

Short communication

Short-term functional plasticity in the human auditory cortex: an fMRI study

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Abstract

Applying functional magnetic resonance imaging (fMRI) techniques, hemodynamic responses elicited by sequences of pure tones of 950 Hz (standard) and deviant tones of 952, 954, and 958 Hz were measured before and 1 week after subjects had been trained at frequency discrimination for five sessions (over 1 week) using an oddball procedure. The task of the subject was to detect deviants differing from the standard stimulus. Frequency discrimination improved during the training session for three subjects (performance gain: T+) but not for three other subjects (no performance gain: T–). Hemodynamic responses in the auditory cortex comprising the planum temporale, planum polare and sulcus temporalis superior significantly decreased during training only for the T+ group. These activation changes were strongest for those stimuli accompanied by the strongest performance gain (958 and 954 Hz). There was no difference with respect to the hemodynamic responses in the auditory cortex for the T– group and the control group (CO) who did not received any pitch discrimination training. The results suggest a plastic reorganization of the cortical representation for the trained frequencies which can be best explained on the basis of ‘fast learning’ theories. © 2001 Elsevier Science B.V. All rights reserved.

Theme: Sensory systems

Topic: Auditory systems: central anatomy

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Cortical representational plasticity has been well documented after peripheral and central injuries or improvements in perceptual and motor abilities. This has led to inferences that the changes in cortical representations parallel and account for the improvement in performance during the period of skill acquisition. A classical study within the auditory domain was published by Recanzone et al. [28]. They trained owl monkeys for 60–90 daily sessions of 400–750 trials to make fine pitch discriminations in selected regions of the auditory frequency spectrum. Tonotopic mapping carried out invasively afterwards showed that the cortical area tuned to the trained frequencies was enlarged by a factor of 2–3 compared with untrained monkeys. These results and other evidence for

use-dependent plasticity in animals led us to investigate whether training to discriminate small differences in spectral pitch alters neuronal representations for the trained frequencies in the human auditory cortex. However, studies of functional plasticity of the human auditory cortex have rarely been performed and comprise studies on cochlear implant (CI) users applying positron emission tomography (PET) methods and studies in healthy humans applying electroencephalographic (EEG) and magnetoencephalographic (MEG) methods. Studies with CI users have shown that the auditory cortex of these patients rapidly develops the potential for being activated by auditory stimuli [23]. Human MEG studies have revealed that the cortical representation of tones may change within hours after a reversible ‘functional deafferentation’ (short-term plasticity) and that early musical training leads to an expansion in the cortical representation of complex harmonic sounds (long-term plasticity) [8,19,24,25]. Finally, human EEG studies have shown altered neurophysiological

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responses as indexed by evoked potentials (EVP) for subjects with excessive auditory training including professional musicians [18,21,31–33], for subjects with illness-induced hearing loss [22], for near-sighted subjects [9], and also for blind subjects [29,30].

Although considerable progress has been made in elucidating the functional plasticity of the auditory cortex, the exact neurophysiological mechanisms and neuro-anatomical constraints are unknown at present. This study therefore was designed in order to delineate the activation pattern of the different brain areas of the auditory cortex during the course of a pitch discrimination learning task. For this, we utilized functional magnetic resonance imaging (fMRI) allowing us to identify hemodynamic responses within the auditory cortex. Specifically, we addressed the following questions. First, which parts of the auditory cortex are most susceptible to use-dependent learning. Second, in contrast to recent studies in this field we attempted to relate the neurophysiological changes within the auditory cortices directly to the performance in learning the pitch discrimination task. We anticipated differences in the pattern of hemodynamic responses in the auditory cortices between subjects improving their pitch discrimination compared to those subjects not improving their pitch discrimination.

Ten paid female volunteers with no history of neurological disorders were studied. All subjects were strongly right-handed according to standard handedness questionnaires [26]. Six subjects were randomly assigned to the experimental group while the remaining subjects were assigned to the control group. Subjects of the experimental group received auditory training, while those of the control group did not receive any training. All procedures were approved by the local review board of Otto-von-Guericke University, Magdeburg, and written informed consent was obtained from all subjects.

The experiment comprised two experimental sessions during which typical auditory oddball tasks in the context of fMRI scanning were conducted. These two fMRI sessions were separated by an interval of 1 week, during which the experimental group received intensive auditory training (9 h, 5 days) (Fig. 1). During these training sessions they conducted the same auditory oddball tasks as during the fMRI scanning. During each training session and during the fMRI sessions, performance data were recorded for later analysis. Scanner noise was recorded and presented together with the auditory stimuli in order to match the sensory condition. The control group, on the other hand, received no training. The fMRI oddball tasks are similar to those of previously published studies [36]. Specifically, these tasks comprise a more frequent standard tone (950 Hz, sine wave, 200 ms duration, 10 ms fade-in and fade-out time) and three rarely presented target stimuli (952, 954, and 958 Hz; all other characteristics were identical to those for the standard tone) (Fig. 2). Auditory stimuli were presented using a digital playback system and

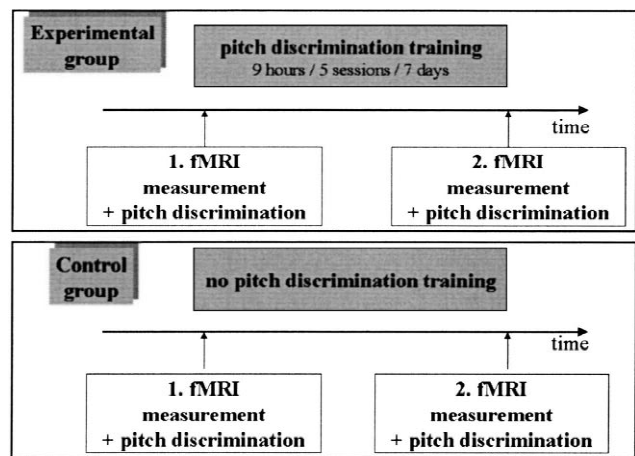


Fig. 1. Schematic description of the experimental setup.

a magnetically shielded transducer system. The acoustic stimulation system terminated in tightly occlusive headphones, allowing unimpeded conduction of the stimulus with good suppression of ambient scanner noise by about 20 dB. Two hundred and ten stimuli were delivered at 2-s intervals in each scanning session. In the stimulus presentation computer program, 30 target stimuli (10 for each frequency) were arranged among non-target stimuli in a pseudo-randomized fashion. The resulting frequency of occurrence of the target stimuli was thus ~14% and that of the non-target stimuli was ~86%. Generation of the target stimuli was inhibited for the next five stimuli. This modification was made to ensure recovery of the task-related signal intensity change to baseline, which has been known to take ~10 s [7]. The subjects were asked to press a button whenever they noticed the particular target stimulus, allowing for counting hits, false alarms, and misses. The subjects closed their eyes during auditory presentation.

Functional magnetic resonance imaging was performed

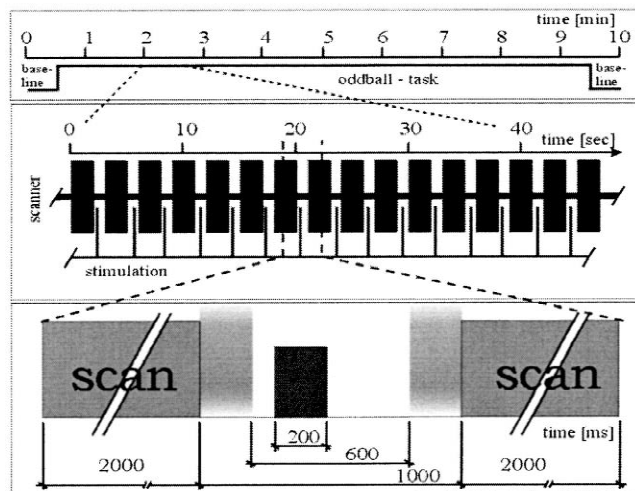


Fig. 2. Schematic description of the fMRI paradigm.

on a 1.5 T MRI system (General Electric, Waukesha, WI, USA), equipped with echo planar imaging (EPI) capabilities using the standard head coil for radio-frequency (RF) transmission and signal reception. Sequences with the following parameters were employed: gradient echo EPI, repetition time TR, 2 s; echo time TE, 40 ms; field of view, $200 \times 200 \text{ mm}^2$; 90° flip angle; matrix size, 64×64 ; voxel size, $3.125 \times 3.125 \times 5 \text{ mm}^3$. Using a midsagittal scout image, 24 axial slice positions (0.5 mm inter-slice gap) were oriented parallel to the bi-commissural plane with the lowermost slice positioned to be 25 mm below the AC–PC line, thus covering the whole auditory cortex. Initiation of each scan was triggered by a computer and synchronized with stimulus presentation. Each session consisted of 210 acquired images, during which standard and target stimuli were presented in randomized order. These sessions were repeated six times each with different randomization of the target and standard stimuli. In addition, 3D anatomical images of the entire brain were obtained using a strongly T1-weighted gradient EPI pulse sequence (3D-GE-EPI) with the following parameters: TR, 24 ms; TE, 8 ms; 30° flip angle; FOV, $250 \times 250 \text{ mm}^2$; matrix size, 256×256 ; 124 sagittal slices with 1.5 mm thickness.

Image analysis was performed on a PC workstation using MATLAB (Mathworks, Natick, MA, USA) and SPM99 software (<http://www.fil.ion.ucl.ac.uk/spm>). For analysis, all images were realigned to the first volume, corrected for motion artifacts, co-registered with the subject's corresponding anatomical (T1-weighted) images, resliced and normalised (4 mm^3) into standard stereotaxic space (template provided by the Montreal Neurological Institute [11]), and smoothed using an 8 mm full-width-at-half-maximum Gaussian kernel. The data were analyzed by statistical parametric mapping. The effect of global differences in scan intensity was removed by scaling each scan in proportion to its global intensity. Statistical analysis was performed by modeling the hemodynamic response function (HRF) for each target and for the standard stimuli relative to baseline. Thus, for each subject and each condition, an image was produced containing the effect sizes relative to baseline for each and every voxel (con*. images in SPM). These images were used for later group analysis in the context of the random effects procedure. For all statistical analyses a mask image was used only containing the temporal cortex. Thus, our statistical analysis was restricted to this brain area. In a first step, significantly activated voxels relative to baseline were searched for applying a one-sample *t*-test testing for significant departure from zero (height threshold of $z=2.3$, $P=0.01$ uncorrected for multiple comparisons; spatial extent criterion of $k=14$, $P=0.05$ corrected for multiple comparisons). In a second step, a multi-group and multi-condition procedure was applied to calculate between-group and between-condition differences. The same statistical threshold as for the aforementioned comparison was used. The significantly activated voxels were overlaid

onto a segmented standard T1-weighted brain used for spatial normalization (MNI template).

According to signal detection theory, the performance data were transformed to d' scores in order to correct for differences with respect to the number of false alarms. d' scores were also calculated for the five training sessions. These d' scores were analysed separately for each subject and for each stimulus frequency. This analysis revealed that only three subjects of the training group yielded performance gains during the five training sessions (the average difference between the post- and pre- d' scores across all stimulus frequencies for subjects 1, 2, and 3 was 1.9, 2.9, and 1.9). The other three subjects of the training group only showed very weak or no performance gains (the average difference between the post- and pre- d' scores across all stimulus frequencies for subjects 4, 5, and 6 was 0.1, 0.3, and -0.3). Thus, the training group was divided into two subgroups, those with performance gain (T+) and those without (T-). The average performance gain is shown in Fig. 3.

Fig. 4a shows peak activations and corresponding stereotaxic coordinates for the comparison relative to baseline. As can be seen, there are extended bilateral activations within the superior temporal gyrus (STG) comprising parts of Heschl's gyrus, the planum temporale (PT), the sulcus temporalis superior (STS), the planum polare (PPo), and the inferior frontal gyrus region (IFG). Thus, the activation pattern to auditory stimulation is similar to previous auditory studies applying fMRI [2–6,12–14]. Comparing separately for each group (T+, T-, and CO) the activations obtained before (pre) and after (post) the pitch discrimination training revealed that the T+ group showed increased bilateral hemodynamic responses in the STG before the training while there was no pre>post difference for the T- and CO groups. As can be seen from Fig. 4b and c the stronger bilateral hemodynamic responses for the T+ group during the pre-session were located more in the posterior STG within the PT, but also in an inferiorly located cluster anterior to the descending ramus of the Sylvian fissure, known to be part of Wernicke's area. In addition, there were also activations in the dorsal bank of the STS and the PPo. There was also a cluster of activation in the right Heschl's gyrus and the PPo. The T- group revealed stronger activation in the left STG, slightly extending into the dorsal bank of the STS ($x=-64$, $y=-44$, $z=8$; $T=6.4$) for the post-session. There was no further significant pre–post difference. Additionally, we performed an interaction analysis to directly compare pre–post differences between the groups. The results are shown in Fig. 4c and revealed stronger bilateral hemodynamic responses in the STG and right PPo during the pre-session than during the post-session for the T+ group (compared to the T- and CO groups). We also searched for differences between the hemodynamic responses obtained for the different stimuli. We found that pre>post differences were only evident for the 958 and

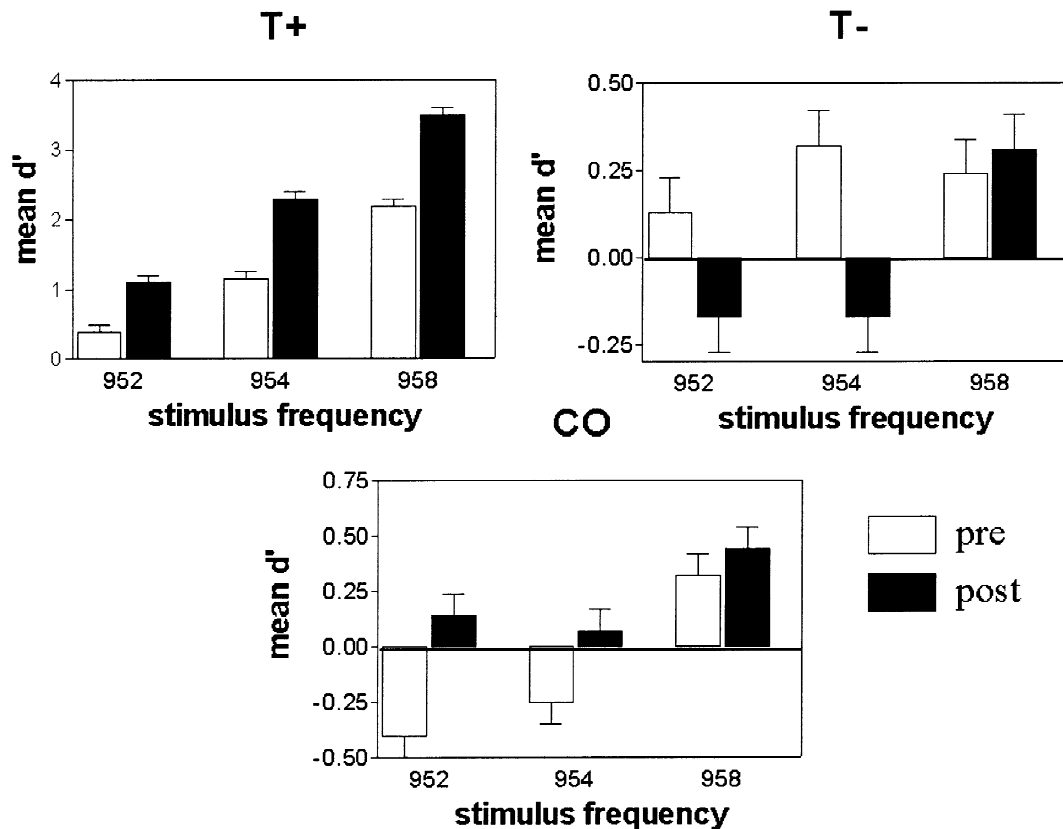


Fig. 3. Mean performance data (as d') for pitch discrimination obtained during the pre- and post-sessions broken down for the three groups (T+, subjects with performance gain; T-, subjects without performance gain; CO, control subjects). Vertical bars indicate standard errors of the mean.

954 Hz tones but not for the much harder to detect 952 Hz tone (Fig. 4d). Finally, the activations obtained during the post-sessions were subjected to a between-group analysis revealing that the T- and CO groups showed stronger activations during the post-session than the T+ group.

This is the first study to show that intensive short-term (1 week) training of pitch discrimination results in a demonstrable neurophysiological change in the hemodynamic response of the human auditory cortex. The change in hemodynamic response is evidenced as a bilateral decrease in the STG for those subjects exhibiting a performance gain (T+ group) during the training sessions. Those subjects exhibiting no substantial performance gain (T- group) and the control subjects (CO) who were not involved in the pitch discrimination training revealed no change of hemodynamic response in the auditory cortex between the pre- and post-sessions despite the fact that the T- group revealed a slight activation increase in the left STG during the post-session. Thus, there is a distinct pattern of activation in the auditory cortex depending on whether or not the subjects are improving their discrimination performance. But what are the underlying neurophysiological reasons for this activation pattern?

A possible mechanism might be that increasing proficiency in detecting a target is associated with perception processes becoming more automatic during the course

of short-term learning. This process may be explained on the basis of 'fast learning theories' put forth in earlier training studies [27]. According to this theory, fast learning could have taken place in the auditory system during training while the brain was selecting optimal sensory units to represent the features of the target tones as a unique population of cells firing in synchrony. Once these codes become efficient, the task becomes automatic with less but more focussed neuronal activation in the auditory areas. These plastic processes may take place either cortically or at subcortical sites that project to the auditory cortex. Possible subcortical sites include the magnocellular division of the medial geniculate nucleus, which is known to recalibrate quickly during learning and to exert a modulatory effect on auditory cortical neurons, making them more sensitive to their preferred spectral inputs [35].

A further possibility might be that, at the beginning of the pitch discrimination training, activation within the auditory cortex is distributed diffusely because the brain is searching for the most appropriate strategy. For example, the posterior auditory areas containing the planum temporale are activated during both sessions for all groups. Hemodynamic responses in the planum temporale decrease after successful pitch discrimination training, thus suggesting that the core region responsible for pitch discrimination is located more anteriorly near the primary auditory

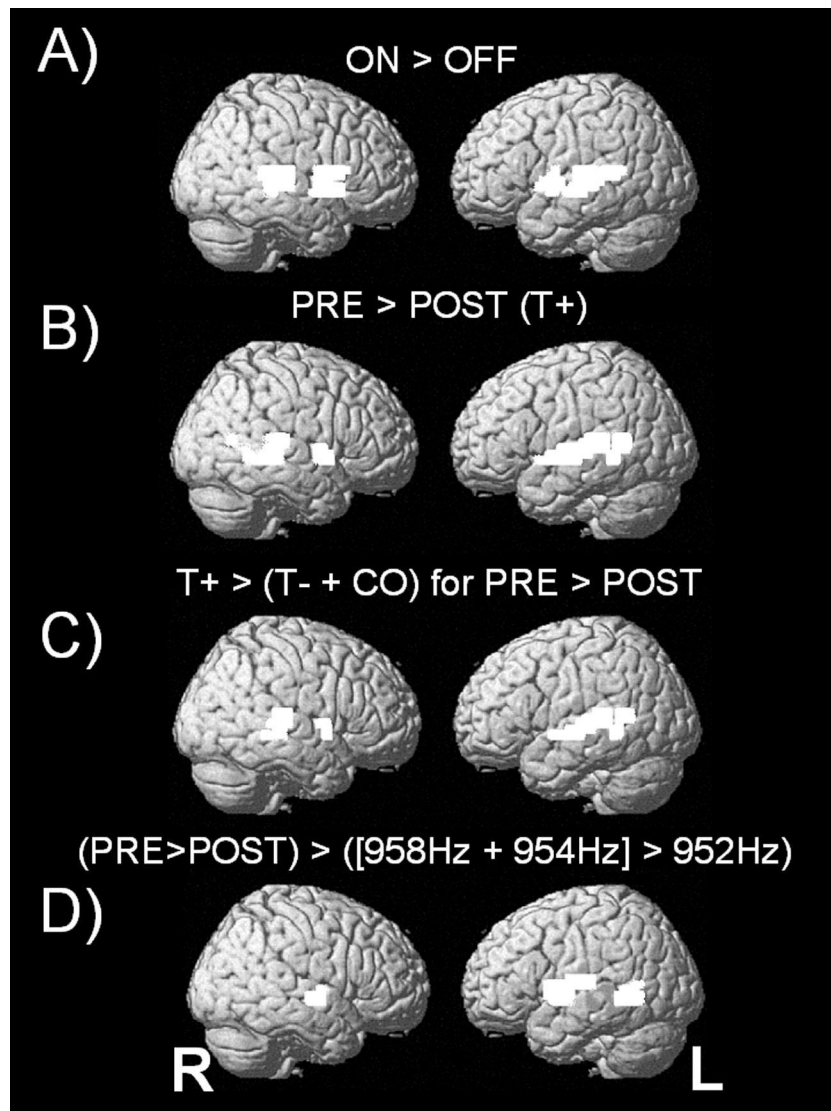


Fig. 4. Significantly activated voxels overlaid onto the MNI standard brain. Presented are the lateral views (L, R, left and right hemispheres). (A) Activated regions for the contrast comparing auditory stimulation with baseline (*ON* > *OFF*). Activation comprises the left Heschl's gyrus ($x, y, z: -52, -24, 12; T=4.1$), left planum temporale ($x, y, z: -60, -40, 8; T=8.3$), the left superior temporal sulcus ($x, y, z: -52, -24, 0; T=7.0$), and the left planum polare ($x, y, z: -40, 0, 4; T=3.9$). Activation on the right hemisphere comprises the superior temporal sulcus extending into the planum temporale ($x, y, z: 56, -36, 0; T=4.4$) and the inferior frontal gyrus including the pars opercularis ($x, y, z: 32, 8, -4; T=5.8$). (B) Activated regions where the pre-session revealed stronger activations than the post-session for the T+ group (*PRE* > *POST* T+). There are extended activations in the left superior temporal gyrus including the planum temporale ($x, y, z: -48, -48, 12; T=6.6$), the dorsal bank of the superior temporal sulcus ($x, y, z: -68, -36, 4; T=4.9$), and the planum polare ($x, y, z: -60, 12, -4; T=4.3$). Activations on the right hemisphere comprise Heschl's gyrus ($x, y, z: 60, -24, 12; T=4.4$), the dorsal bank of the sulcus temporalis superior extending into the planum temporale ($x, y, z: 56, -28, 0; T=4.2$), and the planum polare ($x, y, z: 56, 4, 0; T=6.1$). (C) Anatomical regions revealing significant between-group differences (T+ > [T- + CO]) for the pre > post contrast. Activations are basically the same as for the contrast described in (B). (D) Pre > post differences for the T+ group for the two higher stimulus frequencies (958 and 954 Hz) compared to the lower stimulus frequency (952 Hz). Activations comprise the left Heschl's gyrus ($x, y, z: -64, -20, 12; T=3.0$), the dorsal bank of the left superior temporal gyrus ($x, y, z: -56, -4, 0; T=3.1$), and the left planum polare ($x, y, z: -60, 8, 4; T=2.8$).

cortex. Because the planum temporale contains neural networks thought to be involved more strongly in higher order auditory perception processes, it might be that the activation of these networks during pitch discrimination indicates a less efficient strategy for pitch discrimination.

Neural plasticity has been described for previous experiments as an increase in the neuronal response strength or as an expansion of the representation across cortical areas

associated with the stimulus [16,34]. Increases in amplitude of neuronal responses have been detected using single unit recording techniques in classical conditioning experiments with animals [1,10]. An enlargement of the cortical area representation has been found in monkeys using single unit recording methods [15,28] and in humans using fMRI [17,20]. Most of the studies in humans applying MEG and EEG methods revealed that the N1m,

the mismatch negativity, and the MMF responses to the learned stimuli increased in amplitude during training [18,19,24,33] (for a different finding, see Ref. [8]). Our results seem to be in contradiction to these findings because we found a decrease of activation during the course of a 1-week training session for those subjects who improved their performance. One of the reasons for these possibly contradictory findings might be due to differences with respect to the duration and intensity of the training sessions, the stimuli, or the subjects which participated in these studies. It might also be that the different methods examine different stages of functional plasticity. For example, the EEG and MEG methods are more sensitive to measuring fast neurophysiological processes (within milliseconds) with relatively low anatomical precision, while fMRI methods measure slower neurophysiological processes (within seconds) with relatively high anatomical precision. It will be an endeavour of future studies to uncover similarities and differences of the neurophysiological processes measured with these different methods in the context of functional plasticity studies.

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