Are receptive fields fixed or fluid?

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Neural representations of sensory stimuli are affected by stimulus- and task context. These effects can be long term, such as observed after intensive training or sensory deprivation, or short term, for instance when stimuli are repeated or attended. Long-term effects are generally associated with changes in neural receptive fields, such as expanded representation of, and increased selectivity for, learned features after training, or cortical remapping after hearing loss. In contrast, short-term context effects are usually explained in terms of either suppressive (e.g., repetition suppression) or facilitatory (e.g., attentional facilitation) gain control, without any change in neural coding parameters. More recent models, however, propose that short-term effects, such as repetition suppression or attention, act not only through gain control of neuron populations, but also change the receptive fields of individual neurons. In this view, receptive fields are considered not as fixed, but rather as fluid and instantly adaptable. In this paper, new data are presented, based on non-invasive electrophysiological recordings in humans, which support the notion that short-term context effects cause rapid receptive-field plasticity.

INTRODUCTION

Neural receptive fields

The receptive field (RF) of a sensory neuron describes the selectivity with which that neuron responds to a particular stimulus feature. For example, the RF of an auditory neuron is characterised by the sound frequency that it is most responsive to, and by the steepness with which its responsiveness falls off with distance from this characteristic frequency (CF). This variation of responsiveness with frequency is also referred to as the RF 'tuning'. For primary auditory neurons, the RF is determined by the mechanical frequency tuning of the cochlea, and the neurons particular location along the tonotopic cochlear axis. At more central stages of the auditory pathway, the neural RF is determined by the synaptic input circuitry to the neuron, which receives converging afferent input from multiple units from more peripheral layers. Despite this convergence, the tonotopic arrangement originating from the cochlea is maintained along the ascending auditory pathway all the way to the auditory cortex, where CF varies gradually across the cortical surface, giving rise to a topographic representation of frequency. Such topographic maps of stimulus

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Proceedings of ISAAR 2013: Auditory Plasticity – Listening with the Brain. 4th symposium on Auditory and Audiological Research. August 2013, Nyborg, Denmark. Edited by T. Dau, S. Santurette, J. C. Dalsgaard, L. Tranebjærg, T. Andersen, and T. Poulsen. ISBN: 978-87-990013-4-7. The Danavox Jubilee Foundation, 2014.

features are ubiquitous in the sensory cortices, and form the basis of the neural representations of sensory stimuli that underlie perception.

Experience-related receptive-field plasticity

Theoretically, neural receptive fields must be considered stable entities, in order to support deterministic neural models that provide perceptual constancy. However, in reality, neural receptive fields are known to be susceptible to modification by experience. In the auditory cortex, the cortical area that responds to a given sound frequency has been shown to be *expanded* after a period of intense identification training on that particular frequency (Polley *et al.*, 2006); vice versa, the cortical representation of a sound frequency has been found to *disappear* when peripheral sensitivity at that frequency is lost after noise trauma (Eggermont and Roberts, 2004). These cortical reorganisations are assumed to occur as a result of changes in the receptive fields of individual neurons, reflecting modifications to the neurons input circuitry. This receptive-field plasticity leads to changes in perception, which can be either beneficial, such as perceptual learning after training (Polley *et al.*, 2006), or detrimental, such as development of tinnitus after high-frequency hearing loss (Eggermont and Roberts, 2004). Experience-related receptive-field plasticity is generally assumed to develop over a relatively long time period, in the order of days or weeks. However, it is well-known that both neural and perceptual responses to sensory stimuli can be substantially affected by immediate experience on a much shorter time scale. For instance, attention can be switched between sensory streams within seconds, and is known to drastically and selectively alter the perceptual acuity for and neural responsiveness to sensory stimuli (Scharf *et al.*, 1987, Woldorff *et al.*, 1993). Another example is repetition suppression, or adaptation, which refers to the reduction in neural responsiveness after repeated stimulation. Adaptation is ubiquitous in the sensory cortex, where it acts on a time scale of 100s of milliseconds, and has been implicated in perceptual priming, the improved perceptual acuity for a repeated stimulus, as well as streaming and novelty detection (Grill-Spector *et al.*, 2006). Classically, both attention and adaptation have been considered to act through a gain mechanism, which either increases or decreases the input-output gain of selected neurons, without changing their receptive-field properties. More recently, alternative models have been put forward in which these types of short-term effects also affect the selectivity of neural responses to sensory stimuli. This suggests that neural receptive fields would be susceptible to modifications on a much more rapid time scale than has previously been assumed. Here, new results are presented that investigate this hypothesis by examining the short-term effects of immediate stimulus context and attention on neural receptive fields in the human auditory cortex. For this purpose, we recorded auditory evoked potentials (AEP) non-invasively using electro-encephalography (EEG). In order to infer neural receptive-field properties from the resulting AEPs, we used so-called adaptation paradigms that reveal feature selectivity of the neural population underlying the response. The principle of adaptation paradigms as a tool for measuring neural selectivity is explained below.

Measuring neural receptive fields non-invasively using adaptation paradigms

Adaptation has been observed at each spatial level of neural processing, ranging from single units in the auditory cortex (Wehr and Zador, 2005) to population responses captured in neuroimaging (Grill-Spector *et al.*, 2001; 2006). One particularly interesting property of adaptation is that it is stimulus-specific. This means that the reduction in neural responsiveness after repeated stimulation is greater when the repeated stimulus is identical than when one or more of its features is changed. The increased response elicited by a change in a repeated stimulus is referred to as the 'release from adaptation'. For population responses, a release from adaptation will be elicited only if the underlying neural population is selective for the changed stimulus feature. In this case, the release from adaptation is assumed to arise from activation of a 'fresh' subpopulation of neurons that had not been adapted, because the preceding stimulus fell outside these neurons' receptive fields (May and Tiitinen, 2009; Grill-Spector *et al.*, 2006). According to this 'fresh afferents' model, the release from adaptation will increase with increasing difference between two subsequent stimuli along the relevant feature dimension, as there will be increasingly less overlap between the neural populations responding to the first and second stimulus. In other words, the release from adaptation reflects the receptive-field tuning of the underlying neural population to that particular stimulus feature. A useful practical implication of this is that adaptation can be used to measure receptive-field properties of neural populations using non-invasive neuroimaging methods. Adaptation paradigms were first pioneered by Grill-Spector and colleagues, who applied them to functional magnetic resonance imaging (fMRI) to investigate feature selectivity in different areas of the human visual cortex (Grill-Spector *et al.*, 2001). They used a block design, in which they measured the average blood oxygenation level dependent (BOLD) response to blocked sequences of repeated stimuli, and compared responses between blocks in which the stimuli varied along different feature dimensions. Those feature changes for which the BOLD responses were largest were assumed to have elicited the greatest release from adaptation, and thus that feature was interpreted to be selectively represented by the underlying neural population. An alternative design is used to measure the neural selectivity to one particular stimulus. In this 'event-related' design, discrete trials are presented in which one stimulus (the adapter) is followed by another (the probe), with inter-trial intervals long enough to allow for recovery from adaptation between trials. Here, the response to the probe and the adapter are measured separately, and the amount of adaptation is measured by comparing the size of the (adapted) probe response to that of the (unadapted) adapter. By plotting the amount of adaptation as a function of the difference between adapter and probe along a particular feature dimension, an adaptation tuning curve is constructed that reflects the sharpness of neural tuning to that feature in the particular neural population that responds to the adapter.

METHODS

All experiments reported here recorded cortical AEPs in response to pure-tone stimuli of 100-150 ms duration presented with a stimulus onset asynchrony (SOA) of 500 ms. Stimuli were presented binaurally over headphones at 60 dB SPL to participants seated in a sound-attenuating and electrically-shielded booth. EEG signals were recorded from 33 electrodes placed according to the standard 10-20 arrangement. Data dimensionality was reduced either by fitting the data to a source model and extracting the average source waveform (experiment 1), or by calculating the global field power, which is the root-mean-square over all channels at each time point (experiments 2 and 3). The resulting AEPs showed the typical P1, N1, and P2 deflections, which are obligatory responses originating from the auditory cortex. Individual responses were quantified by the peak-to-peak amplitude difference between consecutive deflections. The difference between P1 and N1 is referred to as ‘N1’, and the difference between N1 and P2 as ‘P2’. The ‘N1’ component is thought to represent neural responses from the more peripheral input layer into the auditory cortex, whereas the ‘P2’ component is assumed to reflect more central, intra-cortical connections. All participants were normally-hearing young adults. 15 participants were tested in experiment 1, 24 in experiment 2, and 12 in experiment 3.

EXPERIMENT 1: DOES REPEATED EXPOSURE TO AN ADAPTER SHARPEN ADAPTATION TUNING?

Background

Both evoked potential studies (May and Tiitinen, 2009) and invasive recordings from the auditory cortex (Ulanovsky *et al.*, 2003) have reported that the neural response to the same stimulus increases as its occurrence in an oddball sequence becomes rarer. At first glance, this effect might be ascribed to stimulus-specific adaptation, as the response to a more often repeated stimulus would be more adapted and thus smaller. However, a study by Taaseh and colleagues reported that this ‘deviant’ response is elicited even when adaptation effects are controlled for (Taaseh *et al.*, 2011). Based on a modelling approach, the authors proposed that the deviant response results from a sharpening of adaptation tuning after repeated presentation of the adapting stimulus. This sharpening would decrease the overlap between the neurons activated by the probable and the rare stimuli in the oddball sequence, compared to a sequence in which the two stimuli are equally probable. This would cause a greater release from adaptation for the rare stimulus, resulting in the observed deviant response. While this hypothesis explained the results well, the sharpening hypothesis is not unequivocally supported by the findings. This is because the responses were measured in continuous sequences, in which the effect of single versus repeated adapters could not be evaluated separately. In order to test the sharpening hypothesis proposed by Taaseh and colleagues directly, we performed an experiment which compared the amount of adaptation after a single, two, or three identical adapters.

Design

An event-related paradigm was used in which discrete adapter-probe trials were presented with an inter-trial interval of 5 s. Based on current estimates of adaptation recovery time, this ensured that no adaptation effects from a preceding trial spilled over to a subsequent trial. The probe frequency was fixed at 1 kHz, and the adapter frequency ranged between 0 to 1.5 octaves above the probe frequency. The amount of adaptation was calculated as the ratio of the P2 amplitude of the probe to that of the first adapter in each trial, which represents the unadapted response.

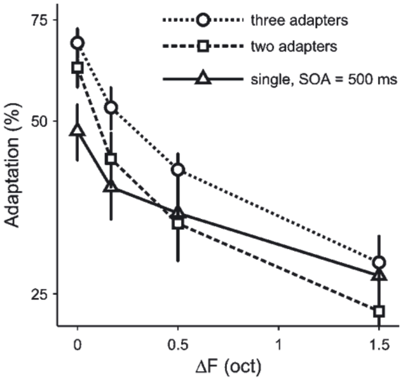

Fig. 1: Adaptation tuning curves compared for probes preceded by a single (triangles, solid line), two (squares, dashed line) and three (circles, dotted line) adapters presented in discrete trials. Plots show mean and standard error across participants of the percent adaptation of the P2 component of the AEP. [From Briley and Krumbholz, in revision.]

Results

The adaptation tuning curves measured for the single, two, and three adapter conditions are compared in Fig. 1. At zero frequency difference between the adapter and the probe (DF = 0), the amount of adaptation increases progressively with the number of adapters. This would be expected, as the effect of the successive adapters on the probe add up. However, as the frequency difference between adapter and probe increases, it can be seen that the amount of adaptation falls off more rapidly for multiple adapters than a single adapter. Notably, at the largest frequency difference, the multiple adapters are in fact no more effective than the single adapter. These effects were found to be significant, and suggest that multiple adapters are relatively less effective at adapting a deviant frequency than a single adapter. This supports the hypothesis put forward by Taaseh and colleagues that adaptation tuning is sharpened after repeated presentation of an adapter.

EXPERIMENT 2: DOES EXPOSURE LEAD TO LONGER-TERM SHARPENING OF ADAPTATION TUNING?

Background

The findings of experiment 1 suggest that the neural population that underlies the adaptation effect after multiple adapters is more sharply tuned than the neural population that is adapted after a single adapter. This could imply either that the adaptation effects observed for multiple versus single adapters involve different neural populations, or that the same neural population has become more sharply tuned after repeated exposure to the adapter. This latter effect could form a neural basis of perceptual priming, as a sharper representation of the repeated stimulus would be expected to improve the perceptual acuity for that stimulus. Priming has been proposed to be a short-term precursor to longer-term perceptual learning. By analogy, we hypothesized that the short-term sharpening observed here might form a precursor for longer-term receptive-field plasticity. In order to test this hypothesis, the next experiment investigated the longer-term effect of repeated exposure on adaptation tuning.

Design

AEPs were recorded in response to stimuli presented in random sequences in which one stimulus, here referred to as the adapter, was presented in 40% of trials, and six different stimuli, here referred to as the deviant probes, were presented in 10% of trials each. The deviant probes had frequencies spaced symmetrically within half an octave around the frequency of the adapter. Here, the average response to the adapter represents the amount of adaptation for a zero frequency difference, whereas the average response to the deviant probes reflects the release from adaptation as a function of frequency difference between adapter and probe. Two conditions were compared: in the ‘fixed’ condition, the adapter frequency was fixed throughout the recording at 1000 Hz; in the ‘roving’ condition, the frequency of the adapter was changed every two minutes, ranging within an octave around 1000 Hz. It was hypothesized that if any longer-term (i.e., > 2 minutes) sharpening effects occurred, this would lead to a difference in the adaptation tuning between the fixed and the roving condition. This is because in the roving condition, there would be no time for longer-term effects of exposure to the adapter to develop.

Results

First, the data were analyzed to estimate short-term sharpening effects. To this purpose, the responses to each stimulus were separately averaged depending on whether they were preceded by one, two, or three adapters in the random sequence. This analysis mimics the multiple and single adapter trials in experiment 1, but here the ‘trials’ were not discrete but embedded at random locations within the continuous random sequence. As these are very short-term effects, the data were averaged over the fixed and roving conditions, and over the entire duration of stimulus presentation and recording, which was 1.5 hours (interrupted by short breaks every 15 minutes). The resulting adaptation tuning curves are shown in Fig. 2A and 2B for the N1 and P2 components, respectively. It is immediately evident that the release from adaptation with frequency difference increases as the number of preceding adapters increases. This effect is significant at all deviant frequencies. Importantly, however, at zero frequency difference there is no significant change in response size for either the N1 or the P2 with increasing number of adapters. These results are analogous to the findings of experiment 1, and similarly suggest that the adaptation effect is more sharply tuned after multiple than after single presentations of the adapter.

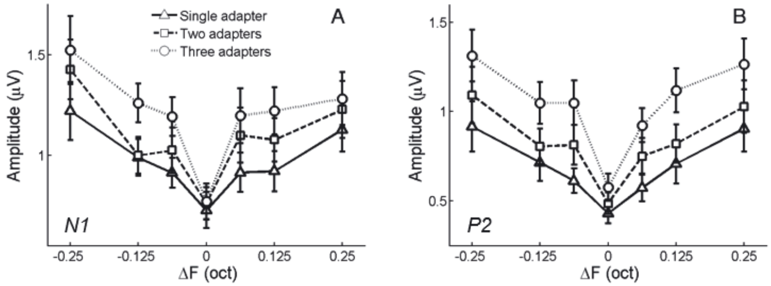

Fig. 2: Adaptation tuning curves compared for probes immediately preceded by one (triangles, solid line), two (squares, dashed line), and three (circles, dash-dot line) adapters in a random sequence. A: N1 B: P2.

Next, the data were analyzed for medium-term effects of exposure to the adapter. Responses to each stimulus were averaged separately over a consecutive time period of 15 minutes. If exposure to the adapter caused effects with memory spans of between 2 and 15 minutes, we would expect a difference between the fixed and the roving condition in the average tuning curve over the first 15 minutes. This comparison is shown in Fig. 3A and 3C for the N1 and P2 components, respectively. As can be observed, there was no significant difference between the two conditions for either component. Figures 3B and 3D show the same comparison for the average over the last fifteen minutes of the recording. Here, we would expect differences that might have developed over the preceding 45 minutes of exposure to the adapter. In fact, the only significant difference observed was a larger decrease in the N1 in the fixed versus the roving condition, which developed gradually during the recording session. This indicates that there is an exposure effect on the N1 with a memory span of up to 45 minutes, but this effect was not frequency-specific. The fact that the P2 did not show this effect may indicate that it is already maximally adapted after seconds of exposure, which is in line with previous findings. In summary, the results of experiment 1 provide further evidence that adaptation tuning is sharpened after repeated exposure to the adapter, but indicate that this is a purely short-term effect, with a memory span in the order of seconds.

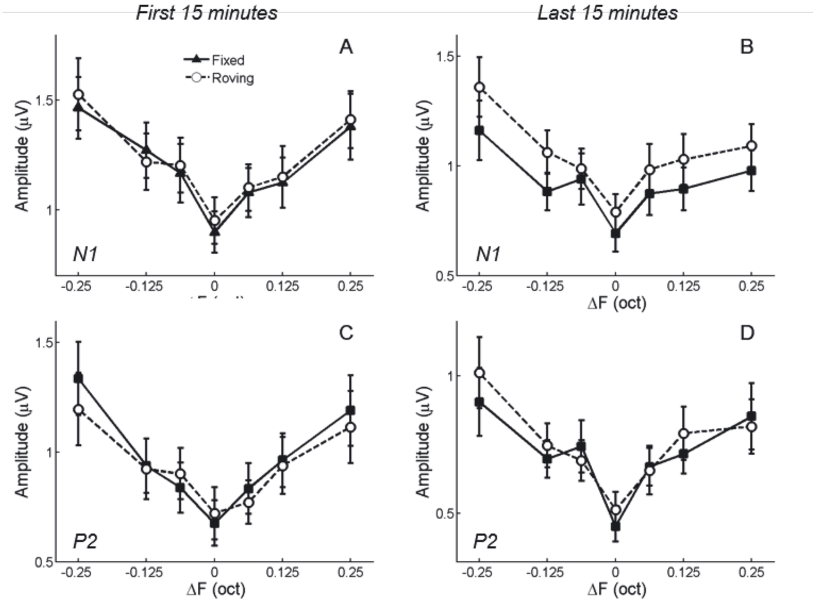

Fig. 3: Adaptation tuning curves obtained with a fixed (filled squares, solid lines) and a roving (open circles, dashed lines) adapter frequency. A and C: First 15 minutes of recording. B and D: Last 15 minutes of recording. A and B: N1; C and D: P2.

MECHANISMS UNDERLYING SHORT-TERM SHARPENING?

Two alternative mechanisms have been hypothesized to underlie the sharpening of adaptation tuning after repeated adapters. These different models explain the effect as arising from bottom-up and top-down processes, respectively.

Bottom-up explanation

Mill and colleagues developed a computational model in which sharpening of adaptation tuning is an emergent property of a convergent network of depressing synapses (Mill *et al.*, 2011). The model assumes that adaptation results from synaptic depression, which is supported by neurophysiological evidence (Wehr and Zador, 2005), and provides a good match to the time course of adaptation. An essential feature of the model is that, as a result of convergence, receptive-field tuning becomes broader from peripheral to central synaptic layers. It is then posited that more peripheral synapses are not depressed after a single adapter, but become depressed after repeated adapters. As a result, the peripheral synapses stop firing, which in turn allows more central synapses, which receive input from the peripheral layers, to recover and resume firing. In this situation, the adaptation tuning measured at the more central layer will actually reflect the tuning at the more peripheral, and thus more sharply tuned, neural layer. Thus, in this model the adaptation observed after multiple adapters reflects the tuning of a different neural population, rather than a change in tuning in the same population. Although this parsimonious model is compelling, it provides only a qualitative explanation of the findings, and is as yet not supported by any direct neurophysiological evidence.

Top-down explanation

An alternative hypothesis is that repeated stimulation elicits top-down feedback processes that modify neural receptive fields through efferent pathways that alter the synaptic input circuitry of individual neurons. Clearly, such a top-down feedback effect would have to act very rapidly to explain the short-term effects observed here. There is some evidence that rapid receptive-field sharpening can be elicited by top-down mechanisms from studies of selective attention. In an fMRI study, Murray and Wojciulik measured release from adaptation in the visual cortex in response to a change in the orientation of a visual stimulus (Murray and Wojciulik, 2004), and found that when the stimulus was selectively attended, the release from adaptation was increased. This indicates that attention caused an increased neural selectivity, i.e., a sharpening of receptive-field tuning, to stimulus orientation. As attention acts in a very immediate manner and can be switched rapidly, these findings suggest that top-down modulation of neural receptive fields can occur within a very short time.

EXPERIMENT 3: DOES ATTENTION SHARPEN NEURAL TUNING?

Background

In the auditory system, evidence of rapid task-related receptive-field plasticity has been reported from single neuron recordings in auditory cortex, which were suggested to result from top-down attentional modulation (Fritz *et al.*, 2003). However, results from human neuroimaging have been confounded by the use of paradigms in which apparent changes in selectivity could have resulted from changes in attentional load (e.g., Ahveninen *et al.*, 2011). In the final experiment presented here, we tested the hypothesis that attention sharpens neural tuning in the human auditory cortex directly, using a similar approach to Murray and Wojciulik.

Design

AEPs were recorded while participants performed a dichotic listening task. Pseudo-random tone sequences (Brimijoin and O’Neill, 2010) comprising four equally-probable frequencies were presented to one ear, while simultaneously a sequence of amplitude-modulated noises was presented to the other ear. The participants were instructed to attend to one ear at a time, which was changed every 2.5 minutes, and detect rare oddballs in the attended stream. In the tone sequences, the oddball was frequency modulated, whereas in the noise sequences, the oddball had a rising rather than falling amplitude profile. The modulation parameters of both types of oddballs were set to achieve an equal hit rate of ~75%. The noises were presented with an SOA of 666 ms plus a jitter ranging between 0 and 100 ms, to avoid synchronization to the tones. Only AEPs to the tones were recorded.

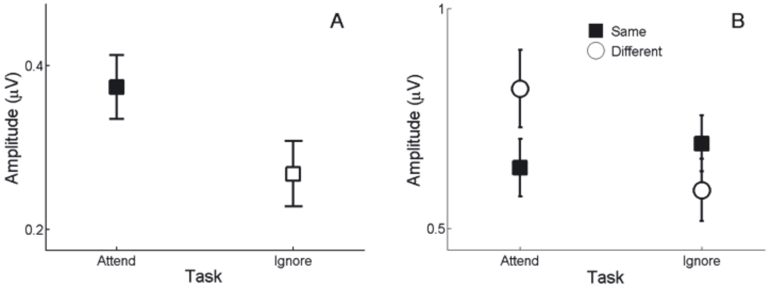

Fig. 4: Effect of attention on P2 amplitude of the AEP. A: Average response to all tones. B: Responses to tones preceded by the same frequency (‘Same’, filled squares) or by a different frequency (‘Different’, open circles).

Results

As expected, the response to the tones was significantly larger when participants attended to the tones (‘attend’) than when they ignored the tones and attended to the noises (‘ignore’). This illustrated for the P2 amplitude in Fig. 4A. In order to evaluate whether attention caused a sharpening of neural tuning, the responses were separately averaged depending on whether they were immediately preceded by the same frequency (‘same’) or by a different frequency (‘different’). The difference between these two conditions reflects the degree of frequency-dependent release from adaptation, with the ‘different’ response expected to be larger than the ‘same’ response. If attention sharpens frequency selectivity, we would expect a greater release from adaptation in the ‘attend’ versus the ‘ignore’ condition. In figure 4B, this comparison is shown for the P2 component. Note that in the ‘attend’ condition, the response to the ‘different’ tone is larger than the response to the ‘same’ tone, whereas in the ‘ignore’ condition, the ‘same’ response is slightly larger than the ‘different’ response. Statistical analysis revealed that the release from adaptation was significantly larger in the ‘attend’ than in the ‘ignore’ condition. This is similar to the findings of Murray and Wojciulik, and supports the hypothesis that attention sharpens neural tuning.

CONCLUSIONS

The close agreement between the results of experiment 1 and 2 and the findings of Taaseh and colleagues provides compelling evidence of sharpening of adaptation tuning after repeated adapters. However, the neural mechanism that underlies this effect has not yet been ascertained. Nevertheless, the results from experiment 3 suggest that receptive-field tuning is susceptible to rapid modulation via top-down pathways. It is plausible that the sharpening elicited by a repeated adapter results from a similar top-down mechanism. The stage of processing at which this top-down modification is effected is not necessarily at the cortex, but could be inherited from earlier stages of processing, via efferent connections that reach back towards the periphery. Efferent effects can even reach as far down as the cochlea, where they have been reported to mediate frequency-specific attentional modulation of cochlear gain (de Boer and Thornton, 2007; Maison *et al*., 2001). Such peripheral effects could alter cortical receptive fields by changing the synaptic input into the cortex.

ACKNOWLEDGEMENTS

We thank Sarah Gibbs, Dominic Friston, and Margareta Szymczak for their assistance in data acquisition and processing; Owen Brimijoin for assistance with creation and analysis of tone sequences; Rob Mill, Cris Lanting, and Julien Besle for helpful discussions. This research was funded by the Medical Research Council (UK).

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