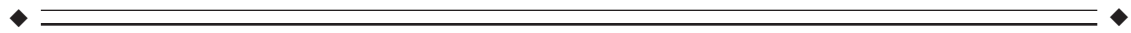# Modulation of Activity in Temporal Cortex During Generation of Inner Speech

Sukhwinder S. Shergill,* **Michael J. Brammer, Rimmei Fukuda, Ed Bullmore, Edson Amaro Jr., Robin M. Murray, and Philip K. McGuire**

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Abstract: Monitoring one's thoughts (in the verbal modality) is thought to be critically dependent on the interaction between areas that generate and perceive inner speech in the frontal and temporal cortex, respectively. We used functional magnetic resonance imaging (fMRI) to examine the relationship between activity in these areas while the rate of inner speech generation was varied experimentally. The faster rate was associated with activation in the left inferior frontal gyrus, the right pre- and postcentral gyri and both superior temporal gyri. Thus, temporal cortical activation was associated with increasing the rate of covert articulation, in the absence of external auditory input, suggesting that there is effective fronto-temporal connectivity. Furthermore, this may provide support for the existence of feed forward models, which suggest that activity in regions responsible for verbal perception is modulated by activity in areas that generate inner speech. *Hum. Brain Mapping 16:219–227, 2002.* © **2002 Wiley-Liss, Inc.**

Key words: inner speech; temporal lobe; frontal lobe; modulation; functional neuroimaging

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INTRODUCTION

Electrophysiological recordings in non-human primates [Müller-Preuss and Ploog, 1981] and man [Creutzfeldt et al., 1989; Numminen and Curio, 1999] indicate that neuronal activity in the temporal cortex is powerfully modulated by vocalization. This modulation can precede articulation by hundreds of milliseconds, suggesting that it is related to the intention to speak (rather than articulation per se) and may be mediated by the direct anatomical connections that link areas that generate and perceive speech [Pandya and Yeterian, 1985; Romanski et al., 1999], in the frontal and temporal cortex respectively. Similarly, some positron emission tomography (PET) studies have indicated that when subjects generate words, the left dorsolateral prefrontal cortex (DLPFC) is activated whereas the bilateral temporal cortex is de-activated [Friston et al., 1991; Frith et al., 1991]. These studies suggest that output from regions involved in verbal generation may modulate activation in areas involved in speech perception, perhaps to inform them that impending verbal stimuli are self-generated.

Most of the neuroimaging evidence for modulation of temporal activation during verbal generation is derived from studies of verbal fluency. As well as articulation, generating a word in response to a cue involves phonological and semantic processing, processes that could also account for changes in frontal and temporal activation [Binder et al., 2000; Burton et al., 2000; Poldrack et al., 1999; Wise et al., 1999]. In the present study, we used functional mag-

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netic resonance imaging (fMRI) to assess the relationship between frontal and temporal activation during the generation of the same word at different rates, to minimize phonological and semantic processing. We studied covert as opposed to overt articulation, as this eliminated the possibility that any changes in temporal activation with increasing verbal output were simply a function of increased auditory input, rather than cortico-cortical modulation. We were also interested in establishing whether fronto-temporal modulation occurred during the generation of inner speech, as the interaction between areas that generate and monitor inner speech is putatively defective in patients with auditory hallucinations [Frith et al., 1995; McGuire et al., 1996]. Covert articulation during other paradigms has been associated with activation in the left inferior frontal gyrus and the superior temporal gyrus [McGuire et al., 1996; Paulesu et al., 1993; Shergill et al., 2001], but the relationship between the responses in these areas has not examined. Both increasing the complexity of covert inner speech [Shergill et al., 2001] and the frequency of overt articulation [Wise et al., 1999] have been demonstrated to increase lateral temporal activation. Thus, we predicted that: 1) increasing the rate of covert articulation would be associated with greater activation in both the left inferior frontal and the left superior temporal gyrus; and 2) there would be a positive correlation between the magnitude of activation in these regions.

MATERIALS AND METHODS

Subjects

Eight male volunteers, right-handed according to Annett's [1970] scale, aged 23–37 years (mean age = 29, SD = 5) participated in the study. They did not suffer from medical or psychiatric disorders and were not receiving medication, and had no family history of psychiatric disorder. Their mean IQ estimated with the National Adult Reading Test [Nelson, 1991] was 115 (range = 106–117, SD = 5). Before inclusion, potential subjects were assessed on their ability to overtly repeat a word at the three rates (once every 1,2, or 4 sec) to be used during scanning. They proceeded to scanning when they consistently achieved a 1:2:4 ratio in the number of repetitions, at the respective rates, over a minute. Subjects provided written informed consent, and the local hospital ethical committee approved the study.

Tasks performed during fMRI

Fast vs. slow covert articulation (categorical comparison)

Subjects covertly generated the word "rest" repeatedly at two self-paced rates (once every 1 or 4 sec = 60 or 15 words/min), without speaking. Their accuracy was checked by asking them to tap their finger at the two different rates both before and immediately after scanning. During scanning, the two conditions alternated in an ABAB design, with each condition lasting 30 sec and 5 cycles of each condition in one 300-sec run. The order of conditions was counterbalanced across subjects. The desired rate during each condition was indicated by a number visible throughout in the centre of a computer screen ("1" for one word every second and "4" for one word every 4 sec).

Fast/intermediate/slow covert articulation (parametric task)

Subjects covertly generated the word "rest" repeatedly at three rates (once every 1, 2, or 4 sec = 60, 30 and 15 words/min) without articulating the word. Their accuracy was checked before and after the task, as described above. Each condition lasted 30 sec, with a minimum of 3 cycles of each condition during one 300-sec run; the desired rate was indicated by a number on a computer screen ("1," "2," or "4") as above. The order of conditions was pseudo randomized. All subjects achieved a consistent timing ratio (on finger tapping) of 1:2:4 between the fast, intermediate and slow rate, immediately before and after scanning.

Image acquisition

Gradient-echo echoplanar MR images were acquired using a 1.5 T GE Signa System (General Electric, Milwaukee, WI) fitted with Advanced NMR hardware and software (ANMR, Woburn, MA) at the Maudsley Hospital, London. A quadrature birdcage head coil was used for RF transmission and reception. In each of 14 non-contiguous planes parallel to the inter-commissural (AC-PC) plane, 100 T2*-weighted MR images depicting BOLD contrast (11) were acquired with TE = 40 msec, TR= 3,000 msec, in-plane resolution = 3.1 mm, slice thickness = 7 mm, slice skip = 0.7 mm; 100 images were collected in each 5-min run. Head movement was limited by foam padding within the head coil and a restraining band across the forehead. At the same session, a 43 slice, high-resolution inversion recovery echoplanar image of the whole

brain was acquired in the AC-PC plane with TE = 73 msec, TI = 180 msec, TR = 16,000 msec, in-plane resolution = 1.5 mm, slice thickness = 3 mm.

Image analysis

Image analysis was performed on a SPARC Ultra 10 workstation (Sun Microsystems, Palo Alto, CA) using MATLAB (version 5.3, The Mathworks Inc., Natick, MA) and SPM99 software (Statistical Parametric Mapping, The Wellcome Department of Cognitive Neurology, London; http://www.fil.ion.ucl.ac.uk/spm). All data sets were automatically realigned to the first image to correct for head movement, normalized using sinc interpolation and transformed into Talairach space using sinc interpolation. The transformed data set for each subject was smoothed with a Gaussian filter (Full width half maximum = 8 mm) to compensate for normal variation in anatomy across subjects. The time series were high pass (126 sec) filtered to remove low frequency artifacts.

Statistical analysis was performed for each subject, and the stereotaxically normalized fMRI time series data from all the subjects pooled for random effects group analysis. Analysis of the two condition task (15 vs. 60 words/min) used a categorical design (using a box-car function with hemodynamic response function to create the general linear model) comparing activation evident during fast greater than slow rate of generation, and vice versa. Analysis of the three-condition task (15, 30 and 60 words/min) used a parametric design to identify areas where activation was linearly correlated (positively and negatively) with the rate of covert articulation. Subsequently we also performed a post-hoc analysis of the parametric design using a second order polynomial term (incorporating linear and squared components). Cluster level statistics corrected for multiple comparisons were thresholded at $P < 0.05$.

Correlational analysis of time series data

To clarify the polarity of any fronto-temporal modulation (i.e., to determine whether it was positive or negative), we examined the BOLD response over time at the focus of maximal activation in six regions during the categorical task; three regions showing activation during each of the faster and slower rates were selected. These comprised the areas where we predicted modulation (the left inferior frontal and left superior temporal cortex), plus the four other most prominently activated regions. The fMRI time series, adjusted for motion correction and linear trends via a high pass filter, at the voxel showing peak response within each region was extracted for all subjects. The time series data were placed in an interregional correlation matrix to examine the functional connectivity in more detail.

RESULTS

Behavioural data

All subjects were able to perform the task within the scanning environment and showed a consistent 1:2:4 timing ratio for the 3 conditions, both pre and post scanning. As a result, data from all subjects were included in the analysis. At one per 1 sec the mean number of taps was 64 (SD 6); at one per 2 sec the mean was 31 (SD 3); and at once every 4 sec the mean was 16 (SD 2).

Categorical comparison

Relative to covert generation at 15 words/min, covert generation at 60 words/min was associated with activation in foci in the dorsolateral and the orbital portions of the left inferior frontal gyrus, and in the anterior part of the left superior temporal gyrus. There was also a large area of activation centered on the right precentral gyrus, which included foci in the postcentral and superior temporal gyri, and further activation in the frontal pole (Fig. 1, Table I). The slower rate of generation was associated with activation in the supplementary motor area (SMA), the left precentral gyrus and the right inferior parietal lobule (Table I).

Parametric analysis

The parametric analysis (increased activation with increased rate) revealed that as the rate of generation increased, there was activation in the left inferior frontal gyrus, the left hippocampus and precuneus, and in the right precentral gyrus, and the posterior part of the right superior temporal gyrus (Table II). Conversely, there was relatively decreased activation in the left precentral and occipital gyri, the right inferior frontal and superior temporal gyri, and the right inferior parietal lobule and precuneus (Table II).

Correlational analysis of time series data

The time series at the extracted voxel consisted of 800 time points across the eight subjects, and two-tailed tests were reported. There was a significant positive correlation between the BOLD response in the
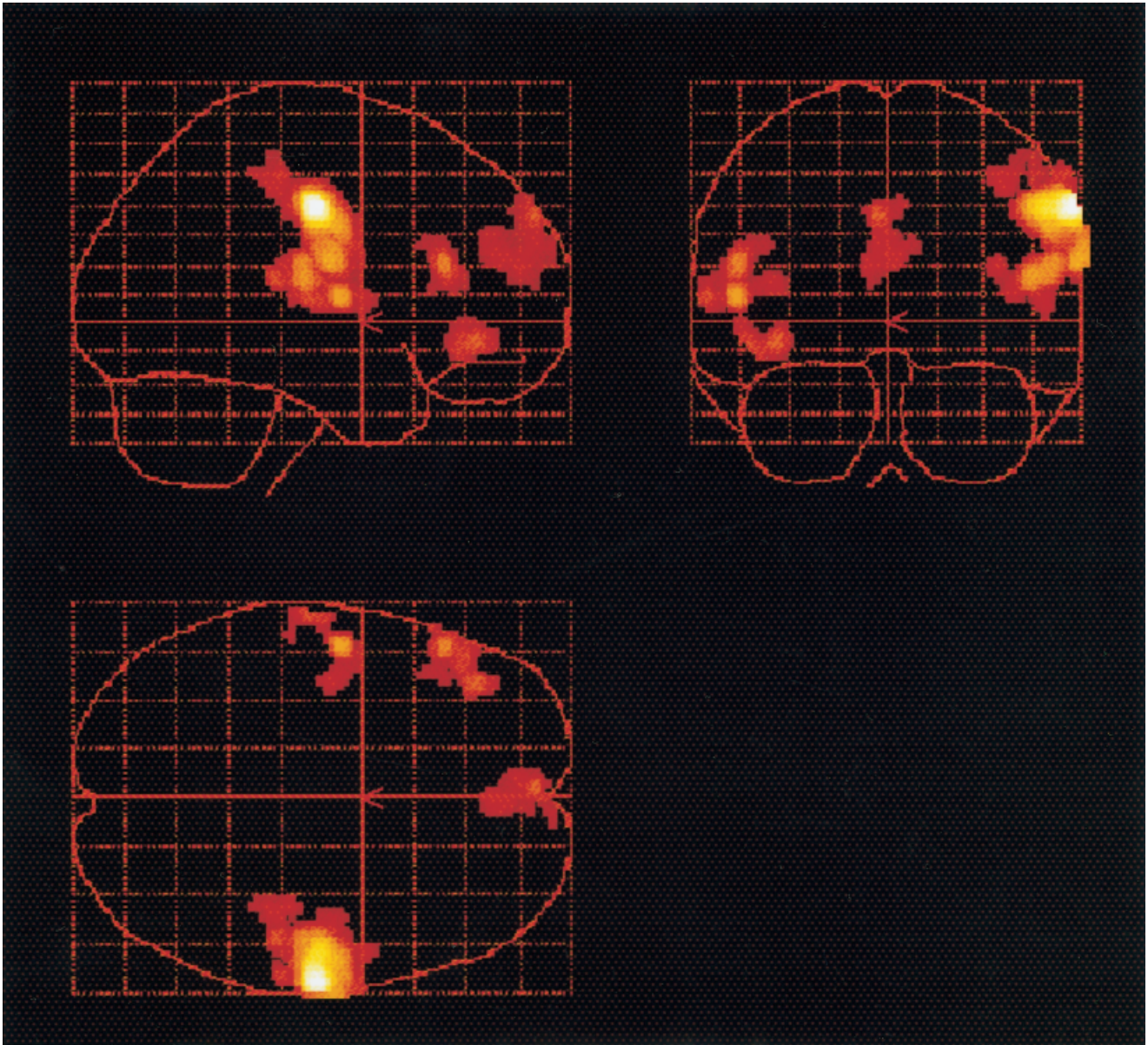
Figure 1.

Regions associated with faster rate of generation of inner speech (60 vs. 15 words/min). Areas shown in red/gold depict clusters significantly activated during the faster rate of covert articulation relative to slower rate. Group activation maps from all eight subjects are displayed on a glass brain, and correspond to Ta-lairach space and are described in Table I. Axial slices are displayed parallel to the anterior commissure-posterior commissure plane, with the right side of the figure representing the right side of the subject's brain.

foci in the left inferior frontal and the left superior temporal gyri (Table III, Fig. 2). The results show significant values of the Pearson coefficient, although the results were still significant when the Kendall tau or Spearman coefficient were computed. There were also negative correlations between the left inferior frontal signal and the responses in the left precentral and the right inferior parietal foci (Table III). The

BOLD responses in the SMA, the left precentral gyrus and the right inferior parietal lobule were significantly inter-correlated (Table III).

DISCUSSION

In this study we examined the neural correlates of covertly articulating the same word at different rates,

TABLE I. Regions demonstrating significant activation during faster and slower rates (categorical analysis)

REGION	X	Y	Z	Cluster size (Number of voxels)	Z score	P (cluster)
Greater activation at FASTER rate						
Left inferior frontal gyrus						
(BA 45/46)	−52	30	20	154	4.9	0.008
(BA 47)	−38	40	−8	134	4.5	0.015
Left superior temporal gyrus (BA42)	−52	−8	8	239	5.4	0.001
Right precentral gyrus (BA 6/4)	64	−16	40	[	8.0	]
Right postcentral gyrus (BA 1,2,3)	66	−12	22	[1549	5.5	0.0001]
Right superior temporal gyrus (BA42)	50	−20	16	[	5.3	]
Frontal pole	−2	60	36	367	4.6	0.0001
Greater activation at SLOWER rate						
Right inferior parietal lobule (BA 40)	54	−48	40	541	6.0	0.0001
Supplementary motor area	4	6	58	143	4.7	0.01
Left precentral gyrus (BA 4)	−38	−8	30	124	4.4	0.02

to investigate the relationship between activity in frontal and temporal cortex. Although the key difference between our conditions was the rate of covert articulation, there may also have been differences in the demands on attention and concentration. Our subjects reported being able to perform all conditions within the scanning environment, without using any explicit timing strategies (excluding subvocal counting or using their respiration rate as a cue), but indicated that they found covert articulation at 60 words/min to be less demanding than at slower rates, presumably because the timing of the generation (that was self-paced) at 30 and 15 words/min was more difficult. Ideally, functional imaging studies of cognitive tasks should involve the measurement of behavioral performance "on-line," to assess how well subjects are performing during image acquisition. Covert

speech, however, cannot easily be measured without introducing additional and potentially undesirable cognitive demands. We sought to minimize the influence of variation in performance by training subjects on the tasks before scanning, obtaining ratings of their performance immediately after each task, and excluding those who reported or demonstrated marked difficulties with task execution. Moreover, there was left inferior frontal cortical activation in association with faster rate of generation of inner speech consistent with that seen in previous studies of inner speech [Paus et al., 1996; Shergill et al., 2001]; this pattern of activation offers some support that the subjects were actually carrying out the tasks during the scanning.

There was no null baseline condition included in the design, because we were primarily interested in the cortical regions showing activation in line with

TABLE II. Regions demonstrating increasing activation with increasing rate (parametric analysis) of generation

Region	X	Y	Z	Cluster size (Number of voxels)	Z score	P (cluster)
Greater activation with FASTER rate						
Left inferior frontal gyrus (BA 45/46)	−54	32	22	145	5.4	0.01
Right precentral gyrus (BA 6/4)	58	−4	42	280	5.5	0.0001
Right superior temporal gyrus (BA22)	66	−50	12	604	5.3	0.0001
Left hippocampus	−28	−16	−8	183	5.1	0.003
Left precuneus (BA 7)	−26	−82	42	114	4.7	0.03
Greater activation with SLOWER rate						
Right inferior parietal lobule (BA 40)	58	−42	50	158	5.2	0.007
Left precentral gyrus (BA 4)	−40	−10	50	123	6.2	0.02
Right inferior frontal gyrus (BA 47)	50	28	−4	173	5.1	0.004
Right superior temporal gyrus (BA22)	58	−24	0	117	4.8	0.03
Right precuneus (BA 7)	16	−82	48	327	5.3	0.0001
Left middle occipital gyrus (BA 18)	−28	−74	12	136	4.7	0.01

TABLE III. Correlation matrix of time series from selected foci[†]

	SMA	R Precen	R IPL	L STG	L Precen	LIF
SMA						
R Precen	NS					
R IPL	0.20**	NS				
L STG	NS	NS	NS			
L Precen	0.12*	NS	0.14*	NS		
LIF	NS	NS	−0.08	0.11*	−0.07	

LIF, left inferior frontal gyrus (Talairach x,y,z = −52, 30, 20); L Precen, left precentral gyrus (−38, −8, 30); L STG, left superior temporal gyrus (−52, −8, 8); R IPL, right inferior parietal lobule (54, −48, 40); R Precen, right precentral gyrus (64, −16, 40); SMA, supplementary motor area (4, 6, 58).
NS, not significant $P > 0.05$; *$P < 0.005$; **$P < 0.0001$.

changes in the rate of inner speech production. The inclusion of a null baseline would have permitted a better examination of the parametric experiment as there would have then been three different rates to assess; however, in the absence of such, only two rates could be compared because one rate had to act as a baseline, reducing the explanatory power of the parametric design and perhaps contributing to the discrepancy between the results of the two different analyses. It may also have assisted in clarifying increases and decreases of activation during the individual tasks.

As expected, there was activation of the left inferior frontal gyrus as the rate of covert articulation increased, and this was evident with both the categorical and parametric comparisons. The predicted activation of the left superior temporal gyrus was seen with the categorical, but not the parametric comparison, whereas both comparisons indicated that faster generation was also associated with activation of the right superior temporal gyrus. Our data are thus consistent with an association between activity in the left inferior frontal gyrus and the temporal cortex bilaterally; although the associations did not all show a linear relationship. Moreover, because our paradigm involved the covert generation of a single word, it is unlikely that the changes in temporal activation reflected increased semantic or phonological processing, or were secondary to changes in auditory input. Although fMRI is not an appropriate technique to allow the detailed examination of timing differences sufficient to confirm a modulatory effect of frontal on temporal cortices, the electrophysiological literature in primates [Müller-Preuss and Ploog, 1981] and man [Creutzfeldt et al., 1989; Numminen and Curio, 1999] would support this interpretation of these results. These studies demonstrated differences in brain activation patterns between identical externally generated and self-generated actions in the auditory modality; auditory cortices were activated in response to vowel changes in heard speech but not when the same vowel changes are *self-uttered* suggesting that motor-to-sensory priming of the auditory cortex dampens the response to self-produced "expected" sounds and occurs at a millisecond time scale.

The absence of activation in the left superior temporal gyrus with the parametric analysis may reflect an incorrect assumption that the relationship between the rate of covert articulation and temporal activation would be linear. Even when hearing words presented at different rates, the response in the left posterior temporal cortex differs from that in bilateral and more anterior temporal regions [Price et al., 1992]. Indeed a post hoc parametric analysis of our data using a combination of a linear and second order polynomial expansion, as opposed to the linear, model demonstrated additional activity within the left middle temporal cortex and hippocampus.

Our subjects reported that they found self-paced generation at 15 and 30 words/min comparably difficult, but more demanding than at 60 words/min. This is in accordance with established models of timing assessment, which propose that temporal units of less than (or around) a 1 sec are perceived as a unit, as distinct from time intervals greater than ~3 sec, which have to be actively estimated [Posner and Petersen, 1990]. Both the categorical and parametric analyses revealed an unpredicted activation of the right superior temporal gyrus and the right precentral gyrus at faster rates of generation. The right temporal cortex demonstrates a linear response to increasing rates of overt articulation [Wise et al., 1999] and is also deactivated (relative to repetition) during overt verbal fluency [Spence et al., 2000]. In the absence of substantial direct connections between the left prefrontal and right temporal cortex [McGuire et al., 1991; Pandya and Yeterian 1985], its activation may be more closely allied to the activation in the right precentral gyrus. The right precentral region we identified is close to an area (52, −6, 41), activated by whispering at a faster rate [Paus et al., 1996], and during covert singing [Reicker et al., 2000]. This activation could be due to subvocalization, although subjects were instructed not to articulate the word, and the method of assessing changes in frequency (tapping rather than vocalizing) was selected to reduce any tendency to articulate the word; alternatively the explanation could be that increased task demands led to the recruitment of contralateral homologous regions, as evident in a recent fMRI study of mental rotation [Carpenter et al., 1999].
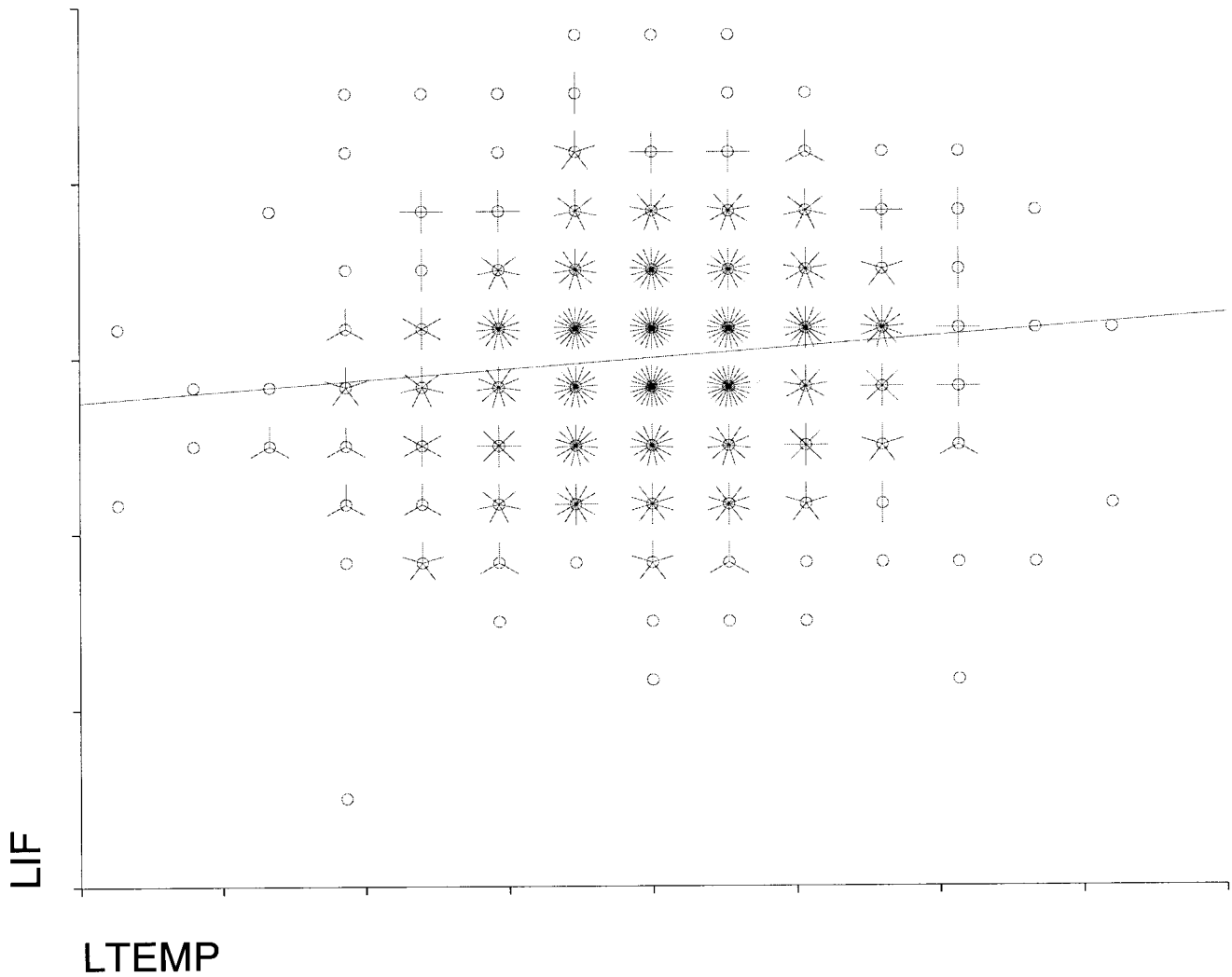
Figure 2.
A graph of the regression between inferior frontal and temporal BOLD signal. Each petal represents a single time point; where the two time series are very close together a line has been fitted through the data.

Another interpretation of these results is that the observations are secondary to making a judgment of timing interval, and less responsive to inner speech generation. A similar experiment that required subjects to tap their right finger in response to a visual cue [Rubia et al., 1998] found activation of the left pre- and post-central gyrus and medial parietal cortex during the faster rate (1.7 Hz); the slower rate (0.2 Hz) was associated with activation of the SMA, left supramarginal gyrus and the medial frontal cortex. This suggests that activation within the left inferior frontal and superior temporal cortices, in our study is not a function of timing related judgments per se. Other studies, however, have found activation of the prefrontal and

inferior parietal lobules in both prospective time judgment [Maquet et al., 1996] and although directing attention to the time interval [Coull and Nobre, 1998]; the right inferior parietal lobule shows activation during the slower rate in our study. Verbal working memory is another potential confounder relevant to time estimation, but one would anticipate that this would be more relevant when there is a longer duration between stimuli, i.e., during the slower rate (where the rate is slower than once every 3 sec) rather than the faster rate (1 Hz); in this study there is activation within the right inferior parietal lobule and left precentral gyrus. The bilateral inferior parietal cortex has been implicated in verbal short term memory [Paulesu

et al., 1993], whereas a recent study of verbal working memory has demonstrated that the left premotor area was associated with the rehearsal of temporal ordering of stimuli [Henson et al., 2000].

The time series data from selected foci indicated that activity in the left inferior frontal and left superior temporal gyri activation were positively correlated. This suggests that the left temporal cortex was activated during the fast rate of verbal generation, rather than being de-activated during the slower rate, as its response was not correlated with that in the other regions, which were more activated at the slower rate. We cannot, however, exclude the possibility of a third region mediating activity in both these regions. A positive modulation of left temporal activity during verbal generation accords with data from a PET study of whispering [Paus et al., 1996] and reading [Price et al., 1996] at different rates, and electrophysiological studies [Alexander et al., 1976; Creutzfeldt et al., 1989; Müller-Preuss and Ploog, 1981], but is at odds with data from some PET studies of overt verbal fluency [Friston et al., 1991; Frith et al., 1995]. The latter involved the comparison of verbal generation with verbal repetition, however, and more recent evidence suggests that the 'deactivation' of temporal cortex during verbal fluency may be a function of changes in the repetition condition per se [Spence et al., 2000; Warburton et al., 1996].

Considering the results from the categorical and the parametric analyses together, the slower rate was particularly associated with activation in the SMA and the right inferior frontal, superior temporal and inferior parietal cortex, and the left precentral gyrus. Many of these areas are activated during relatively demanding tasks that entail covert articulation e.g., imagining a sentence being spoken in someone else's voice [Shergill et al., 2000a]. The engagement of these regions during slower rates of verbal generation may thus have reflected greater task demands. The time series correlation matrix confirms the strong association between the SMA, frontal and parietal areas that have been demonstrated to be activated during the planning, preparation and initiation of voluntary movement [Seitz et al., 2000], and are anatomically interconnected [McGuire et al., 1991]; the temporo-parietal junction has often been demonstrated to be associated with increased attentional demands [Johannsen et al., 1997; Kawashima et al., 1999; Pardo et al., 1991].

CONCLUSION

Although the temporal resolution of fMRI makes it difficult to assess whether temporal cortical activation is secondary to frontal modulation, electrophysiological data in non-human primates and in man suggests that the frontal activity precedes the temporal [Alexander et al., 1976; Creutzfeldt et al., 1989; Müller-Preuss and Ploog, 1981; Numminen and Curio, 1999]; there are also dense connections between these regions that could mediate a direct interaction [Pandya and Yeterian, 1985; Romanski et al., 1999]. Our findings would support a frontal modulation of temporal cortical regions during verbal generation, and indicate that this is not simply secondary to increased phonological or semantic processing. A similar process is evident in other modalities, within the visual system visual cortical activity is modulated by areas involved in the generation of eye movements [Bahcall and Kowler, 1999; Sperry, 1950], there is an inverse correlation between the frequency of saccade generation and the magnitude of the visual cortical activation, in the absence of changes in visual input [Paus et al., 1995]. This may serve to control for the effects of retinal stimulation during eye movements on visual cortical activity. In the somatosensory system, there is greater activation of somatosensory cortex in response to an external stimulus, compared to an identical stimulus that is self-generated [Blakemore et al., 1998]. Thus, communication between frontal and temporal areas during the generation of inner speech may inform areas involved in language perception that verbal output is self-generated [Frith et al., 1995]; as it is evident during the generation of covert speech, it may occur in association with thoughts as well as actions. Defective communication between these areas could lead to the mis-identification of internally generated verbal material as 'alien' speech, and may be a critical factor underlying auditory hallucinations in schizophrenia [Shergill et al., 2000a,b].

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