A., Wise, R.J., Rosen, S., and Scott, S.K. (2006). Positive emotions preferentially engage an auditory-motor “mirror” system. *J. Neurosci.* *26*, 13067–13075.
- Beaucousin, V., Lacheret, A., Turbelin, M.R., Morel, M., Mazoyer, B., and Tzourio-Mazoyer, N. (2007). fMRI study of emotional speech comprehension. *Cereb. Cortex* *17*, 339–352.
- Lieberman, A.M., and Mattingly, I.G. (1985). The motor theory of speech perception revised. *Cognition* *21*, 1–36.
- Hickok, G., Houde, J., and Rong, F. (2011). Sensorimotor integration in speech processing: computational basis and neural organization. *Neuron* *69*, 407–422.
- Pulvermüller, F., and Fadiga, L. (2010). Active perception: sensorimotor circuits as a cortical basis for language. *Nat. Rev. Neurosci.* *11*, 351–360.
- Saur, D., Kreher, B.W., Schnell, S., Kümmerer, D., Kellmeyer, P., Vry, M.S., Umarova, R., Musso, M., Glauche, V., Abel, S., et al. (2008). Ventral and dorsal pathways for language. *Proc. Natl. Acad. Sci. USA* *105*, 18035–18040.
- Rauschecker, J.P. (2011). An expanded role for the dorsal auditory pathway in sensorimotor control and integration. *Hear. Res.* *271*, 16–25.
- Scott, S.K., Blank, C.C., Rosen, S., and Wise, R.J. (2000). Identification of a pathway for intelligible speech in the left temporal lobe. *Brain* *123*, 2400–2406.
- Bouchard, K.E., Mesgarani, N., Johnson, K., and Chang, E.F. (2013). Functional organization of human sensorimotor cortex for speech articulation. *Nature* *495*, 327–332.
- Möttönen, R., and Watkins, K.E. (2009). Motor representations of articulators contribute to categorical perception of speech sounds. *J. Neurosci.* *29*, 9819–9825.
- D'Ausilio, A., Pulvermüller, F., Salmas, P., Bufalari, I., Begliomini, C., and Fadiga, L. (2009). The motor somatotopy of speech perception. *Curr. Biol.* *19*, 381–385.
- Banissy, M.J., Sauter, D.A., Ward, J., Warren, J.E., Walsh, V., and Scott, S.K. (2010). Suppressing sensorimotor activity modulates the discrimination of auditory emotions but not speaker identity. *J. Neurosci.* *30*, 13552–13557.
- D'Ausilio, A., Bufalari, I., Salmas, P., Busan, P., and Fadiga, L. (2011). Vocal pitch discrimination in the motor system. *Brain Lang.* *118*, 9–14.
- Houde, J.F., and Chang, E.F. (2015). The cortical computations underlying feedback control in vocal production. *Curr. Opin. Neurobiol.* *33*, 174–181.
- Guenther, F.H., and Hickok, G. (2016). Neural models of motor speech control. In *Neurobiology of Language*, G. Hickok, and S.L. Small, eds. (Academic Press), pp. 725–740.
- Fernández-Miranda, J.C., Wang, Y., Pathak, S., Stefaneau, L., Verstynen, T., and Yeh, F.-C. (2015). Asymmetry, connectivity, and segmentation of the arcuate fascicle in the human brain. *Brain Struct. Funct.* *220*, 1665–1680.
- Thiebaut de Schotten, M., Ffytche, D.H., Bizzi, A., Dell'Acqua, F., Allin, M., Walshe, M., Murray, R., Williams, S.C., Murphy, D.G., and Catani, M. (2011). Atlas location, asymmetry and inter-subject variability of white

- matter tracts in the human brain with MR diffusion tractography. *Neuroimage* 54, 49–59.
39. Forkel, S.J., Thiebaut de Schotten, M., Dell'Acqua, F., Kalra, L., Murphy, D.G., Williams, S.C., and Catani, M. (2014). Anatomical predictors of aphasia recovery: a tractography study of bilateral perisylvian language networks. *Brain* 137, 2027–2039.
  40. Catani, M., Allin, M.P.G., Husain, M., Pugliese, L., Mesulam, M.M., Murray, R.M., and Jones, D.K. (2007). Symmetries in human brain language pathways correlate with verbal recall. *Proc. Natl. Acad. Sci. USA* 104, 17163–17168.
  41. Petkov, C.I., Logothetis, N.K., and Obleser, J. (2009). Where are the human speech and voice regions, and do other animals have anything like them? *Neuroscientist* 15, 419–429.
  42. Obleser, J., and Eisner, F. (2009). Pre-lexical abstraction of speech in the auditory cortex. *Trends Cogn. Sci.* 13, 14–19.
  43. Belin, P., and Zatorre, R.J. (2003). Adaptation to speaker's voice in right anterior temporal lobe. *Neuroreport* 14, 2105–2109.
  44. Makris, N., Papadimitriou, G.M., Kaiser, J.R., Sorg, S., Kennedy, D.N., and Pandya, D.N. (2009). Delineation of the middle longitudinal fascicle in humans: a quantitative, in vivo, DT-MRI study. *Cereb. Cortex* 19, 777–785.
  45. Wong, F.C., Chandrasekaran, B., Garibaldi, K., and Wong, P.C. (2011). White matter anisotropy in the ventral language pathway predicts sound-to-word learning success. *J. Neurosci.* 31, 8780–8785.
  46. Weiller, C., Bormann, T., Saur, D., Musso, M., and Rijntjes, M. (2011). How the ventral pathway got lost: and what its recovery might mean. *Brain Lang.* 118, 29–39.
  47. Zatorre, R.J., Belin, P., and Penhune, V.B. (2002). Structure and function of auditory cortex: music and speech. *Trends Cogn. Sci.* 6, 37–46.
  48. Giraud, A.L., Kleinschmidt, A., Poeppel, D., Lund, T.E., Frackowiak, R.S., and Laufs, H. (2007). Endogenous cortical rhythms determine cerebral specialization for speech perception and production. *Neuron* 56, 1127–1134.
  49. Cogan, G.B., Thesen, T., Carlson, C., Doyle, W., Devinsky, O., and Pesaran, B. (2014). Sensory-motor transformations for speech occur bilaterally. *Nature* 507, 94–98.