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A Hydrodynamic Model of an Outer Hair Cell

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A HYDRODYNAMIC MODEL OF AN OUTER HAIR CELL

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ABSTRACT

A 10 000 times enlarged hydrodynamic model of the outer hair cell sterocila in the inner ear was built. On the model it was possible to measure the force and the force direction for each individual hair as a function of the flow direction and velocity. Measurements were made at the mean flow velocity 10^{-2} m/s, which is equivalent to a flow velocity in the real ear of about 1 μm/s. The kinematic viscosity of the liquid used in the model was 10 000 times higher than the viscosity of perilymph to attain hydrodynamic equallity. Two different geometries for the sterocilia pattern were tested. First the force distribution for a W-shaped sterocilia pattern was recorded. This is the sterocilia pattern found in all real ears. It was found that the forces acting on the hairs were very regular and perpendicular to the legs of the W when the flow was directed from the outside of the W. When the flow was reversed, the forces were not reversed, but were much more irregular. This can eventually explain the half wave rectification of the nerve signals. As a second experiment, the force distribution for a V-shaped sterocilia pattern was recorded. Here the forces were irregular both when the flow was directed into the V and when it was directed against the edge of the V.

KEYWORDS

Hydrodynamic, model, outer hair cell, force measurements, sterocilia.

INTRODUCTION

Since von Békésy's experimental research (3-9) about the geometry of and nerve signals from the inner ear, many authors have described both theoretical and experimental work about cochlear mechanics. (1-2, 10-15) There have been mathematical models of the basilar membrane vibrations showing some correlation between the location of the maximum vibration amplitude and the frequency of the exitation. There has also been a lot of work done in the area of measuring the actual nerve signals from ears of different animals including humans.

The gap to fill now, is to connect the mechanical side of the sensory cells with the nerve signals from the cell. One way to explain the strange nerve signals coming out of the inner ear is to look at the individual forces, acting upon each hair of an outer hair cell, and see if the rectification of the nerve signals can be explained by the hydrodynamic forces on the sterocilia.

Another important question to answer is: why are the sterocilia of the outer hair cells placed in the form of W:s. In the present hydrodynamic model of the hair cell it is possible to fill in the missing hairs in the W to make it a V and measure the change in forces acting upon the sterocilia.

EXPERIMENTAL MODEL

To measure the forces and the force directions of each hair on a hair cell, a model was built. In the model the force and the force direction were measured by using hydrostatic manometers. Each hair was connected to four manometers and there were 102 hairs in the model, giving a total of 408 manometers. The geometry of the manometer connections can be seen in Figs. 1 and 2.

Figure 2 also shows the locations of the hairs relative to each other and the channel system going from the hairs and to the manometers. To make it possible to manufacture the channel system, the model had to be very much larger than the real hair cell, so the model was built in the scale 10 000:1. This means that the hairs became 50-100 mm:s long and 10 mm in diameter, and the total size of the model was about half a meter in diameter. See Fig. 3.

To get the same flow pattern in the model as in a real ear the fluid had to be about 10 000 times more viscous than the perilymph, if the density was the same. As model fluid a heavy lubricating oil was chosen with the viscosity at room temperature about 10 Ns/m^2 and with the density 900 kg/m^3.

The working principle for the model is, that a variator motor drives a wing-pump (Figs. 4 and 5). This gives a flow of oil through the hair cell hairs (see Fig. 4). The direction of the flow velocity can be changed to any direction from 0° to 360° by rotating the oil tank relative to the table and the hair cell, shown in Figs. 5 and 6. The flow gives a force on each hair. This force makes the hair tilt in the direction of the force. Through the bottom of each hair, see Fig. 1, oil comes into channel A from a hydrostatic oil pressure source. The same pressure source is connected to all the hairs with equally long tubes, so the pressure in channel A is the same for all hairs. The oil then flows through the 4 channels B and out to the manometers through the 4 channels C for each hair.

The level of the liquid in the manometers will then rise to different heights depending on the force and force direction on the hair. The hairs are not fitting exactly into the holes in the "hair cell", but have a radial clearance of 0,1 mm. This means that when the hydrodynamic flow force has tilted the hair over, so that the channel B is tightly connected with channel C, for instance at the left side of the hair in Fig. 1, the oil will flow into this manometer. The oil will also flow into the manometer at the opposite side of the hair through that channel B, but there a lot of the oil will leak away through the 0,2 mm clearance between hair and the hole in the hair cell. The oil level in the manometers will rise until the pressure at the connection point between channel B and channel C is such, that the hydrostatic forces acting upon the hair will balance the hydrodynamic forces from the outer flow. Then the hair will tilt back so that the leakage at the connection between the channels B and C will be exactly the same as the flow through the channel B. This means that the oil level in the manometer will be stationary.

The time, for the oil levels in the manometers to become stationary, was about 5 hours.

MEASURING TECHNIQUE

It was not possible to just start the apparatus, wait 5 hours and then make a set of measurements.

As the hairs were not standing on a point, but a circular ring, see Fig. 1, it was not possible to guarantee that zero force on the hair gave equally high pressures in all four manometers connected to the hair. To overcome this difficulty, all measurements were made as differential measurements. First the pressure was put on in the pressurizing system for 5 hours. The wing pump was not driven during that time. At the end of the pressurizing time the manometer readings were registered. Then the wing pump was put on, circulating the oil with a velocity which could be varied between zero and a maximum speed. The maximum speed was much higher than the speed in a real ear. (It was given by the maximum slope of the free oil surface). After 5 hours, pressure readings were made.

The force components on the hair, caused by the flow, were proportional to the second difference of the pressure. The flow force in the x-direction, see Fig. 7, was then

$$F_x = A[(p_2 - p_1)_{flow} - (p_2 - p_1)_{no\ flow}]$$

and in the y-direction

$$F_y = A[(p_4 - p_3)_{flow} - (p_4 - p_3)_{no\ flow}]$$

where A is a constant.

The constant A is the same for all hairs, as it is assumed that the nerve signals in a real ear will be caused by bending of the hairs and not so much by shearing of the hairs (the bending strains and stresses are 50-100 times higher than the ones caused by shearing).

The total hydrodynamic force on a hair was

$$F = F_x^2 + F_y^2$$

and the direction of the force was given by the angle

$$\alpha = \arctan (F_y/F_x)$$

MEASUREMENTS

The size and direction of the force on each hair is shown in Figs. 9 and 10 for the normal geometry. In Fig. 9 the flow is coming from the top of the figure, that is hitting the W from the outside. In Fig. 10, the flow comes from the bottom of the figure, that is hitting the W from the inside.

The forces acting on the hairs were very symmetrical relative to the center line of the hair group (±10 percent), why in the Figs. 9 and 10 the the force distribution was made completely symmetrical by adding, hair by hair, a force on a hair on the left side to the force on a hair on the right side and divide by two.

The sizes and directions of the forces acting on the hairs when they are placed in a V-form are shown in Figs. 11 and 12. This geometry of the outer hair cell hairs is <u>not</u> found in animals or humans. As can be seen from Figs. 11 and 12, the forces are not symmetrical around the center line of the model, why the measured forces in this case could not be made symmetrical. A possible explanation of the unsymmetrical force distribution can be a slight inclination ($\sim 1°$) of the mean flow velocity to the geometrical center line of the hair pattern. Figures 11 and 12 show that the force distribution on the hairs is very irregular, both when the flow goes into the V and when it comes from the outside of the V.

DISCUSSION OF THE RESULTS

The forces acting on the hairs, placed in W-form, (Figs. 9 and 10), are not at all equal for all hairs. When the flow comes from the outside of the W, the direction of the forces is fairly constant and perpendicular to the legs of the W. This is true except for the center of the W and the outer most parts of the W, see Fig. 9. When the flow comes from the inside of the W, the forces on the hairs are much more irregular, see Fig. 10. Both the sizes and the directions of the forces are changing from hair to hair. The maximum force, acting on a hair in Fig. 10 is about 60 percent bigger than the maximum force on any hair in Fig. 9. There is one thing in common with the Figs. 9 and 10. That is the variation of the force from hair to hair.

Over big areas of the sterocilia pattern, the size of the force on the hair is changing almost sinusodial from hair to hair or with a longer wavelength. A very strange behavior is shown by the sterocilia nr 73 and 97 in the inner row of hairs. The forces on these sterocilia change the direction with 90° and the size with a factor 5 when the flow direction is reversed.

The forces, acting on the hairs placed in V-form (Figs. 11 and 12), are irregular for both the flow directions tested. It seems as if the missing hair in the W-form has a strong stabilizing effect on the forces, when the flow comes from the outside of the W. The measurements also show that the sensitivity for misalignment is much less for the W-form than for the V-form. The misalignment was the same for the two geometries within 0.05°.

CONCLUSION

When the flow across a hair cell is reversed, the forces on the hairs are not reversed. This can explain the rectification effect of the cochlea when it transforms mechanical signals to nerve signals. Depending on the structure of the sensory cells, they can either fire a signal when the forces on the hairs are all in the same direction or when the difference between the hairs is as big as possible. In both cases, the result will be a rectification of the signals when it transforms from a mechanical signal to a nerve signal.

When the hairs are placed in a V-form, the force distribution is irregular even when the flow comes from the outside of the V. The force distribution for the V-form is much more sensitive to misalignment of the flow velocity than the W-form.

ACKNOWLEDGEMENT

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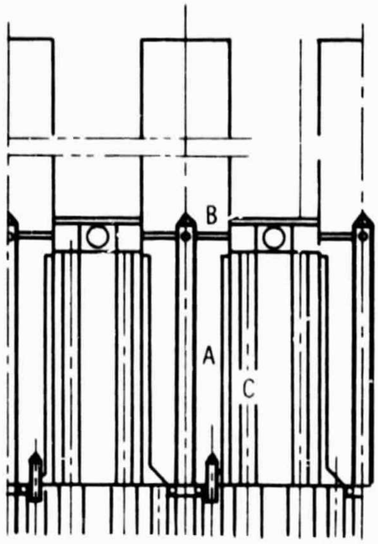

Figure 1. - Hair and manometer connections.

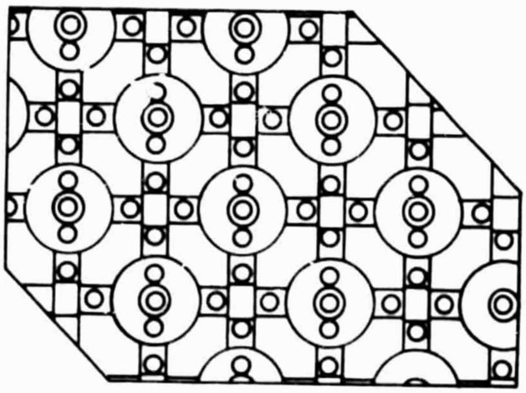

Figure 2. - The hair locations and channel systems.

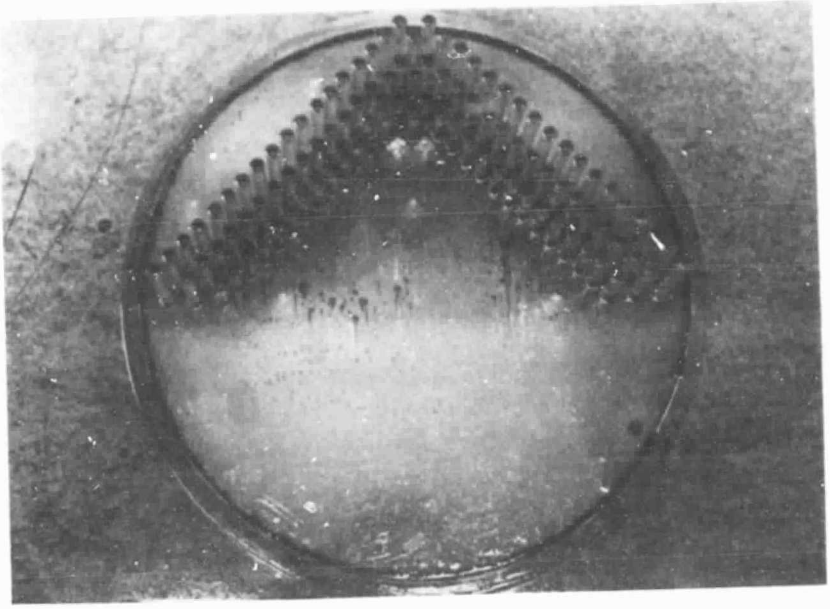

Figure 3. - Hair cell model.

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BLACK AND WHITE PHOTOGRAPH

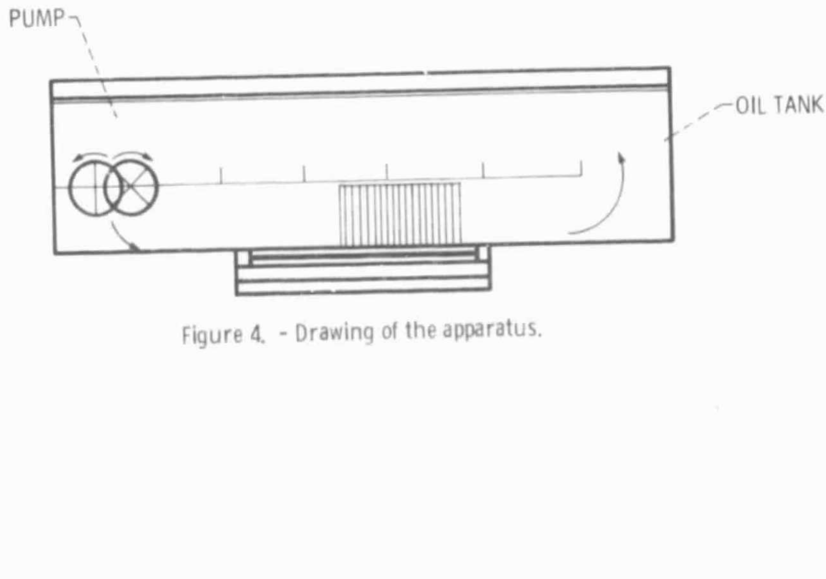

Figure 4. - Drawing of the apparatus.

Figure 5. - Photo of the apparatus and the manometers.

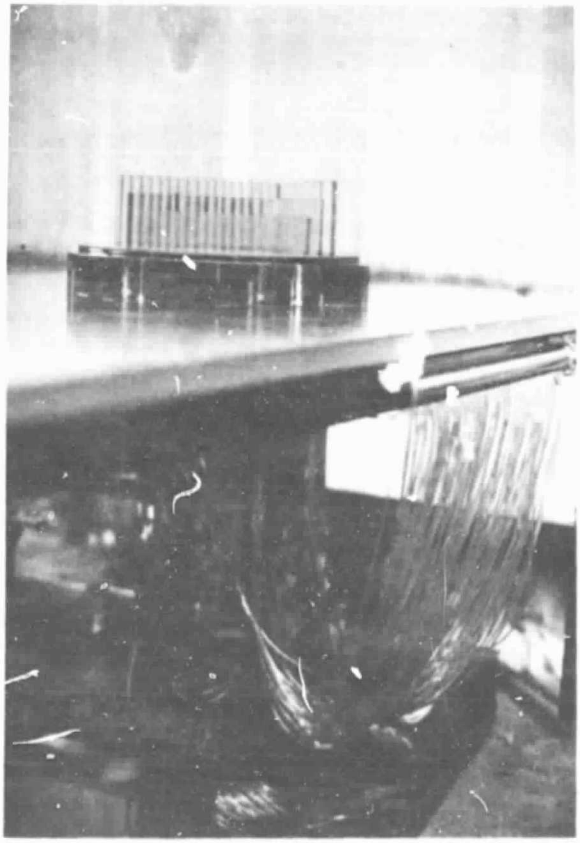

Figure 6. - Photo of the hair cell model and the manometer connections.

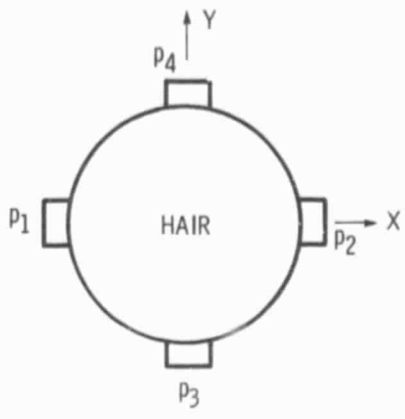

Figure 7. - Pressures acting on the hair.

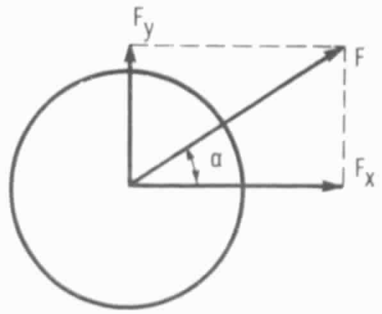

Figure 8. - Force components.

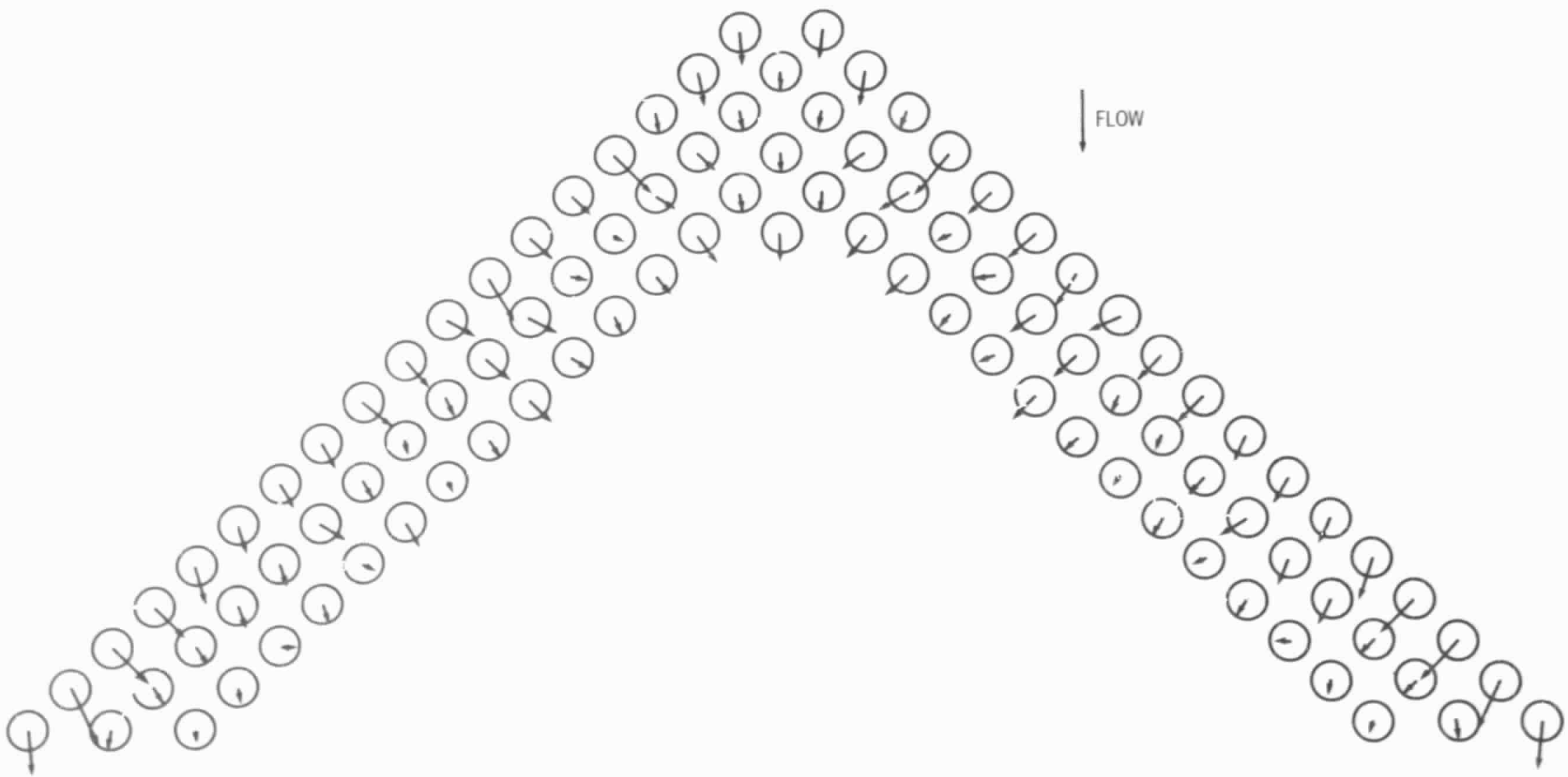

Figure 9. - Hair forces. Mean flow velocity $v = 0.01$ m/s. W-geometry.

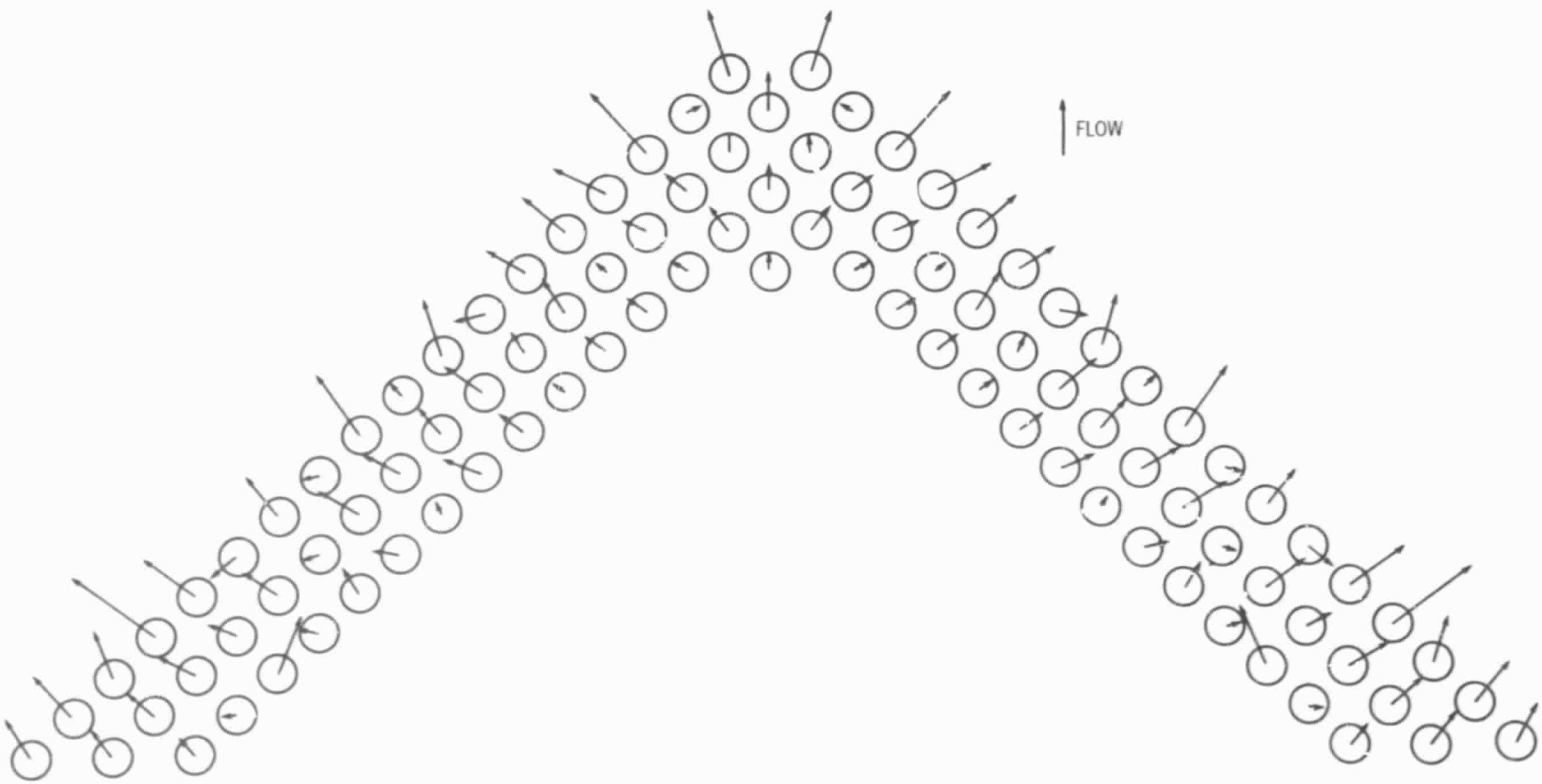

Figure 10. - Hair forces. Mean flow velocity $v = 0.01$ m/s. W-geometry.

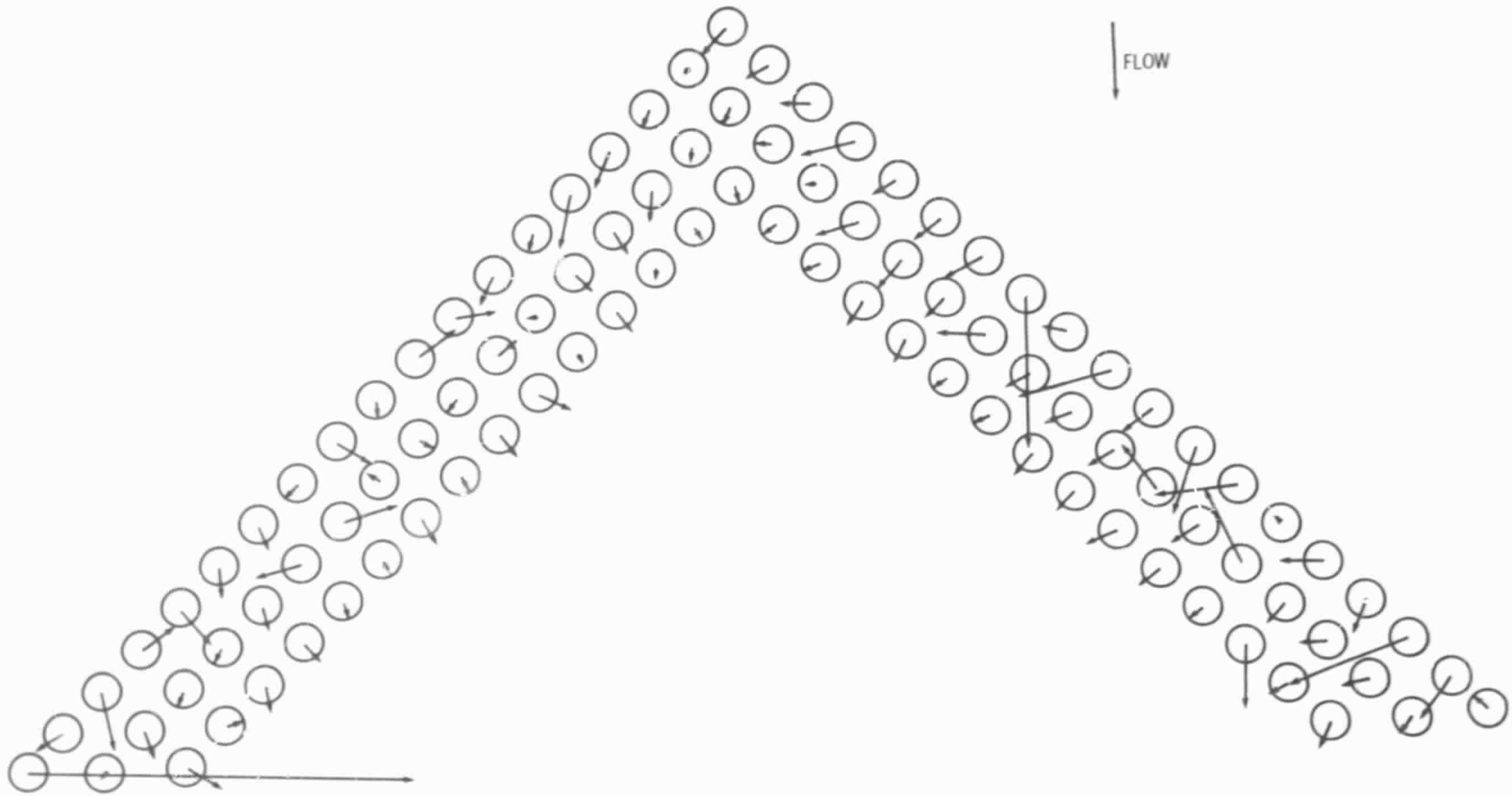

Figure 11. - Hair forces. Mean flow velocity $v = 0.01$ m/s. V-geometry.

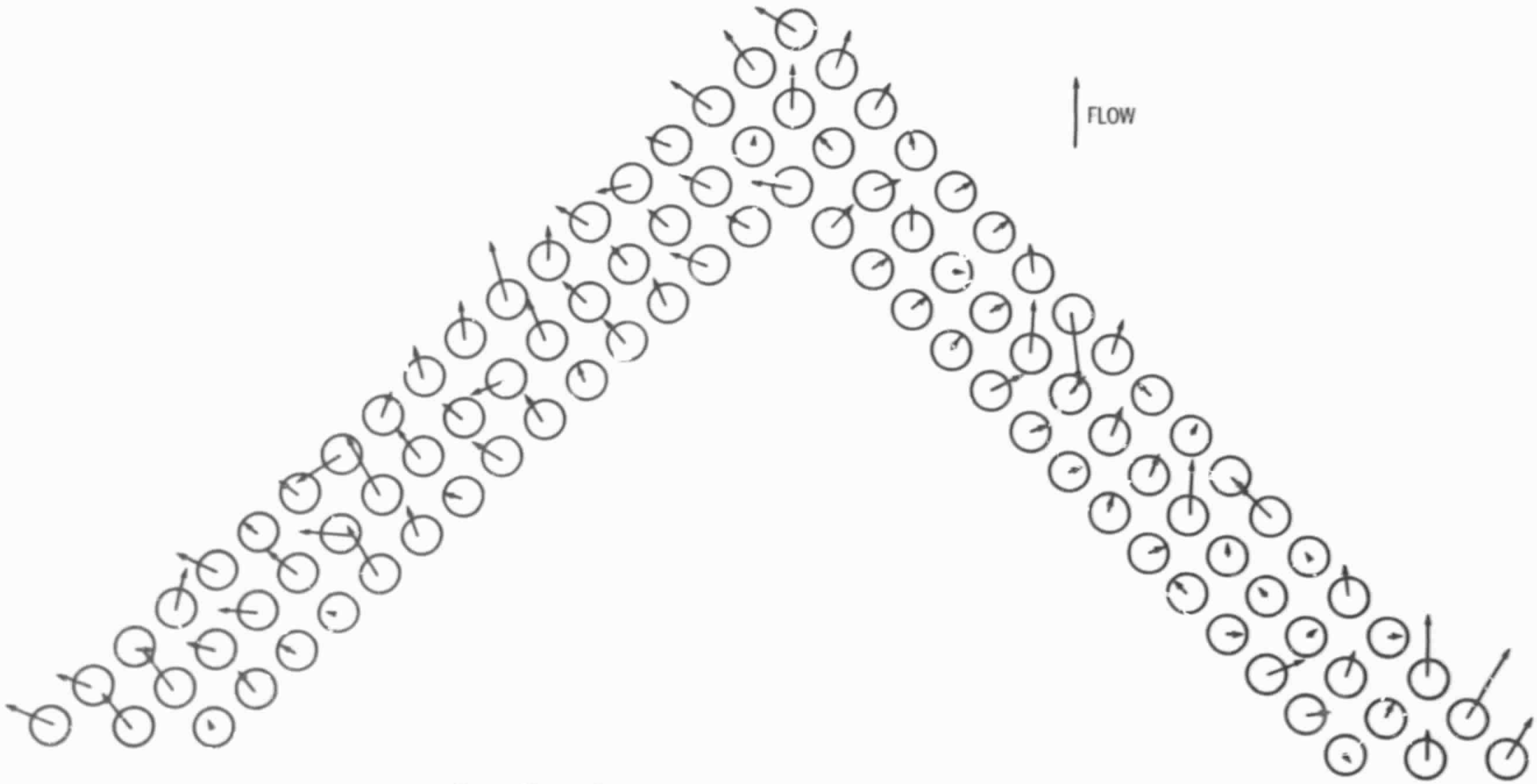

Figure 12. - Hair forces. Mean flow velocity v = 0.01 m/s. V-geometry.