LETTERS

The neuronal representation of pitch in primate auditory cortex

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Pitch perception is critical for identifying and segregating auditory objects[1], especially in the context of music and speech. The perception of pitch is not unique to humans and has been experimentally demonstrated in several animal species[2,3]. Pitch is the subjective attribute of a sound's fundamental frequency (f_0) that is determined by both the temporal regularity and average repetition rate of its acoustic waveform. Spectrally dissimilar sounds can have the same pitch if they share a common f_0. Even when the acoustic energy at f_0 is removed ('missing fundamental') the same pitch is still perceived[1]. Despite its importance for hearing, how pitch is represented in the cerebral cortex is unknown. Here we show the existence of neurons in the auditory cortex of marmoset monkeys that respond to both pure tones and missing fundamental harmonic complex sounds with the same f_0, providing a neural correlate for pitch constancy[1]. These pitch-selective neurons are located in a restricted low-frequency cortical region near the anterolateral border of the primary auditory cortex, and is consistent with the location of a pitch-selective area identified in recent imaging studies in humans[4,5].

Many natural sounds (or biologically significant sounds) have periodic acoustical waveforms. These sounds can be spectrally decomposed into a sinusoid at the frequency of periodicity (f_0) and a series of sinusoids at frequencies that are integer multiples of f_0 (harmonics). Although these individual spectral components are represented within the cochleotopic organization of the auditory system in a distributed fashion, they are perceptually grouped together into a single sound with a pitch equivalent to a pure tone at f_0 (ref. 1). In the auditory periphery, the f_0 of complex sounds—such as missing fundamental harmonic complex sounds (MFs)—is represented by a distributed neural code involving both the discharge rates and temporal firing patterns of auditory nerve fibres[6,7]. How this information is used to encode pitch within the central auditory system is poorly understood.

Deficits in pitch discrimination have been observed in animals[8], including humans[9,10], following auditory cortical lesions, indicating a cortical role in pitch perception. However, electrophysiological recordings in macaque monkeys suggest that primary auditory cortex (AI) does not contain a representation of pitch, as AI neurons do not respond to MFs with a pitch matching their characteristic frequency[11,12]. Alternatively, pitch may be processed in non-primary auditory cortex, as recent human imaging studies have revealed a cortical pitch processing region anterolateral to primary auditory cortex[4,5]. The organization of primary and secondary areas of auditory cortex is largely conserved across primate species[13,14], and a similar 'pitch centre' may exist in non-human primate auditory cortex. In this study, we searched for pitch-selective neurons in the auditory cortex of the common marmoset (*Callithrix jacchus*): a New World primate species sharing a similar hearing range with humans[15]. Using single-unit extracellular recordings (see Methods), we found a restricted cortical region near the anterolateral low-frequency border of AI in the marmoset containing neurons that respond significantly to both pure tones and MFs with similar pitches.

In order for a neuron to be considered pitch-selective, we required that it satisfy two criteria. First, the neuron had to respond significantly to both pure tones and MFs with a similar pitch. Second, all of the harmonics of the MF had to be outside the neuron's excitatory-frequency response area. An example of a neuron's response to acoustic stimuli to test these criteria is shown in Fig. 1 (see also Supplementary Fig. 1). A total of 53 neurons from three marmosets met our criteria for pitch-selectivity. Fifty-one of these neurons were located within a restricted low-frequency region near the antero-lateral border of AI and neighboured by the low-frequency regions of R (rostral field) and laterally situated non-primary areas (Fig. 2a, Supplementary Fig. 2a–c). These pitch-selective neurons accounted for 39% (51/131) of the neurons recorded in this region that responded to pure tones. Pitch-selective and non-pitch neurons in this area spanned a similar range of characteristic frequencies (Fig. 2b). Owing to recording time constraints, we initially searched for MF responses using fundamental frequencies near the neuron's characteristic frequency (determined by pure tone). In some pitch-selective neurons, we systematically varied an MF's f_0 in order to determine the neuron's best fundamental frequency. In general, pitch-selective neurons were similarly tuned for their peak responses to pure tones and MFs (Fig. 3b) and always overlapped in their frequency and fundamental frequency tuning for pure tone and MF responses, respectively (Fig. 3a, Supplementary Fig. 3a, b). We did not have any evidence from our experiments to support the existence of neurons with MF and pure tone responses that failed to overlap along the frequency axis. An additional 50 neurons in this region were encountered that did not respond significantly to pure tones, but did respond to narrowband or wideband stimuli such as harmonic complex tones, sinusoidally amplitude- or frequency-modulated tones (sAM, sFM), click trains, or band-pass noise. A subset of these neurons ($n = 10$) only responded to harmonic complex and sAM tones with repetition rates similar in frequency to the characteristic frequencies of neighbouring neurons. These neurons may play a role in processing the pitch of complex sounds; however, they were not included in our analysis of pitch-selective neurons due to an insufficient sample size.

Once we characterized neurons as pitch-selective, we further tested these cells with a variety of complex sounds whose pitch salience were parametrically varied. A click train (see Methods) has a pitch corresponding to its average repetition rate and a pitch salience determined by the regularity of the time intervals between successive clicks. When the timing of individual clicks is 'jittered' to create an irregular click train, the pitch salience decreases with increasing irregularity[16]. We tested the effect of a click train's temporal irregularity on neuronal responses in a subset of pitch-selective neurons and found an overall decrease in their discharge rates (Fig. 4a,

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Supplementary Fig. 4a, b). For another subset of pitch-selective neurons, we tested their sensitivity to pitch salience using iterated-ripple-noise (IRN) stimuli, which were constructed by adding broad-band noise iteratively to itself with a constant delay[17]. Because each iteration of this delay-and-add process increases the temporal regularity of the resulting sound, the pitch strength of the stimulus also increases. Overall, pitch-selective neurons increased their discharge rate as the strength of pitch in the IRN also increased (Fig. 4b, Supplementary Fig. 4c).

Pitch salience is also dependent on the harmonic composition of an MF. Data from studies in humans indicate that the salience of pitch is greater in MFs composed of lower-order harmonics rather than those composed of higher-order harmonics[1]. It is the third to fifth harmonics of a harmonic complex tone that contribute the most to its pitch[1]. However, it is unknown if this is also the case in marmosets. We observed that pitch-selective neurons usually responded most strongly to harmonic complex sounds containing lower-order harmonics (first to sixth harmonics) (Fig. 4c).

Several important distinctions must be made between this study and previous reports of a neural representation of periodicity in the auditory cortex of the gerbil[18,19]. In the present study, the pitch-selective neurons had characteristic frequencies that were mostly below 800 Hz (Fig. 2b) and, given the correspondence between characteristic frequency and preferred missing fundamental frequency (Fig. 3b), this closely matches the human perceptual limit of missing fundamental pitch[20]. Responses at higher best-modulation frequencies (2–3 kHz) were observed in previous studies investigating periodicity-encoding in gerbil auditory cortex[18,19]. Another difference between these studies was the frequency range of harmonics to which neurons responded. In our study, only MFs

containing harmonics below ~5 kHz evoked significant responses in most pitch-selective neurons (Fig. 4d). This matches the upper frequency limit of an MF's harmonics for its pitch to be perceivable by humans[1]. In contrast, the carrier frequencies of sAM tones used in previous studies investigating periodicity responses in gerbil auditory cortex[18,19] were above 5 kHz. Finally, a crucial distinction between the present study and previous work was the sound level at which MF and sAM acoustic stimuli were delivered, respectively. When the ear is stimulated with two tones (f_1 and f_2), combination tones ($2f_1 - f_2$, $f_2 - f_1$, and so on) are generated by the non-linear mechanics of the cochlea[1]. Psychophysical studies show that missing MFs with two components generate combination tones at the f_0 that are 20–25 dB lower than the sound level of individual components[21]. The magnitude of this combination tone increases by 3 dB for every doubling of the number of components. Physiological studies in the inferior colliculus of guinea pigs[22] suggest that combination tones at the f_0 can be produced in the range of 17–34 dB below the sound level of the carrier of an amplitude-modulated tone. To avoid the confound of neural responses evoked by combination tones, we strictly limited the sound level of the individual components of MFs used in our experiments to be no more than 10 dB above the neuron's tone response threshold at its characteristic frequency. The outer ear provides an additional amplification to the harmonics of the MF and may affect our estimation of the sound level of combination tones. Although the spectral-specific gain of the outer ear has not been measured in the marmoset, other animal models indicate that the gain increases with frequency (over the frequency range 100–5,000 Hz) with a maximum relative gain between high frequencies and low frequencies of about 10 dB. More than 75% of the pitch-selective neurons (40/53) responded significantly to an MF when the
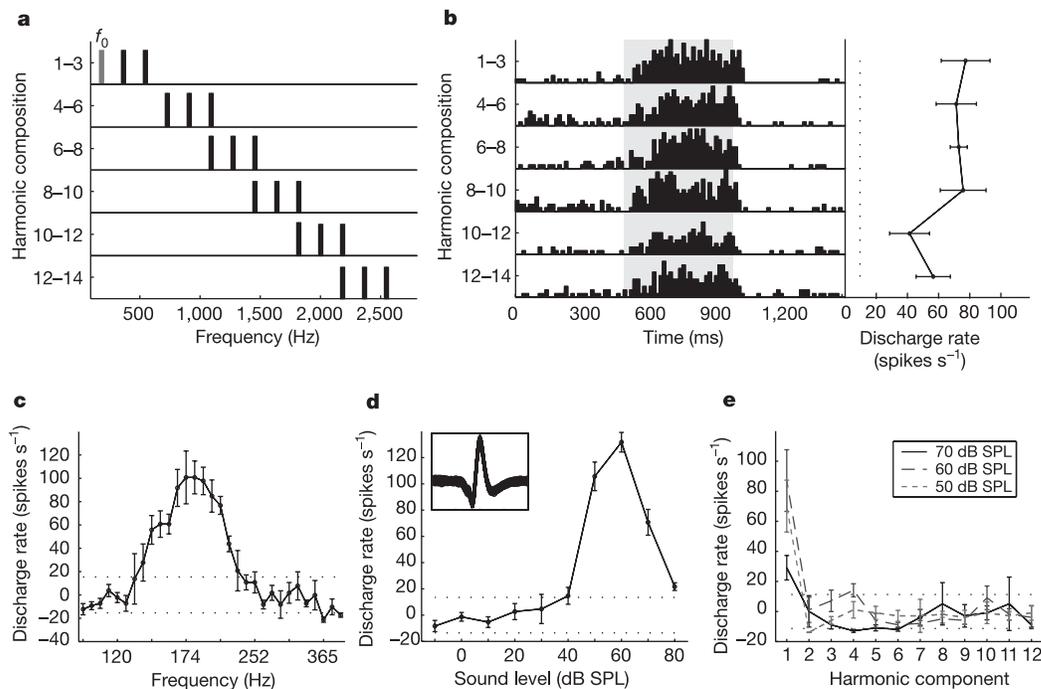
Figure 1 | **An example of a pitch-selective neuron (unit M36n-532).** Error bars represent standard error of the mean (s.e.m.). The dotted black lines indicate the significance level for discharge rate (± 2 standard deviations away from the spontaneous discharge rate). **a**, Frequency spectra of a series of harmonic complex stimuli. The fundamental frequency component (f_0) and its higher harmonics have equal amplitudes of 50 dB SPL. **b**, Peristimulus time histogram (left) and tuning curve (right) of the neuron's response to the stimuli in **a**. Stimuli were presented from 500 to 1,000 ms (indicated by the shaded region on the left plot). **c**, Frequency

tuning of the neuron derived from pure tones. **d**, Response of the neuron to a pure tone at characteristic frequency (182 Hz) across sound levels (rate-level function). Inset plot shows an overlay of 2,434 digitized action potentials recorded from this neuron (displayed within a 2 ms window). **e**, The neuron's responses to individual harmonics (number 1–12) at three sound levels, respectively. All the harmonics above the f_0 component (first harmonic) were outside the neuron's excitatory frequency response area, and did not elicit significant responses. SPL, sound pressure level.

individual components were set at the neuron's pure tone sound level threshold at its characteristic frequency (Fig. 5a); a situation where combination tones at the neuron's characteristic frequency would be at least 20 dB below its response threshold (or 10 dB assuming the maximum outer-ear differential gain between f_0 and the harmonics of the MF) as estimated by previous studies[21,22]. As such, the procedures implemented in the present study ensure that the MF responses reported here are not the result of combination tones. Previous studies[18,19] employed sAM tones delivered at 30 dB or more above a neuron's sound level threshold, making the interpretation of the reported periodicity representation difficult.

Combination tones can be perceptually masked by spectrally overlapping band-pass noise[1]. We compared responses to MFs with and without a noise masker for a subset of pitch-selective neurons ($n = 20$). The masker was generated using 1–2 octave band-pass noise centred at the f_0 of the MF and at a sound level −10 to +10 dB

relative to the levels of individual components of the MF. None of the pitch-selective neurons studied failed to respond significantly in the presence of the noise masker (Fig. 5b). The approximate 50:50 ratio of neurons whose discharge rates increased or decreased in the presence of the noise masker may be due to the proximity of this cortical pitch area to both the core and belt regions of auditory cortex that show preferences for tonal or noisy sounds, respectively[23]. Less than half of the neurons from Fig. 5b that were tested responded significantly to the noise masker when it was played alone (Supplementary Fig. 5a, b).

Magnetoencephalography studies in humans suggest both a parallel[24] and orthogonal[25] topographical organization of pitch relative to the cochleotopic map in AI. In addition, a recent optical imaging study in gerbils[19] has suggested a horseshoe-shaped topographical map for periodicity that is superimposed on a linear cochleotopic map. Due to the small size of the cortical area containing pitch-selective neurons ($\sim 1 \, mm^2$) (Fig. 2a, Supplementary Fig. 2a, b), we could not determine any topographical arrangement of best pitch encoded by these neurons. Pitch-selective and non-pitch neurons within this region had characteristic frequencies spanning the same frequency range (Fig. 2b). However, given that non-pitch neurons encoding low frequencies are present in the same region of auditory cortex, these data support a parallel topographical representation of pitch and frequency. The two characteristic frequency distributions were significantly different ($P = 0.0251$, Wilcoxon rank-sum test) with pitch-selective neurons biased towards lower-frequency characteristic frequencies; however, bandwidth and peak latency were not significantly different between these two groups of neurons. While the range of characteristic frequencies encountered from pitch-selective neurons fell below the f_0 of most marmoset vocalizations

Figure 2 | **Location and characteristic frequency distribution of the pitch area in marmoset auditory cortex. a**, Characteristic frequency topographical map from the left hemisphere of one marmoset. Pitch-selective neurons (black squares) were found clustered near the anterolateral border of AI. Frequency reversals indicate the borders between AI/R and R/RT (rostral temporal field). **b**, The characteristic frequency distribution from pitch-selective and non-pitch neurons within the pitch area of three marmosets. M, medial; C, caudal; L, lateral; R, rostral; CF, characteristic frequency.

Figure 3 | **Pitch-selective neurons share a similar tuning for pure tones and MFs. a**, An example of an individual pitch-selective neuron's tuning to pure tone frequency and the fundamental frequency of MFs respectively. (unit M2p-201) **b**, A comparison of the characteristic frequency and the best missing-fundamental frequency responses from 15 pitch-selective neurons. The Spearman correlation coefficient (r) is displayed on the plot and is statistically significant ($P < 0.05$).
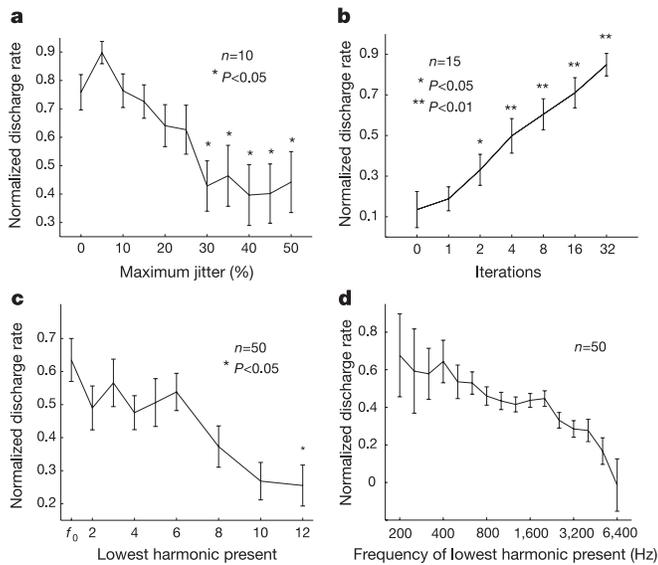
Figure 4 | Pitch-selective neurons are sensitive to pitch salience. Error bars represent s.e.m. Statistical significance was determined using Wilcoxon rank-sum test. Responses were normalized by the maximum response elicited within the stimulus set. **a**, Averaged population response of pitch-selective neurons to irregular click trains as a function of maximum jitter. The response to a regular click train was used as a reference for statistical comparison at other jitter values. **b**, Averaged population response as a function of the iterations of IRN stimuli. The response to IRN stimuli with 0 iterations was used as a reference for statistical comparison at other iterations. **c**, Averaged population response as a function of the lowest harmonic presented in the MF stimuli. The reference for statistical comparison was harmonic complex sounds with their fundamental frequency present. **d**, Averaged population response as a function of the frequency of the lowest harmonic presented in the MF stimuli.

Figure 5 | MF responses are not caused by combination tones.
a, Distribution of sound level threshold for individual components of the MF response relative to the sound level threshold for a pure tone response at the neuron's characteristic frequency. Inset plot shows rate-level functions from a pitch-selective neuron (unit M41o-294) for pure tones and MFs. The two dotted lines indicate two standard deviations from the spontaneous discharge rate. Error bars represent s.e.m. **b**, Scatter plot comparing responses to MFs with and without the presence of a noise masker for 20 pitch-selective neurons. All the neurons tested had significant discharge rates for both conditions. The two dotted lines parallel to the axes indicate two standard deviations (s.d.) from the spontaneous discharge rate. The diagonal line has a slope of 1.

(4–8 kHz), marmosets produce several call types (for example, 'egg' call, $f_0 \approx 800$ Hz) that have fundamental frequencies near the upper range of the characteristic frequencies of pitch-selective neurons[26]. It is important to note that marmosets hear sounds containing harmonic structure from other animals and the environment in their natural habitat.

The cortical region containing pitch-selective neurons appears to be on the border of core areas AI and R, and lateral belt areas AL (anterolateral) and ML (middle lateral), without spanning the entire tonotopic representation of any one of these four areas. This may be a frequency-specific and functionally specialized area of auditory cortex in primates, analogous to areas of auditory cortex of the mustached bat (*Pteronotus parnellii*) that contain combination-sensitive neurons[27].

Lower-order harmonics of a complex tone are resolved by the auditory system, and the estimates of the frequencies of these components can be used to determine the pitch[28]. However, when the harmonics of a complex tone are not resolved by the auditory system, only the temporal information (repetition rate) of the acoustic waveform can be used to determine the pitch[29]. How marmosets perceive these MFs and, more specifically, to what extent they use spectral and temporal pitch mechanisms remains to be studied in future behavioural and physiological experiments. Given that the size of the cochlea is smaller in marmosets than in humans, it is probable that some of the lower-order harmonics resolved in the human are unresolved in the marmoset. As such, the MF responses that we observed were most probably evoked by both resolved and unresolved harmonics. Spectral and temporal processing strategies may ultimately be unified in auditory cortex, providing a single central neural correlate for the perception of pitch.

METHODS

Animal preparation and recording. Details of experimental procedures can be found in recent publications from our laboratory[30]. Single-unit recordings were conducted in awake marmosets (subjects 1–3: M2p (left hemisphere), M36n (right hemisphere), M41o (left hemisphere)) sitting quietly in a semi-restraint device with their head immobilized, within a double-walled soundproof chamber (Industrial Acoustics) whose interior is covered by 3-inch acoustic absorption foam (Sonex). Because the auditory cortex of the marmoset lies largely on the lateral surface of the temporal lobe, high-impedance tungsten microelectrodes (3–5 MΩ) could be inserted perpendicular to the cortical surface. Electrodes were mounted on a micromanipulator (Narishige) and advanced by a manual hydraulic microdrive (Trent Wells). Action potentials were detected on-line using a template-based spike sorter (Multi-Spike Detector; Alpha Omega Engineering) and continuously monitored by the experimenter while data recording progressed. Typically 5–15 electrode penetrations were made within a miniature recording hole (diameter ~1 mm), after which the hole was sealed with dental cement and another hole opened for new electrode penetrations. Neurons were recorded from all cortical layers, but most commonly from supragranular layers.

Generation of acoustic stimuli. Acoustic stimuli were generated digitally and delivered by a free-field loudspeaker located one metre directly in front of the animal. All sound stimuli were generated at a 100 kHz sampling rate and

low-pass filtered at 50 kHz. Harmonic artifacts were at least 43 dB lower than the fundamental at 80 dB SPL (sound pressure level). The difference grew as the sound level of the fundamental decreased. The sound level of individual frequency components used in this study was no higher than 80 dB SPL.

Frequency tuning curves and rate-level functions were generated using pure-tone stimuli of 200 ms in duration with interstimulus intervals of >500 ms, and had a minimum of 5 repetitions. MF, IRN, and click-train stimuli were 500 ms in duration with intertrial intervals of least 1 s, and had a minimum of 10 repetitions. All stimuli were presented in a randomly shuffled order. Pure-tone stimuli intensity levels were generally 10–20 dB above threshold for neurons with monotonic rate-level functions, or at preferred levels for non-monotonic neurons. Harmonic complex tones were composed of 3 or 9 components in either cosine or Schroeder negative phase. The individual components of all harmonic complex tone stimuli were presented at no more than 10 dB above the neuron's sound level threshold at its characteristic frequency. Components of the MF were considered outside the neuron's excitatory frequency response area if each component, when played individually at 0, +10 and +20 dB relative to its sound level within the harmonic complex, did not evoke a significant response. Sound levels were varied in 10 dB steps.

Noise maskers were typically 1–2 octave band-pass noise centred at the missing fundamental frequency (near the unit's characteristic frequency). The sound level of the noise masker ranged from +10 to −10 dB relative to the individual harmonics. Noise maskers were played simultaneously with MFs.

Regular click trains had inter-click intervals equal to $1/f_0$ where f_0 was the preferred fundamental frequency of the neuron. Rectangular clicks (broadband) or narrowband clicks made of brief pulses of white noise or a tone (at an integer multiple of the f_0) were used to generate click trains. Rectangular click trains had a width of 0.1 ms while narrowband clicks[30] had each pulse windowed by a gaussian envelope with a sigma of 0.1–0.4. An irregular click train was constructed by shifting each click of a regular click train relative to a previous click by an amount of time proportional to the ISI and randomly selected from a uniform distribution $S_x = [-J,J]$, where J equals the maximum possible jitter. The maximum jitter in the irregular click train stimulus set was varied between 5 to 50%.

Generation of cortical characteristic frequency maps. Single units with significant neuronal discharges to tones, band-pass noise, or other narrowband stimuli (for example, sAM, sFM) were used to generate cortical characteristic frequency maps. The characteristic frequency of each location on the map is determined by the median characteristic frequency of all electrode tracks within 0.25 mm. Electrode track characteristic frequencies were calculated by computing the median characteristic frequency of units within the track.

Data analysis. The mean spontaneous discharge rate was subtracted during the calculation of a neuron's mean driven discharge rate over the entire duration of the stimulus. Mean driven discharge rates greater than 2 standard deviations above the spontaneous discharge rate were considered significant. The peak MF response from every pitch-selective neuron was also determined to be significant ($P < 0.05$) using a Wilcoxon rank-sum test.

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