A practical course for preclinical medical students was developed to illustrate aspects of binocular vision and mechanisms of primary visual transduction. It is based on a graphic analysis of two optical illusions, the Pulfrich and the Mach-Dvorak phenomena. A pendulum swinging in a plane perpendicular to the direction of observation appears to follow an elliptical path when viewed binocularly with a filter in front of one eye (Pulfrich illusion) or with alternating occlusion of the right and left eye above a critical frequency (Mach-Dvorak illusion). The Pulfrich phenomenon permits us to determine the relationship between perceived illusory depth and filter density. Analyzing the Mach-Dvorak phenomenon allows us to determine the dependence of illusory depth on interocular delay. Comparison of both determinations (depth against transmission and depth against time) permits us to establish, without complex calculations, the effect of luminescence on visual processing time. In addition, this course illustrates a general methodological concept mentioned by Popper: students make an unexpected observation, put forward a testable hypothesis, and try to falsify it.

Key words: physiology education; psychophysics; stereopsis; luminescence; visual processing time; Pulfrich phenomenon; Mach-Dvorak phenomenon

Psychophysical observations are excellent examples for analysis of the physiological mechanisms causing them. Therefore, our physiology course curriculum for preclinical medical students includes many psychophysical experiments. To demonstrate mechanisms of binocular vision and primary visual transduction, an additional course in visual physiology was developed. The course is based on a graphic analysis of two optical illusions, the Pulfrich (15) and the Mach-Dvorak phenomena (4). In both illusions, because of different interferences with visual perception, a pendulum swinging in a plane perpendicular to the direction of observation appears to follow an elliptical path. A graphic analysis of the two phenomena permits us to determine, without complex calculations, the effect of luminescence on visual processing time.

The Pulfrich phenomenon can easily be demonstrated to a whole group of students. A bob is attached by threads of equal lengths to a ceiling at two different points in a line parallel to the direction of observation. Therefore, the pendular movement will be restricted to a plane that is perpendicular to the direction of observation. A fixation mark is placed directly underneath the pendulum's resting position. Binocular observation of the pendulum with a filter in front of one eye results in an illusory
An illusion occurs when a swinging pendulum bob is viewed binocularly with a neutral density filter in front of one eye. Although the bob is restricted to move in a plane perpendicular to the direction of observation, the path of the pendulum seems to be elliptical. This phenomenon, known as the Pulfrich illusion, is best described as elliptical. For convenience, the term “elliptical” will be used further on, despite the fact that the apparent path is not strictly an ellipse. This is due to the fact that the short axis away from the point of fixation is longer than the short axis toward the observer (Fig. 2 and Appendix). The sense of rotation changes upon holding the filter in front of the other eye, and the magnitude of the illusory depth perception increases upon an increase in the filter density.

The students realize that an asymmetrical luminance for the two eyes causes the illusion. Then they measure the relationship between transmission of the filter and apparent depth of the pendulum path. They learn a technique to determine in a quantitative way a psychophysical illusion and obtain information about the reproducibility of such measurements. On the basis of their knowledge about perception of crossed and uncrossed images of objects, the working hypothesis is put forward that an additional delay in visual processing time causes the illusion. This hypothesis can be tested by studying whether asynchronous exposure of both eyes to scenes of equal luminance produces the same kind of illusion. For different interocular exposure delays, the students determine the depth of the pendulum path.

Comparison of both illusions (depth against transmission and depth against time) permits us to establish, without complex calculations, the effect of luminance on visual processing time. This relationship is qualitatively compared with the influence of stimulus intensity on the rate of change in membrane potential of isolated photoreceptors (1, 7). The rate of hyperpolarization increases and the time to reach a hypothetical threshold decreases with increasing stimulus intensity. The students compare this dependence to the working hypothesis and deduce that it is not in contradiction to it. Furthermore, it is possible to directly calculate the additional visual processing time on the sole basis of a geometric analysis of the data obtained from the Pulfrich illusion (9). The students are informed about this possibility; however, we prefer not to derive the equation, because for many of them the result remains too theoretical.

**Pulfrich phenomenon.** As mentioned above, the most generally accepted explanation for the Pulfrich illusion is that the signals from the eye getting more light arrive at the cortex sooner than the signals from the eye getting less light. As a consequence, information about scenes imaged on the two retinas at different times arrives simultaneously at the cortex (temporal disparity). Information about scenes imaged on the two retinas at the same time arrives asynchronously at the cortex (spatial disparity of moving objects). Therefore, aside from being seen under different angles, the two scenes differ only for moving objects, which are seen at a wrong distance. Data from several psychophysical (2, 8–10, 19) and electrophysiological investigations (3, 17) do not contradict the delay hypothesis.

A geometric analysis permits us to assess the additional visual processing delay induced by the filter. Figure 2 shows a horizontal plane of observation through the point of fixation and the nodal points of...
Parameters determining the Pulfrich phenomenon. The graph shows the parameters used in APPENDIX to calculate the visual processing delay induced by a neutral density filter (F), which is placed in front of the left eye; ZR is the nodal point of the right eye, and ZL is the nodal point of the left eye. The lines W1–W2 correspond to the plane in which the pendulum oscillates. A: apparent position of the pendulum P1 if determination is done when the bob passes the midpoint from right to left. B: apparent position of the pendulum P2 if the determination is done when the bob passes the midpoint from left to right.

To avoid influences of saccadic eye movements and changes in convergence, the observers fixed on the resting target and did not follow the oscillating rod. (From the point of view of an observer fixing on the resting target, the imaging of the oscillating target may be described as follows: objects in a plane behind or in front of the point of fixation project on disparate retinal areas. According to the delay hypothesis, retardation of processing in one eye leads to spatial disparity in perception of moving objects (P1 to P2). Both disparities are interpreted as depth by the visual system. However, there is a distance of fixation where the two effects cancel out each other. To measure this, the observer adjusts his distance of fixation until light perceived simultaneously from the two disparate points in the plane of oscillation, P1 and P2, seems to originate from his plane of fixation above Pn.

The simple harmonic motion of the pendulum is achieved by a Scotch-yoke arrangement described in detail in MATERIALS AND METHODS (Fig. 3). On the basis of the laws of space perception and because the fixation point has to be brought closer to the observer, the information about the positions P1 and P2 must be processed at the same time in the visual cortex (Fig. 2A). Accordingly, excitation of the left eye was initiated when the bob was at the point P1, and excitation of the right eye was initiated when the bob was at the point P2. The time taken for the bob to move from P1 to P2 is the theoretical additional visual processing delay induced by the filter.
Schematic representation of the mechanical pendulum. A Scotch-yoke arrangement was used to oscillate a rod in a plane perpendicular to the direction of observation. Parameters used to calculate (APPENDIX) visual processing delay induced by a neutral density filter are shown. Two exemplary rod positions at two different times are shown. M (solid lines) and P₁ (interrupted lines). A constant-speed motor drives the radius (r). Movement of r results in a displacement (k) of the rod from M to P₁. Amplitude of oscillation is 2r.

In analogy, if the pendulum swings in the opposite direction, its apparent position is P₄ (Fig. 2B).

According to Lit (9), the additional visual processing time can be calculated for each attenuation by experimentally determining the distance cₒ or cᵢ (Figs. 2 and 3 and APPENDIX). This has been done over the range of filter transmissions from 100 to 0.1% at various levels of illumination (9). Furthermore, the calculated predictions for perceived depth as a function of varying spatial conditions, such as observation distances (11) and target velocities (10) over a wide range, are in good agreement with the measurements. Because the derivation of the formula (see APPENDIX) is for many students slightly difficult to grasp and the result remains theoretical, we prefer to analyze the relationship between perceived depth and delay via the Mach-Dvorak phenomenon (4). As will be shown later, quantitative comparison of the measured depth in the Pulfrich and the Mach-Dvorak illusions allows a much more obvious graphic determination of this delay.

Mach-Dvorak phenomenon. Figure 4 represents a horizontal plane of observation through the point of fixation and the nodal points of the eyes. To study the Mach-Dvorak effect, the two eyes are alternately occluded (solid, horizontal bars in Fig. 4) while observing a swinging pendulum. Zᵣ is the nodal point of the right eye, and Zᵢ is the nodal point of the left eye. The lines W₁-W₂ indicate the true planes of oscillation. In Fig. 4, A and B, it is assumed that the right eye sees before the left, and position determination is done when the pendulum passes the midpoint from left to right. Then the right eye sees the pendulum between the positions P₁ and P₁' (Fig. 4A). Later, while the after image produced by the right eye is still effective, the left eye sees the pendulum between P₂ and P₂' (Fig. 4B). In Fig. 4B the overlap of the two scenes is shown. Therefore, during this period of observation, the pendulum seems to move on the elliptical path from P₄ to P₄'.

In analogy, when the pendulum swings in the opposite direction, it seems to be behind the plane of oscillation (Fig. 4, C and D). Adjusting the phase shift between the two disks controls the degree of asynchrony. As seen in the Pulfrich effect, the pendulum appears to move on an elliptical path, and the depth of the ellipse increases with increasing asynchrony. The classic explanation suggests that the visual response persists for each eye after the cessation of the temporary stimulus (interrupted lines in Fig. 4, B and D) and that the processing of the two monocular images can overlap in time. This overlap is the basis for a stereoscopic response (6, 13).

Alteration of the following variables has been analyzed by Michaels et al. (12): interocular delay, exposure duration, and velocity of the pendulum. Provided that the interocular delay is shorter than 60 ms, the pendulum position can be predicted correctly by geometric calculation by using the interocular delay time (onset to onset rule).

MATERIALS AND METHODS

Pulfrich phenomenon. An apparatus similar to that described by Lit (9) was used to measure the Pulfrich and the Mach-Dvorak phenomena (Fig. 5). To observe the Pulfrich phenomenon, the disks
Mach-Dvorak illusion. Schematic representation shows 4 different situations for a horizontal plane of observation through the center of fixation and the 2 ocular nodal points. One monocular viewing condition for each eye is shown. $Z_R$ and $Z_L$ are nodal points of the eyes, and lines $T_1-W_2$ indicate the true planes of oscillation. In A and B, it is assumed that the right eye sees before the left one, and position determination is done when the pendulum passes the midpoint from left to right. With the right eye the pendulum is seen between the positions $P_1$ and $P'_1$ (A); with the left eye it is seen between $P_2$ and $P'_2$ (solid lines, B). B shows as well the overlap of the 2 scenes (solid and interrupted lines). Therefore the pendulum seems to follow the trace $P_N$ to $P'_N$. C and D: analogous pendulum swinging in opposite direction (pendulum seems to be behind the plane of oscillation). Similar to Pulfrich effect, pendulum appears to move on an elliptical path.

(item 6 in Fig. 5) did not rotate. They were fixed at $0^\circ$ phase shift in a position allowing a continuous binocular view through the aperture of a filter box (Fig. 5 shows this setting). The oscillating target was a metal rod of 4 mm diameter painted black (item 3 in Fig. 5). A motor-driven Scotch-yoke arrangement ensured that the target oscillated strictly in one plane and that amplitude and maximal speed remained constant within $\pm 1\%$ (Fig. 3 and item 2 in Fig. 5). In Fig. 3, two exemplary rod positions at two different times of a cycle are shown, position $M$ (solid lines) and position $P_1$ (interrupted lines).
Apparatus used to quantify Pulfrich and Mach-Dvorak illusions: filter box (1), Scotch-yoke arrangement (2), oscillating target (3), fixation target (4), adjustment of fixation target (5), and rotating disks (6). Illumination unit and black screen between oscillating target and filter box to restrict view to rods in vertical direction are not shown.

full revolution of the radial bar attached to the axis of the motor moved the rod back and forth from left to right. A 30 V DC constant-speed motor drove the radius. The distance of the pendulum from the observer (d) was 100 cm, the angular size of the rod was 14 min, the period of oscillation was 5.55 s, the amplitude was 30 cm (2π), and the velocity at midposition was 28.13 cm/s, corresponding to 15.7°/s. The depth of the ellipse in the near direction was measured by adjusting the distance of fixation target in the midsagittal plane (Fig. 5) until the moving target seemed to move directly over it. The fixation target looked like the oscillating target and was placed directly below it (item 4 in Fig. 5). The offset from the fixation bar from the plane of oscillation was read to an accuracy of ±0.5 mm by a second person. To avoid influences of saccadic eye movements and changes in convergence, the observers fixated on the resting target and did not follow the oscillating rod. A black screen (aperture 330 mm wide and 40 mm high) between the oscillating target and the filter box restricted the view to the two rods in the vertical direction (not shown in Fig. 5). About 20 mm of the fixation and the oscillating target were visible. They were seen against a uniform white background illuminated by a 60-W opaque filament lamp (not shown in Fig. 5). For the Mach-Dvorak phenomenon, the fast flicker of a gas discharge lamp can interfere with the alternating viewing conditions. The bulb was cylindrical, 195 mm long and 29 mm in diameter, and was placed directly above the aperture of the black screen. The luminosity of the white background in front of which the target oscillated was 125 cd/m².

The measurements were performed on two of the authors, D. Mojon (D. M.) and H. Oetliker (H. O.). They had in both eyes a visual acuity of 20/15, a stereoacuity of 40 arcsec in the Titmus stereotest, and ability to see all three figures of the Lang stereotest II. An ophthalmological examination showed normal eyes. Interpupillary distances while subjects were fixating at 100 cm were 66 mm for D. M. and 70 mm for H. O. To avoid an increase of the Pulfrich effect due to dark adaptation of the filter-covered eye (16), a single determination had to be made in < 10 s. In addition, between two measurements a uniform light adaptation was performed for both eyes.

Mach-Dvorak phenomenon. The oscillating target, the fixation target, the black screen, and the lighting were the same as those used for observation of the Pulfrich phenomenon (Fig. 5). The two black disks were driven by the same motor to ensure the same speed (item 6 in Fig. 5). Six equal holes of 24 mm diameter were located at a distance 115 mm from the rotation center. Adjustment for individual interpupillary distance was possible by vertical displacement of the empty filter box (item 1 in Fig. 5). The rotation speed of the disks was 800°/s. At this speed, during one observation cycle each eye could see through the hole for 15 ms and its vision was obstructed for 60 ms. The phase shift between the two disks was adjustable. The interocular delay was always kept shorter than one-half the time between two exposures for the same eye. This ensured that the two scenes separated by the shorter time interval had to be matched together, and therefore ambiguity in the direction of perceived depth could be avoided. The interocular delay (ms) was calculated by dividing the phase shift (°) by the rotation speed of the disks (°/s). Again D. M. and H. O. performed the measurements. Linear regression
Filter density and near displacement. Near displacements (means ± SD) are plotted as a function of transmission of neutral density filter in front of left eye for D. M. (A) and H. O. (B). Dotted line, a logarithmic curve fit. An exemplary graphic determination for 20% transmission is shown. For D. M. and H. O. this corresponds to an illusionary displacement of 3.2 and 2.5 cm, respectively.

RESULTS

Pulfrich phenomenon. In Fig. 6 (for D. M., Fig. 6A and for H. O., Fig. 6B) near displacement (means ± SD) is plotted against transmission of the filter in front of the left eye. Arrows show an exemplary graphic determination of perceived depth for a 20% filter. The transmission of 20% corresponds to a displacement of 3.2 cm for D. M. and of 2.5 cm for H. O. The dotted line represents a logarithmic curve fit.

Mach-Dvorak phenomenon. In Fig. 7 near displacement (means ± SD) is plotted against interocular delay. Arrows show exemplary graphic determinations of interocular delays corresponding to perceived depth at 20% transmission (see also Fig. 6). Displacements of 3.2 cm (D. M.) and 2.5 cm (H. O.) correspond to visual processing delays of 8.0 and 8.6 ms, respectively. The dotted line represents a linear curve fit.

Effect of luminescence on visual processing time. In Fig. 8, transmission of the filter in front of the left eye is plotted against interocular delay. Filled symbols show values obtained by graphic determinations; open symbols represent values calculated...
Transmission and interocular delay. Interocular delays are plotted against transmission of neutral density filter in front of left eye for D. M. (A) and H. O. (B). Filled symbols, graphic determinations; open symbols, values calculated by using Eq. 7. Interrupted line, logarithmic fit for graphic determinations; dotted line, logarithmic fit for calculated values; arrows, exemplary determinations for 20% transmission (see Figs. 6 and 7). In D. M. and H. O., a 20% transmission filter in front of left eye causes a visual processing delay of 8.0 and 8.5 ms, respectively, if determined graphically. Calculation of visual delays for 20% transmission using Eq. 7 (APPENDIX) yields 7.9 and 6.3 ms for D. M. and H. O., respectively.

Using Eq. 7 (APPENDIX). The interrupted line represents a logarithmic fit for the graphic determinations; the dotted line represents a logarithmic fit for the calculated values. Arrows show values for 20% transmission determined by using the graphic method (see Figs. 6 and 7). A 20% transmission filter in front of the left eye causes an additional visual processing delay of 8.0 ms in D. M. and of 8.5 ms in H. O. Calculation using Eq. 7 yields for transmission of 20% delays of 7.9 ms for D. M. and of 6.3 ms for H. O.

DISCUSSION

Didactics. The Pulfrich phenomenon is one of the optical illusions that can be demonstrated easily and in an impressive way to a group of students. They observe a swinging pendulum hanging from the ceiling with a fixation mark directly underneath its resting position. If the target is attached at two different points on two threads of equal length, the pendulum movement will be restricted to one plane. While observing binocularly the pendulum, the students hold a filter in front of one eye. The unexpected elliptical pendulum path (Fig. 1) impresses all people capable of stereoscopic vision. They can change the sense of apparent rotation by moving the filter in front of the other eye. By repeating the observation with a filter of higher density, they observe that the depth of the illusion increases. After realizing that the illusion depends on an asymmetrical luminance of the scenes seen by the two eyes, the students measure quantitatively the dependence of the apparent depth impression on the transmission of the neutral density filter (Fig. 6). They learn a general technique to quantize a psychophysical illusion and obtain information about the reproducibility of such measurements on themselves. They draw a graph similar to Fig. 2 by applying their knowledge about crossed and non-crossed images of objects. This enables them to formulate a working hypothesis that the Pulfrich illusion is caused by an additional delay in visual processing time. To falsify this hypothesis, a situation has to be found in which asynchronous exposure of both eyes to scenes of equal luminescence does not produce an illusion of the same kind. The Mach-Dvorak experiment does of course produce such an illusion. For different interocular exposure delays, the students determine the depth of the pendulum path (Fig. 7). Then they graphically derive the relationship between the additional visual processing delay and the relative difference in luminosity by comparing the results obtained from the analysis of the Pulfrich phenomenon with the results of the Mach-Dvorak phenomenon (Fig. 8). They do
not need to derive Eq. 7 or 8 given in the APPENDIX. These equations allow a direct calculation of the additional visual processing delays by using only the data obtained by analysis of the Pulfrich illusion. The derivation of the equations is quite long, and the result remains too theoretical for many of the students. After graphic determination of the relationship between luminescence and visual processing delay, the result is qualitatively compared with the influence of stimulus intensity on the rate of change in membrane potential of isolated photoreceptors (1, 7). The velocity of hyperpolarization increases, and the time to reach a hypothetical threshold decreases with increasing stimulus intensity.

The students realize that this dependence of rate in change of membrane potential on stimulus intensity does not contradict their working hypothesis. At the end of the course they are confronted with the fact that the illusory depth increases with increasing observation distance. This is best shown by observing the pendulum hang on the ceiling at two different distances with a filter in front of one eye. For most people this finding is contrary to intuition. Interested students can derive Eqs. 9 and 10, showing that the depth of the illusion is proportional to the observation distance.

General implications. This practical course illustrates to students some general concepts of methodology suggested by Popper. The students are confronted with an unexpected observation, must put forward a testable hypothesis to explain it, and can go through the procedure of trying to falsify it (14). Furthermore, many students remain impressed about the reproducible determination of differences in visual processing time in the range of milliseconds by a simple psychophysical method.

Technical aspects. Each year this course is attended by ~200 students in groups of ~16 within a total time of 3 wk. In 4 h each student performs the Pulfrich/Mach-Dvorak experiments, together with the determination of visual acuity and near accommodation. About 2 h are needed to perform the Pulfrich and the Mach-Dvorak experiments. For each experiment four setups are provided. A single setup is used by two students. One performs the experiments while the other notes the displacements. Two tutors assist the whole group during the 4 h of the course. Some weeks before the course starts, the students can attend lectures in physiology of the eye, including principles of binocular vision. These lectures assure that their knowledge is sufficient to perform this course in only 2 h.

APPENDIX

Knowing the geometric parameters, distance of the pendulum from the observer (d), interpupillary distance (2b), and the parameters of movement of the pendulum, amplitude (2\theta) and period (T), the student can calculate additional visual processing time (t) from the depth perception (similar triangles, Figs. 2 and 3)

\[ a = \frac{bc_N}{d - c_N} \quad \text{and} \quad a = \frac{bc_F}{d + c_F} \]  

(1)

\[ c_N \quad \text{and} \quad c_F \]  

are the respective distances from the plane of oscillation to the point of fixation, and \( a \) is one-half the distance from \( P_1 \) to \( P_2 \). If we know the amplitude and the period of the pendulum, the time for the bob to move from \( P_1 \) to M can be calculated. The displacement \( k \) of the rod from its midposition as a function of time \( t \) with use of a Scotch-yoke arrangement (Fig. 3) is given by the formula

\[ k = r \sin \left( \frac{2\pi t}{T} \right) \]  

(2)

where \( r \) is the length of the radially affixed bar on the driveshaft, and \( T \) is the time for one complete revolution of the driveshaft.

If the displacement corresponds to the distance \( P_1M \), then \( a \) is equal to \( k \), and the time \( t' \) to move from \( P_1 \) to M is

\[ t' = \frac{T}{2\pi} \arcsin \left( \frac{a}{r} \right) \]  

(3)

Near the midposition, the time \( t'' \) to move from \( P_1 \) to \( P_2 \) is twice as much

\[ t'' = \frac{T}{\pi} \arcsin \left( \frac{a}{r} \right) \]  

(4)
If $c_N$ was measured, substitution of $a$ from Eq. 1 yields for the time $t_N$

$$t_N = \frac{T}{\pi} \arcsin \left( \frac{bc_N}{(d-c_N)r} \right)$$

(5)

Correspondingly, if $c_F$ was measured, substitution of $a$ from Eq. 1 yields for the time $t_F$

$$t_F = \frac{T}{\pi} \arcsin \left( \frac{bc_F}{(d+c_F)r} \right)$$

(6)

If the value of $a$ is sufficiently small that the sine of the angles between the two lines $Z_L P_N$ and $Z_R P_N$ equals the value of the angles in radians, we obtain for the time $t_N$

$$t_N = \frac{Tb}{\pi r} \frac{c_N}{(d-c_N)}$$

(7)

and for the time $t_F$

$$t_F = \frac{Tb}{\pi r} \frac{c_F}{(d+c_F)}$$

(8)

The two time values ($t_F$ and $t_N$) have to be equal within experimental error. This can be used as a further test of the hypothesis in applications in which the phenomenon is studied more rigorously. It is not done in our course because of lack of time.

Solving Eq. 7 for $c_N$ and Eq. 8 for $c_F$ gives the relationship between distance of the pendulum from the observer ($d$) and illusory depth impression toward the observer $c_N$

$$c_N = d - \frac{t_N \pi r}{Tb}$$

(9)

and away from the observer

$$c_F = d - \frac{t_N \pi r}{Tb}$$

(10)

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Teachers and their students may find the following articles from *News in Physiological Sciences* useful when exploring the physiology of vision:

**Saibil, H. R.** From photon to receptor potential: the biochemistry of vision. *NIPS* 1: 122–125, 1986.
