A novel mechanism of cochlear excitation during simultaneous stimulation and pressure relief through the round window

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The round window (RW) membrane provides pressure relief when the cochlea is excited by sound. Here, we report measurements of cochlear function from guinea pigs when the cochlea was stimulated at acoustic frequencies by movements of a miniature magnet which partially occluded the RW. Maximum cochlear sensitivity, corresponding to subnanometre magnet displacements at neural thresholds, was observed for frequencies around 20 kHz, which is similar to that for acoustic stimulation. Neural response latencies to acoustic and RW stimulation were similar and taken to indicate that both means of stimulation resulted in the generation of conventional travelling waves along the cochlear partition. It was concluded that the relatively high impedance of the ossicles, as seen from the cochlea, enabled the region of the RW not occluded by the magnet, to act as a pressure shunt during RW stimulation. We propose that travelling waves, similar to those owing to acoustic far-field pressure changes, are driven by a jet-like, near-field component of a complex pressure field, which is generated by the magnetically vibrated RW. Outcomes of research described here are theoretical and practical design principles for the development of new types of hearing aids, which use near-field, RW excitation of the cochlea.

1. Introduction

The round window (RW) membrane acts as a pressure relief valve for the almost incompressible fluids of the cochlea, making possible movement of the stapes, and hence, movement of the inner ear structures. It has long been known [1] that cochlear function is impaired when the RW membrane is immobilized, thickened, congenitally malformed or absent [2–4]. These observations signify the physiological importance of the RW membrane for audition, and the necessity to retain it, which has been revealed during surgery of the middle and inner ear [5]. Traumatic damage or rupture of the RW membrane can cause hearing loss and deafness owing to perilymph aspiration or loss of the normal pressure-releasing function of a compliant RW [6–9].

It has been established that, while normal function of the RW is important for effective stimulation of the cochlea through the conventional oval window route, the cochlea can be stimulated successfully in non-conventional ways (e.g. through bone conduction, through the RW and through perforations in the cochlea’s apical turn). All of these techniques produce similar patterns of cochlear sensitivity and excitation [10–12]. In recent years, significant recovery of hearing thresholds has been achieved in human patients using active middle ear implants (vibrating electromechanical devices) to stimulate the cochlea through the RW at the frequencies of the incoming sound [13–17]. The RW approach could be an effective and preferable alternative to conventional hearing aids for hearing rehabilitation in patients with, for example, chronic inflammatory middle ear diseases, recurrent...
cholesteatoma, when the anatomy of the middle ear is highly distorted [14], and for patients with congenital malformations of the outer and middle ear, i.e. in cases of conductive hearing loss. In the latter situation, dysplasia and immobilization of the ossicles, often in combination with malformations of the oval window, can make hearing reconstruction through the oval window impossible. The feasibility of the RW approach for the above disorders, and for conditions when the oval window is inaccessible, has been demonstrated in successful attempts to combine outer and middle ear reconstruction with implantation of active middle ear prostheses on the RW [13,15,16]. An understanding of the mechanisms of cochlear excitation through the RW is essential to ensure that the technique is to be predictable and effective in the clinic.

One uncertainty relates to the mechanisms of basilar membrane (BM) excitation using probes that cover only a part of the RW membrane, whereby the area of the RW not covered by the probe provides an effective pressure shunt [11, p. 197]. This might make excitation of the cochlea problematic through shunting pressure changes that would otherwise excite the BM. Mobility of the stapes is probably not essential for successful cochlear excitation through the RW if most of the pressure relief is provided by the non-occluded area of the RW. This paper deals with the mechanisms of cochlear excitation, using a miniature magnet that only partially occludes the RW. With the stapes mobility decreased, a novel form of cochlear excitation is achieved with a sensitivity that matches that of conventional acoustic stimulation.

2. Material and methods

Pigmented guinea pigs (280–390 g) were anaesthetized with the neurolept anaesthetic technique (0.06 mg kg\(^{-1}\) body weight atropine sulfate s.c., 30 mg kg\(^{-1}\) pentobarbital i.p., 500 \(\mu\)g kg\(^{-1}\) Hypnorm i.m.). Additional injections of Hypnorm were given every 40 min. Additional doses of pentobarbitone were administered as needed to maintain a non-reflective state. The heart rate was monitored with a pair of skin electrodes placed on both sides of the thorax. The animals were tracheotomized and artificially respired, and their core temperature was maintained at 38°C with a heating blanket and a heated head holder. The middle ear cavity of the ear used for the measurements was opened to reveal the RW. Compound action potentials (CAPs) of the auditory nerve were measured from the cochlear bony ridge in the proximity of the RW membrane using Teflon-coated silver wire (S in figure 1). Thresholds of the N1 peak for acoustic and RW stimulation were estimated offline using recording of the CAP using 50 averages.

For acoustic stimulation, sound was delivered to the tympanic membrane by a closed acoustic system comprising two Brueil and Kjaer 4134 1/2 inch microphones for delivering tones and a single Brueil and Kjaer 4133 1/2 inch microphone for monitoring sound pressure at the tympanum. The microphones were coupled to the ear canal via 1 cm long, 4 mm diameter tubes to a conical speculum, the 1 mm diameter opening of which was placed about 1 mm from the tympanum. The closed sound system was calibrated in situ for frequencies between 1 and 50 kHz. Known sound pressure levels were expressed in dB SPL, \(2 \times 10^{-5}\) Pa.

A neodymium iron boron disc magnet (M in figure 1; diameter 0.6 mm, thickness 0.2 mm) was placed on the surface of the round window (RW). C labels a miniature coil situated above the magnet. S denotes a Teflon-coated silver wire used for recording of activity of the auditory nerve. IS indicates incudostapedial joint.

Figure 1. Schematic view of the cochlea (CH) through a lateral opening in the temporal bone. M indicates a neodymium iron boron disc magnet (diameter 0.6 mm, thickness 0.2 mm) placed on the surface of the round window (RW). C labels a miniature coil situated above the magnet. S denotes a Teflon-coated silver wire used for recording of activity of the auditory nerve. IS indicates incudostapedial joint.

magnetic field created by alternating current through the coil. Stimulation current through the coil was generated by a Data Translation 3010 board, attenuated and fed to the coil through a current buffer. Maximum voltage applied to the coil in this study was 10 V which corresponded to 0 dB attenuation. High-frequency cut-off of the system for electrical stimulation in situ was above 100 kHz. No signals associated with the coil current were recorded in the absence of the magnet which confirms an absence of electrical interference between the coil and the CAP electrode. The efficacy of the floating magnet RW stimulation varies between preparations (see below). The floating magnet does not, however, impose a variable DC load on the RW, which undergoes large, slow, periodic, movements caused by middle ear muscle contraction in anaesthetized animals. This would not be the case for probes that use a rigid lever in contact with the RW, which would provide a variable DC load depending on the phase of the large RW movement, with the possibility of causing damage to the RW.

Displacements of the magnet and the stapes were measured using a displacement-sensitive laser diode interferometer without the need for reflective beads [19]. The beam of the interferometer was focused centrally on the exposed surface of the magnet or the head of the stapes. The output signal of the interferometer was processed using a signal conditioning amplifier, digitized at 250 kHz with a Data Translation 3010 board, and instantaneous amplitude and phase of the wave were recorded and averaged 10 times using a digital phase-locking algorithm.

Voltage signals to the coil were sinusoidal stimuli of 40 ms in duration (with 110 ms between stimuli) shaped with raised cosines of 0.5 ms duration at the beginning and at the end of each sinusoidal pip. All acoustic stimuli in this work were shaped with raised cosines of 0.5 ms duration at the beginning and at the end of stimulation. White noise for acoustical calibration and tone sequences for auditory and mechanical stimulation were synthesized by a Data Translation 3010 board at 250 kHz and delivered to the microphones or to the coil through low-pass filters (100 kHz cut-off frequency). Signals from the acoustic measuring amplifier were digitized at 250 kHz using the same board and averaged in the time domain. Experimental control, data acquisition and data analysis were performed using a PC with programs written in TestPoint (CEC, MA, USA). All procedures involving animals were performed in accordance with UK Home Office regulations with approval from the local ethics committee.
generates a volume velocity of cancelling piston sources. The sum of that owing to a fixed oval window and that owing to two pistons with volume velocities of the RW.

This will depend on the stiffness, which is the same throughout the cochlea. The magnitude of then made up of two components.

The RW is assumed to be driven by a piston (magnet) over a part of its area and the remaining part of the RW is flexible and generates an equal and opposite volume velocity, because the fluid is assumed to be incompressible and the cochlear wall is rigid. The internal pressure in the cochlea is thus made up of two components.

The first component is an average alternating pressure, $P_M$, which is the same throughout the cochlea. The magnitude of this will depend on the stiffness, $S$, of the freely moving area of the RW. $P_M$ is required to be large enough to force this area to have a volume velocity equal and opposite to that of the driving piston. The force on the freely moving part is thus $Sx$, where $x$ is its mean displacement. Its volume velocity, $q$, is thus $i\omega A x$, where $A$ is the freely moving area and $\omega$ is the stimulation frequency. Because the force on the freely moving part is equal to $P_M A$, we can define

$$P_M = \frac{Sq}{i\omega A^2}. \quad (3.1)$$

Because the average pressure is uniform throughout the volume, it does not cause any excitation of an incompressible cochlear partition. It is worth noting that if the stiffness, $S$, of the freely moving area of the RW is small then the mean pressure generated within the fluid volume is also small.

Even if the volume velocity of the freely moving part of the RW is equal and opposite to that of the piston, the second pressure component, a near-field pressure, is generated close to the RW. This is due to the pressure required to accelerate the fluid from below the piston into the freely moving part of the RW and is thus dependent on the fluid inertia. The spatial distribution of this near-field pressure will depend on the details of the geometry, but its magnitude will be proportional to the fluid density, $\rho$, and to the acceleration of the piston, $i\omega q$. An indicative overall magnitude of $P_N$ can then be defined as

$$P_N \propto i\omega q. \quad (3.2)$$

For a given piston volume velocity, the average pressure (equation (3.1)) decreases with increasing the stimulation frequency, whereas the average near-field pressure (equation (3.2)) increases with the frequency.

It is worth noting that if the cochlear wall is not perfectly rigid, for example if the stapes is not completely fixed, then the internal pressure also generates a volume velocity on the oval window, as illustrated in figure 2a. This would generate a pressure component owing to the flow of fluid across the cochlea that would depend on the fluid inertia rather than on the stiffness of the window. A near-field pressure would then be generated in the vicinity of both the oval window and the RW.

The on-axis near-field pressure, $P_N$, owing to RW stimulation can be estimated using a simple model of cancelling piston sources. The assumed geometry is shown in figure 2b in which an inner piston with a radius of $a_1$ has a velocity of $v_1$ and an annular piston with an inner radius of $a_1$ and an outer radius of $a_2$ has a velocity of $v_2$.

The volume velocity of the inner piston thus is

$$q_1 = \pi a_1^2 v_1, \quad (3.3)$$

and that of the outer piston is

$$q_2 = \pi (a_2^2 - a_1^2) v_2. \quad (3.4)$$

If the cochlea is sealed, then the volume velocities are equal and opposite so that $q_2 = -q_1$, and the ratio of the two

![Figure 2](http://rsif.royalsocietypublishing.org/)

*Figure 2. Pressure distribution during cochlear stimulation through partially occluded RW. (a) Pressure distribution in presence of a mobile stapes. The effect of the mean internal pressure on an imperfectly fixed stapes is to generate a small volume velocity, $-\alpha q$, where $\alpha < 1$. In this case, the freely moving area of the RW generates a volume velocity of $-(1 - \alpha)q$ and these two components cancel the volume velocity, $q$, of the driving piston on the RW. Then, the internal pressure is the sum of that owing to a fixed oval window and that owing to two pistons with volume velocities $+\alpha q$ and $-\alpha q$ on either side of the volume. (b) Sketch of cancelling piston sources.*
linear velocities must be

\[ \frac{v_2}{v_1} = \frac{a_1^2}{a_2^2 - a_1^2} \]  

(3.5)

which is plotted in figure 3.

Assuming free-field conditions, the complex on-axis pressure a distance of \( r \) from a single piston of radius \( a \) vibrating with velocity \( v \) is given [20] as

\[ p(r) = -\rho cv (e^{-iv\sqrt{r^2 + a^2}} - e^{-ivr}), \]  

(3.6)

where \( k = 2\pi/\lambda \) is the wavenumber, \( \lambda \) is the acoustic wavelength and \( c \) is the speed of sound in the fluid. The distance between the RW and the BM, which is less than 1 mm in both guinea pigs and humans [21], is much smaller than the wavelength, which is equal to about 1.5 m at 1 kHz assuming a speed of sound of 1500 m s\(^{-1}\) in the cochlear fluid. Hence, we can assume \( \lambda \gg r \), and

\[ kr = \frac{2\pi r}{\lambda} \ll 1. \]  

(3.7)

In this case, we can take the first-order series approximation to the exponentials in equation (3.6) to give the pressure owing to the inner piston as

\[ p_1(r) \approx ipo a_1 \left( \sqrt{r^2 + a_1^2} - r \right). \]  

(3.8)

The pressure due to the annular piston is equal to that due to a piston of radius \( a_2 \) and velocity \( v_2 \) minus that due to a piston of radius \( a_1 \) and velocity \( v_1 \)

\[ p_2(r) \approx ipo a_2 \left( \sqrt{r^2 + a_2^2} - \sqrt{r^2 + a_1^2} \right). \]  

(3.9)

The total near-field pressure \( P_N(r) \) is the superposition of those owing to the inner and outer pistons in equations (3.8) and (3.9) with \( v_2/v_1 \) given by equation (3.5)

\[ P_N(r) = ipo a_1 \left[ \frac{\sqrt{r^2 + a_1^2} - r}{a_2^2 - a_1^2} \left( \sqrt{r^2 + a_2^2} - \sqrt{r^2 + a_1^2} \right) \right]. \]  

(3.10)

Although this expression is not strictly valid in the present case unless the near-field pressure has died away over the width of the cochlea, the modulus of equation (3.10) is plotted in figure 4 as a function of distance from the centre of the source distribution, \( r \), for various values of \( a_1/a_2 \) and with a constant value of \( v_1 \). The pressure drops quickly with the distance from the piston, especially for small \( a_1/a_2 \), but the shortest distance between the RW and the BM is also only 0.2 mm in guinea pigs [21]. Hence, excitation of the cochlea with a magnet that covers just a part of the RW is possible by the near-field pressure in the vicinity of the RW. A natural consequence of the simple model of canceling piston sources is higher near-field pressure for larger \( a_1/a_2 \) ratios for constant piston velocity. In the real cochlea, however, the RW piston velocity is likely to drop for larger \( a_1/a_2 \) ratios as a consequence of an increase in cochlear impedance as seen by the piston. A model is needed, which takes into account this effect and measurements of the RW impedance for different proportions of the RW covered by the magnet, in order to find an optimum \( a_1/a_2 \) ratio which provides the most efficient stimulation of the cochlea through the RW. It also should be noted that within the validity of equation (3.10), the total near-field pressure \( P_N(r) \) is proportional to the acceleration of the inner piston. The BM is a pressure detector [22], it should, therefore, be expected that BM stimulation is proportional to piston acceleration.

3.2. Placement of magnet on the round window
does not alter the sensitivity of the cochlea
to acoustic stimulation

The cochlear neural threshold to acoustic stimulation, measured as a threshold for the N1 peak of the CAP, did not change after placement of the magnet on the RW and during the entire experiment (up to 3 h after the placement; figure 5). It is well established that increases in the impedance of the RW leads to elevation of the hearing threshold [1], thus the observed stability of the CAP thresholds after placement of the magnet revealed that the RW impedance did not increase and the area of the RW not covered by the magnet could provide effective pressure relief at acoustic frequencies when the cochlea is stimulated conventionally. The RW impedance is much lower than any other leakage impedance in the cochlea [23]. Thus, in view of the stability of the N1 thresholds following placement of the magnet, we can conclude that the RW...
Figure 5. Thresholds of acoustic stimulation (dB SPL) versus frequency (kHz) for N1 peak of the CAP of the auditory nerve measured before (open symbols) and 2.5 h after (filled symbols) placement of the magnet on the RW.

Figure 6. Displacement of the RW magnet as a function of voltage applied to the coil for three different stimulus frequencies (5, 10 and 20 kHz) measured in situ on the RW of a single preparation. The data at each frequency are pooled and normalized from measurements at different gains of the signal conditioning amplifier.

impedance remained the smallest impedance in the system, even after this manipulation.

3.3. Frequency dependence of neural thresholds in response to round window and acoustic stimulation are similar

The coil voltage–magnet displacement relationship was linear in all six preparations where this characteristic was studied (an example is given in figure 6). In all preparations, the frequency dependence of the magnet displacement resembled that of a low-pass filter with the high-frequency slope being between 12 and 18 dB per octave (figure 7a). A slope of 12 dB per octave is to be expected if the magnet is behaving as a mass subject to a constant force caused by the magnetic field. In this case, the magnet acceleration should not depend on frequency, which is indeed observed for most of the frequency range used in this study (figure 7b). Because the high-frequency cut-off of the system for electrical stimulation was above 100 kHz, the relatively steep high-frequency slope of the coil voltage–magnet displacement relationship for frequencies below 10 kHz (figure 7a) most likely reflects the multiple degrees of freedom of the mechanical system formed by the inductively coupled coil and the magnet inertia, together with the RW and the cochlear fluid.

There were no major differences between CAP threshold curves for acoustic stimulation between all preparations used in this study (figure 7c). However, in the same preparations, CAP threshold curves expressed as a function of the coil voltage required to generate threshold CAP for magnetically driven RW stimulation varied by approximately 10 dB over the 8–20 kHz range (figure 7d). Likely, bases for these CAP threshold variations could include differences between preparations in the relative position of the magnet and the coil and to slightly different locations of the magnet on the RW. The smallest coil voltages required to generate the threshold CAP was observed for frequencies between 10 and 11 kHz. Taking into account the linearity of the magnet displacement (figure 6), the corresponding magnet displacements for the threshold coil voltage could be readily derived from the isovoltage response curves at 10 V (figure 7a) and the CAP threshold curves (figure 7d) using the following equation: displacement at threshold = displacement at 10 V/10^attenuation at threshold/20). The derived magnet displacement threshold curves (figure 7e) reveal that the sensitivity of the guinea pig cochlea to RW stimulation is in the subnanometre range. Maximum sensitivity, which corresponds to the smallest magnet displacements at threshold, was observed for frequencies around 20 kHz, which is similar to the frequency of maximum sensitivity for acoustic stimulation (figures 5 and 7c, note different frequency ranges in these figures). The absolute sensitivity of the magnet displacement threshold curves varied between preparations (figure 7e), probably, as pointed out above, because of variations between preparations in the relative locations of the coil, the magnet and the RW membrane. Magnet displacement threshold curves within the range of those shown in figure 7e were obtained for three further preparations but, for clarity, are not shown.

Near-field pressure, which is likely to excite the BM responses in our experiments, is proportional to the acceleration of the magnet (figure 7f) which, at threshold, was calculated from the threshold displacement (figure 7e). The threshold acceleration changes only by about 20 dB within the frequency range studied (figure 7f). This change corresponds better to the changes in the threshold SPL for acoustic stimulation within the same frequency range (figure 7c), whereas threshold displacement changes by more than 40 dB for the same frequencies (figure 7e). This last observation provides an additional confirmation that, in our experiments, the BM is excited by the near-field pressure which is proportional to the magnet acceleration.

3.4. Latencies of neural responses to acoustic and round window stimulation are similar

To gain insights into the mechanisms by which the cochlea is excited through RW stimulation, we compared the CAP latencies for suprathreshold stimulation within 10 dB above the thresholds for acoustic and RW stimulation of the cochlea (figure 8). The latencies were essentially the same. The CAP latency for low-level acoustic stimulation depends on the travelling wave delay and is inversely related to the characteristic frequency of the fibre [24]. Hence, we can conclude that the
mechanisms of energy propagation to the characteristic frequency place were similar for both acoustic and RW stimulation.

3.5. Increase in the stapes impedance does not affect efficiency of cochlear stimulation through the partially occluded round window

As suggested previously, the relatively high acoustic impedance of the middle ear ossicles (as seen from the cochlea), combined with a magnet that only partially occluded the RW, may allow the region of the RW not covered by the magnet to act as a pressure shunt during RW stimulation. It may thus be suggested that stapes mobility plays little or no role in the stimulation of the cochlea through the RW. Indeed, when the cochlea was excited through the RW, movements of the stapes at the frequency of stimulation were observed above the noise floor of the interferometer only at low frequencies less than 7 kHz and high stimulation amplitudes (figure 9a,b). Preparations with the largest and smallest stapes responses are shown in figure 9a,b. Similar results were observed in two further preparations. When the stapes’ impedance was increased by filling the ear canal with superglue, and stapes displacements could not be detected above the noise floor of the interferometer, regardless of the frequency and magnitude of the control voltage to the stimulating coil (figure 9a,b), thresholds of the RW elicited CAPs before and after increase in the stapes impedance were largely similar (figure 9c). According to this observation, it is suggested that stapes mobility is not required for effective excitation.

Figure 7. Magnet displacement and neural thresholds as a function of the stimulation frequency in three representative preparations. (a) Frequency dependence of the magnet displacement at constant voltage (10 V) applied to the coil. (b) Frequency dependence of the magnet acceleration at constant voltage (10 V) applied to the coil calculated from data at panel (a). (c) CAP thresholds during acoustic stimulation. Note a shorter frequency range than in figure 2. (d) Dependence of the coil voltage to generate threshold CAP during the RW stimulation. (e) Corresponding magnet displacement at the CAP threshold. (f) Corresponding magnet acceleration at the CAP threshold calculated from data at (e).
of the cochlea in our experimental configuration, i.e. when relatively large part of the RW was not occluded.

4. Discussion

On the basis of CAP threshold measurements at stimulus frequencies that span almost its entire auditory range, the guinea pig cochlea is sensitive to subnanometre displacements and minute accelerations of the RW (figure 7). The CAP data, set in the context of a model of cochlear stimulation through the partially occluded RW, support the viability of RW stimulation as an effective route for exciting the mammalian cochlea, further building on previous studies of the mechanical properties of the cochlea and recent work concerning the implementation of RW implantable hearing devices [13, 25, 26]. Quantification of the RW transducer displacement/acceleration presented here provides parameters essential for the design of future devices, although these parameters vary within individuals (figures 7 and 9). These factors may include the shape of the transducer and the area of the RW it covers. Most significant is whether the transducer completely covers the RW, as demonstrated by other groups [27–29], or leaves an RW area partially free [26, 30–32]. The outcome of our experiments reveals that partial coverage of the RW may not affect RW impedance sufficiently to affect cochlear stimulation with the exposed portion of the RW membrane acting as a pressure shunt (figure 5). Complete coverage would probably remove this shunt, possibly resulting in a different mechanism of BM stimulation.

Our experiments demonstrate that middle ear prostheses, which partially cover the RW, can be used effectively for simultaneous cochlear stimulation and pressure relief through the RW. The existence of a ‘third window’ (an additional pressure shunt, $Z_{3SV, 3ST}$; figure 10) in the cochlea has been postulated to account for the efficiency of RW stimulation because of the relatively high impedance, as seen from the cochlea, presented by the ossicles [30]. The proposed identity of the third window ranges from the vasculature of the cochlea to the cochlea and vestibular aqueducts [17, 30]. Evidence for the existence of the third window and its ability to shunt pressure is claimed from experiments in which the RW membrane is completely blocked during normal acoustic stimulation or the stapes is immobilized and the cochlea is stimulated through the RW route. Despite blockage or fixation, the air conduction thresholds are raised by between 20 and 50 dB depending on the study cited [3, 30, 33–35]. However, even the comparatively low experimental value of a 20 dB rise in threshold level is significant when compared with the low thresholds achieved in this study (figure 9). Additionally, it is unlikely that a hypothetical third window is responsible and, indeed, required for pressure relief in our experiments. The RW impedance ($Z_{RW}$; figure 10a) is much lower than any other leakage impedance in the cochlea during normal acoustic stimulation [23], i.e. $Z_{RW} \ll Z_{3ST}$ and pressure at point N is determined mainly by $Z_{RW}$. Moreover, the neural thresholds are highly sensitive to increases in RW impedance [1]. In our experiments, the neural thresholds during acoustic stimulation did not change after the magnet placement (figure 5). We took this finding to indicate that the RW impedance remained the smallest impedance in the system even after this manipulation (i.e. $Z_{RW} \ll Z_{3ST}$ after the magnet placement) and provided an effective pressure shunt minimizing the pressure at point N (figure 10b) and the far-field pressure drop across the
impedance of the cochlear partition ($Z_{3,SV}$; figure 10b). This outcome might also be expected from the direct finding that intracochlear pressure differences between the scala vestibuli and scala tympani remained low during RW stimulation [23]. On the basis of our findings reported here, we propose that the pressure shunting occurred through the area of the RW which remained exposed. This proposal is also supported by the findings of Schraven et al. [32], who tested different sized actuator tips and their coupling to the RW. Schraven et al. [32] found that stimulation by actuators with tip sizes well below the dimensions of the RW resulted in reduced stapedial movements compared with those tips that covered most of the RW. This result could be accounted for if the free exposed area of the RW acted as a pressure shunt. This does not discount other ‘windows’ contributing to pressure relief but it is clear from results presented here that their contribution appears to be negligible in our experiments.

We found that CAP thresholds did not change after stapes impedance ($Z_{3,ST}$; figure 10b) was increased (figure 9). CAP threshold elevation was, however, observed in earlier studies using RW stimulation through a partially blocked RW [30]. Furthermore, where we found RW stimulation through the partially occluded RW elicited stapes displacements only at high intensities below 7 kHz, under similar stimulus conditions, Lupo et al. [30] observed stapes movement in chinchillas across a wider frequency range of 0.25–16 kHz. We suggest that tighter hydromechanical coupling between the RW transducer and the stapes, and consequent changes in the hydromechanical properties of the cochlea after stapes immobilization, may account for elevation of the CAP thresholds after stapes fixation observed by Lupo et al. [30]. Correspondingly, differences in transducer shape and the proportion of the RW covered may potentially account for differences in the transducer–stapes hydromechanical coupling reported in this study and by Lupo et al. [30].

Pretension of the RW, which can potentially increase stiffness of the exposed area of the RW, and hence the average pressure within the cochlear (equation (3.1)), can enhance stapedial movement during RW stimulation [31,36]. It is apparent that differences in the outcomes of different studies, including ours presented here, depend on a number of factors, including the choice of both the size and shape of the transducer and pretension of the RW. The finding by Stieger et al. [23] that the stapes velocity is not a good measure of the effectiveness of reverse stimulation of the cochlea might reflect sensitivity of the stapedial responses to variations in the parameters of RW stimulation mentioned above. Control of these parameters is important to ensure that mobility of the ossicular chain is reduced to levels that negate the need for additional intrusive procedures that might cause sensorineural hearing loss.

In our experiments, the RW provided an effective common pathway for both cochlear stimulation and pressure relief. Therefore, we conclude that the mode of cochlear excitation through the RW, in this case, is different from that observed during conventional, acoustical cochlear stimulation or RW stimulation, which does not allow pressure relief through the RW [28,29]. Our results together with direct measurements of the pressure in the cochlea during RW stimulation [23] using a transducer that leaves the RW partially exposed, indicate that under this condition the transducer displacement probably is not able to cause a far-field pressure difference between the cochlear scala, which is the normal stimulus for the cochlea [12]. Far-field pressure differences between the scalae are unlikely to be caused by the type of RW stimulation we used because of the high impedance of the ossicular chain, as seen from the cochlea [27,28], and pressure backflow around the transducer [11]. We propose, instead, that during RW stimulation through the partially occluded RW, the BM is stimulated via the near-field complex pressure generated in the vicinity of the RW (figure 4), i.e. a fluid-jet flow, which, however, results in the generation of conventional travelling waves along the cochlear partition. In this sense, the cochlear excitation in our experiments on the RW stimulation is similar to excitation due to rocking movement of the stapes, which creates only local pressure gradients/flow motion in the cochlea [37,38] resulting, nevertheless, in generation of the travelling waves and neural excitation [39,40]. In our experiments, the near-field pressure is proportional to the acceleration of the transducer which allows effective cochlear stimulation even at extremely small RW displacements at high frequencies. This conclusion should be taken into account during the design of hearing aid devices which stimulate the cochlea through the partially occluded RW. The near-field pressure variations will be limited to the vicinity of the RW membrane (figure 4), but the close spatial relationship between the RW and the BM [21] makes excitation of the BM by these localized near-field pressure variations possible. Once the BM is stimulated in the vicinity of the RW, a conventional travelling wave is generated along the cochlear partition, which is supported by our CAP recordings. This conclusion is based on our finding that the 12–25 kHz region of the cochlea, which is most sensitive to RW magnet stimulation (figure 7c,f), is located in the middle of the basal turn of the cochlea and this region is not adjacent to, or cannot be observed through the RW. Indeed, the CAP latency for low-level acoustic

Figure 10. Schematics of impedances of the cochlea during acoustic (a) and RW (b) stimulation. $Z_{3,SV}$ and $Z_{3,ST}$ are impedances of the cochlear partition and the open area of the RW respectively. $Z_{RW}$ is the stapes impedance as seen from the cochlea. $Z_{3,SV}$ and $Z_{3,ST}$ are impedances of ‘third windows’ in the scala vestibuli and scala tympani, respectively. $q$ indicates a volume velocity generated by stimulation.
stimulation, which depends on the travelling wave delay [24], is similar for both acoustic and RW stimulation (figure 8). Furthermore, CAP threshold tuning curves derived through acoustic (figures 5 and 7c) and RW magnet (figure 7e,f) stimulations have similar maxima in sensitivity between 12 and 25 kHz.

It should be noted that it is not essential for the excitation that the motion of the magnet is strictly piston-like. It is likely that the magnet underwent some rocking motion in our experiments. This possibility, however, does not affect our conclusion about the mode of cochlear excitation and, in terms of the model (figure 2b), simply corresponds to a different ratio \( \alpha_1/\alpha_2 \) which should still provide effective stimulation.

Our investigation of the mechanisms underlying cochlea stimulation through the RW using a transducer that partially covers the RW membrane has important significance for future clinical use of such devices. RW stimulation does not even require mobility of the ossicular chain, as demonstrated in this study, to provide input to the cochlea that is similar to that obtained acoustically in a ‘normal’ ear. RW stimulation does, however, involve a novel mechanism of generating travelling waves along the cochlear partition, which we believe has not previously been considered. Travelling waves are initiated as a consequence of near-field pressure in the immediate vicinity of the RW, rather than far-field pressure differences between the scala vestibuli and scala tympani.

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References