

Pitch processing in auditory cortex: using the temporal information of MEG to augment the spatial information of fMRI

Roy D. Patterson, CNBH, PDN, Cambridge University, email rdp1@cam.ac.uk; Alexander Gutschalk, Dept of Neurology, Heidelberg; Annemarie Seither-Preisler, Exp. Audiology, Muenster; Katrin Krumbholz, MRC IHR, Nottingham

Research supported by the UK Medical Research Council (G9900362, G0500221), the Deutsche Forschungsgemeinschaft (Ru 652/1-3) and the Alexander von Humboldt Foundation

Physiological studies of temporal pitch processing suggest that the processing of temporal regularity begins in the brainstem (e.g., Palmer and Winter, 1992), which suggests that there is a hierarchy of temporal pitch processing in the auditory pathway as would be expected from computational models of auditory perception (e.g., Patterson et al., 1995; Pressnitzer et al., 2001).

These models specify a sequence of processing stages, and they can be used to generate hypotheses about where to look for the stages of pitch processing in the brain. If the signature of one of the processes can be identified at a specific site in the auditory pathway, it places strong constraints on where the remaining processes are instantiated.

Functional magnetic resonance imaging (fMRI) has good spatial resolution, but relatively poor temporal resolution. Magneto-encephalography (MEG) has superb temporal resolution, but relatively poor spatial resolution. Recently, a loose consortium of auditory scientists has combined these techniques to search for pitch and melody processing centres and to measure the dynamics of the processing.

II. Imaging pitch processing with MEG

Magnetoencephalography (MEG) measures the strength and direction of post-synaptic activity in pyramidal cells of cortex. It has millisecond temporal resolution, so it can follow the temporal dynamics of auditory processing.

The most prominent MEG response is a large negative deflection which appears in the interval between 80 and 150 ms post stimulus onset (Fig. 3a, 3c); it is referred to as the N1m. It is the aggregate activity of multiple sources in auditory cortex. To isolate the pitch component of the N1m, Krumbholz et al. (2003) and Rupp et al. (2005) developed continuous stimulation techniques where the sound begins with a noise and then, after the N1m has passed, the noise changes to a RIS with the same energy and similar long-term spectrum. At the transition (Fig. 3b), there is a marked perceptual change from hiss to tone, which is accompanied by a prominent negative deflection referred to as the pitch onset response (POR).

The inverse transition, from RIS to noise produces a marked perceptual change from tone to hiss percept, but there is no corresponding deflection (Fig. 3d, ?).

I. Imaging pitch processing with fMRI

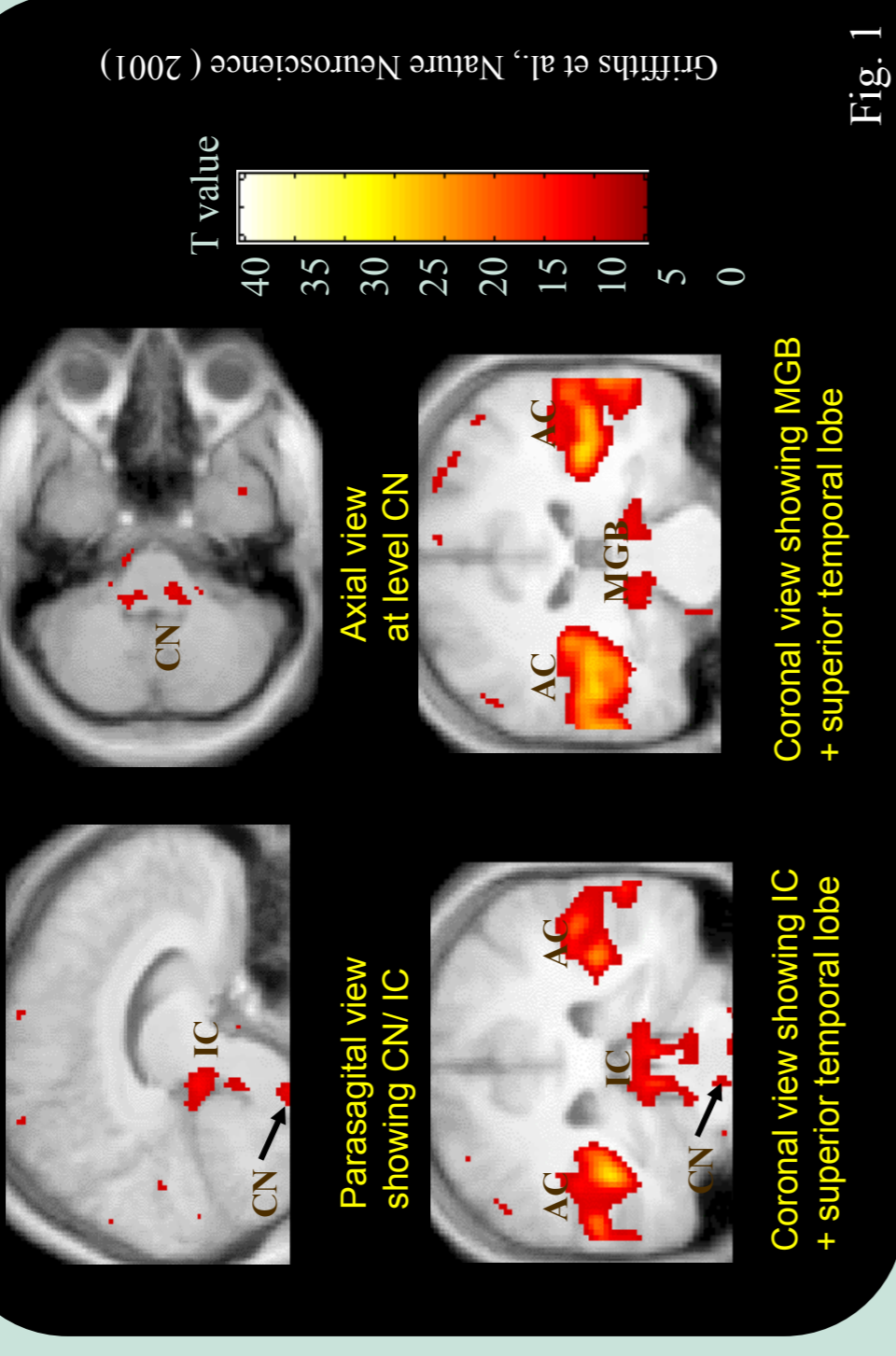
Neural tissue draws oxygen from the blood when it is active, and functional Magnetic Resonance Imaging (fMRI) can be used to measure neural activation through the blood-oxygen-level depletion (BOLD) response.

Griffiths et al. (2001) used Regular Interval Sounds (RIS), which produce a strong pitch, to show that fMRI was sufficiently sensitive to image all of the monaural, subcortical nuclei of the auditory pathway simultaneously. (Fig. 1)

A contrast between the response to RIS and spectrally matched noise showed that pitch processing begins in subcortical structures (CN and IC).

At the same time, a contrast between RIS with varying pitch and fixed pitch revealed that changing pitch does not produce more activation than fixed pitch in these regions.

The results were interpreted to mean that pitch processing begins in the brainstem but is not completed there.



Griffiths et al., Nature Neuroscience (2001)

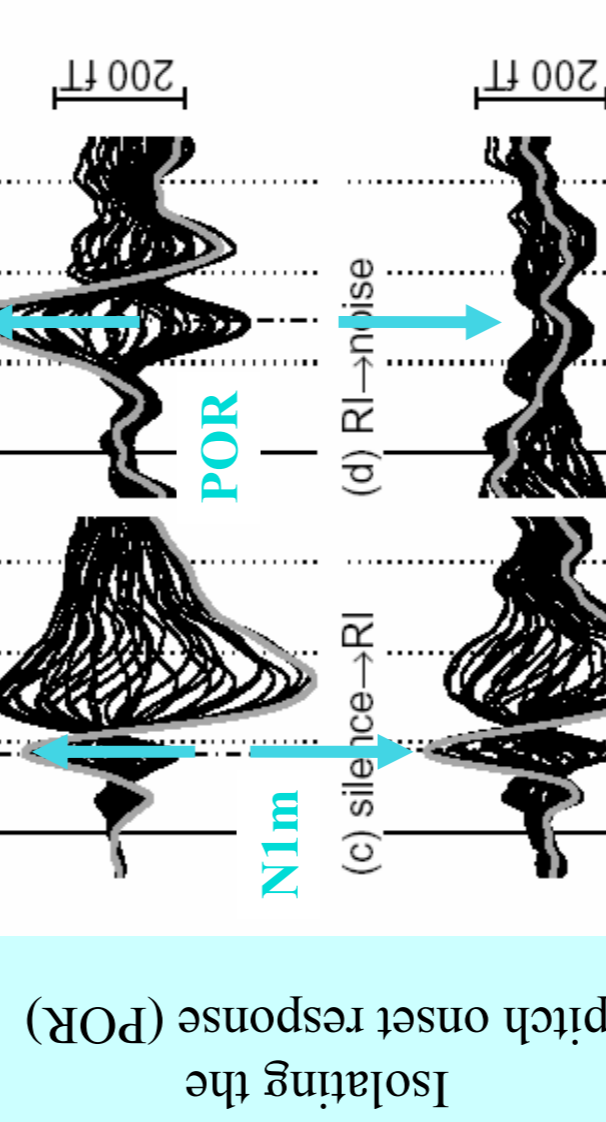


Fig. 3

Krumbholz, Patterson, Seither-Preisler, Lammertmann and Lutkenhoner, Cerebral Cortex (2003)

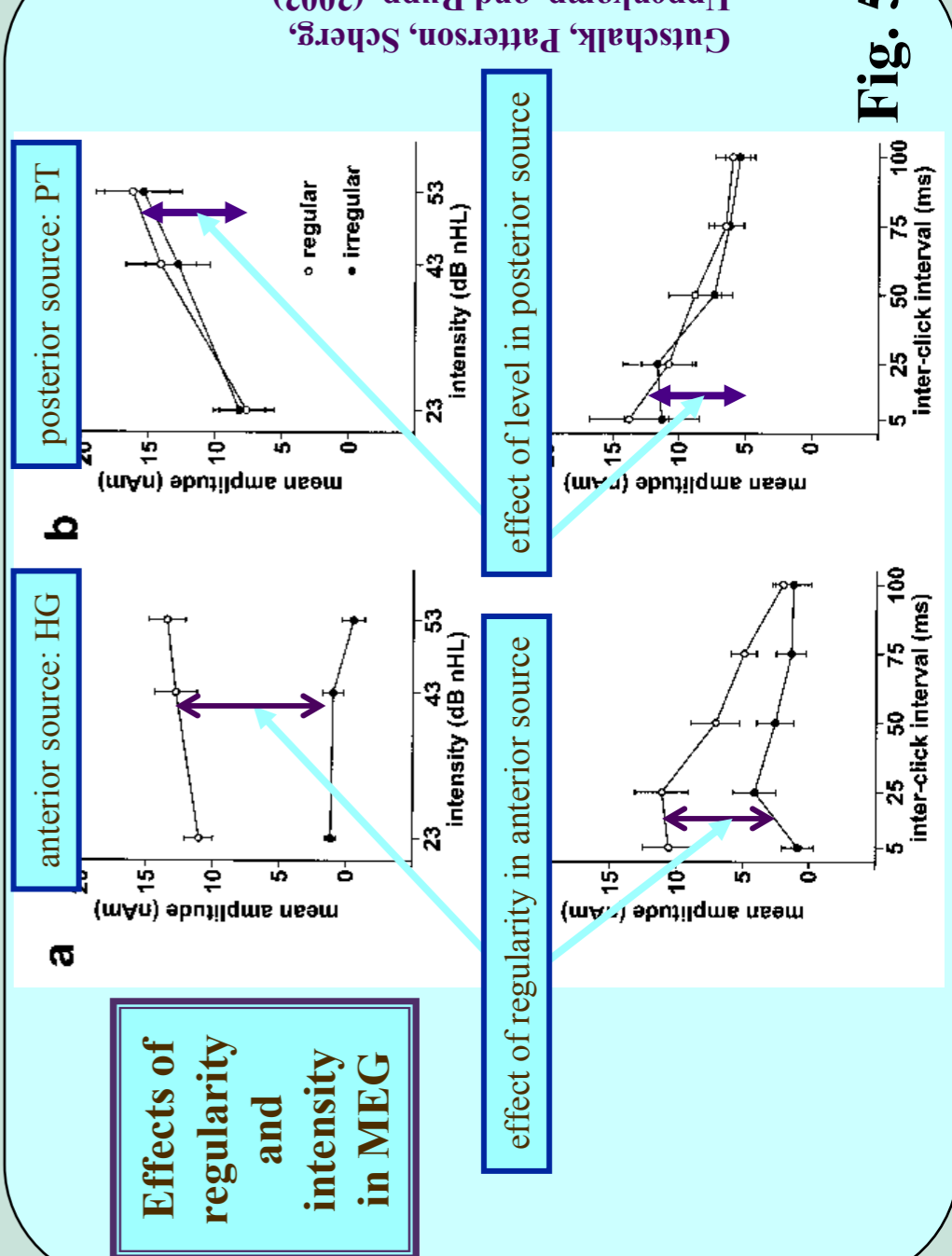


Fig. 5

Gutschalk, Patterson, Seiger, Uppenkamp, and Rupp, (2002)

Both the RIS and noise produced more activation than silence, bilaterally in auditory cortex, along Heschl's gyrus (HG) and behind it in Planum Temporale (PT) (Patterson et al., 2002) (Fig. 2, blue).

- When the fixed-pitch condition was contrasted with noise, there was differential activation in antero-lateral HG bilaterally, just outside PAC (Fig. 2, red), which suggests that al-HG is involved in pitch processing.
- When the melody conditions were contrasted with the fixed-pitch conditions, there was differential activity in the superior temporal gyrus (STG) below HG, and in planum poliare (PP) anterior to HG, with more activation in the right hemisphere (Fig. 2, green, cyan).
- The results suggest that the al-HG region is involved in determining pitch value and pitch strength, rather than the contour of pitch change that defines melody or prosody.

Penagos et al. (2004) found similar activation with harmonic complex tones. Warren et al. (2003) found that pitch chroma changes produce activation in al-HG. Bender and Wang (2005) demonstrated sensitivity to the low pitch of complex tones in the homologous region of marmoset cortex.

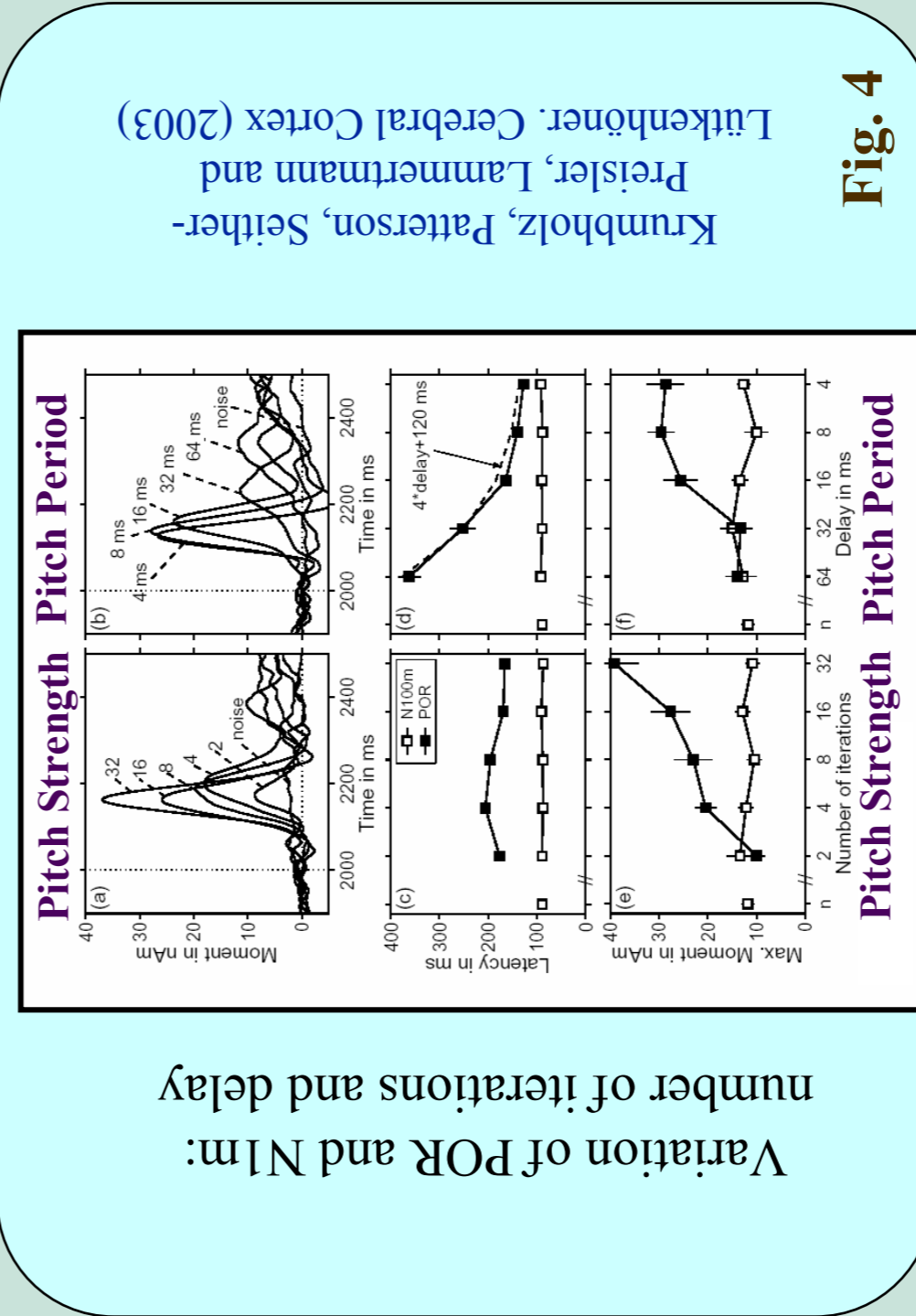


Fig. 4

Krumbholz, Patterson, Seither-Preisler, Lammertmann and Lutkenhoner, Cerebral Cortex (2003)

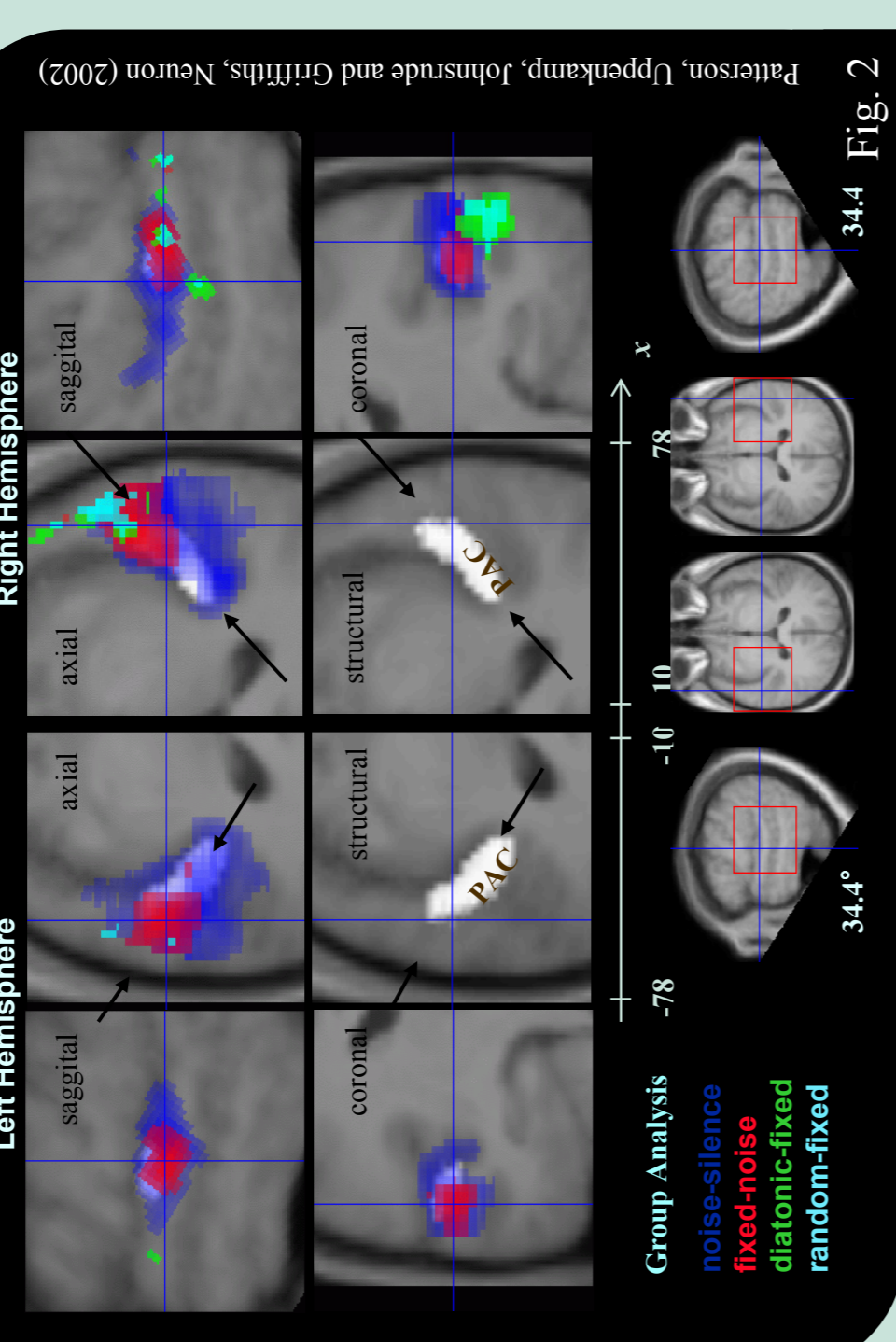


Fig. 2

Patterson, Uppenkamp, Johnsrude and Griffiths, Neuron (2002)

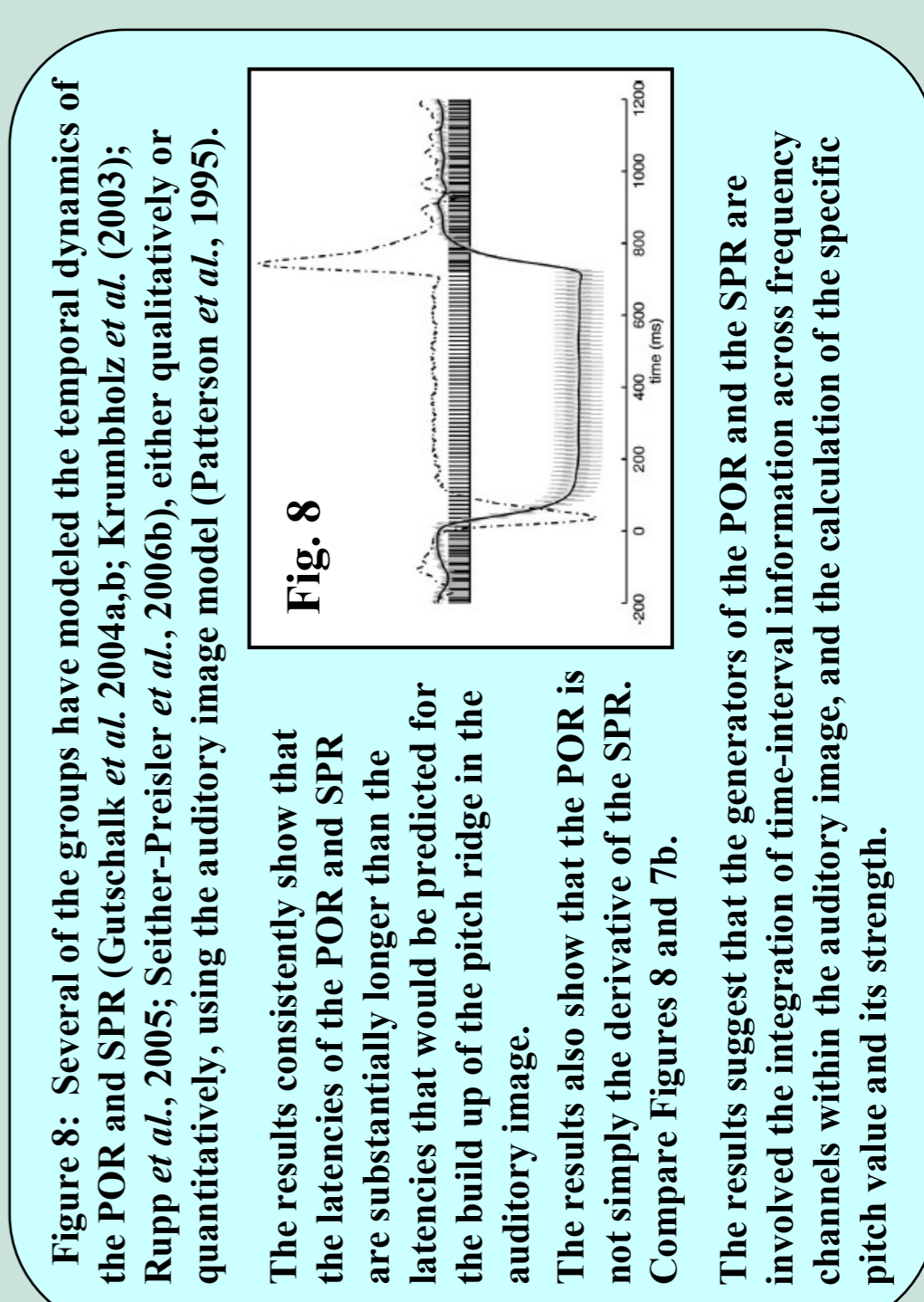


Fig. 8

The latencies of the POR and the SPR are both surprisingly long: The peak latency of the POR is about 120 ms plus four times the 'period' of Fig. 7b (shown as above) (Krumbholz et al., 2003) and the SPR appears in the source wave between 200 and 300 ms post regularity onset (Fig. 7b), and rises to its sustained level over 100-200 ms.