

HORIZONTAL-VERTICAL PREFERENCES IN HUMAN AND PIGEON VISUAL FIELDS

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Perceptual multistability is characterized by the fact that an objectively unchanging stimulus like the famous Necker cube leads to perceptual switching between two or more interpretations. Underlining the importance of endogenous processes in perception, research on this phenomenon therefore has become an intensively investigated paradigm in the field of visual neuroscience (RAMACH-ANDRAN & ANSTIS 1985; BASAR-EROGLU, STRÜBER, KRUSE, BASAR & STADLER 1996; CRICK 1996; LEOPOLD & LOGOTHETIS 1996, 1999; KLEINSCHMIDT, BUCHEL, ZEKI & FRACKOWIAK 1998; LUMER, FRISTON & REES 1998).

VETTER, HAYNES & PFAFF (2000) demonstrated that pigeons show perceptual reversals similar to those reported in human observers. This initial evidence of multistability in animals suggests that it is a general property found in sensory systems. As multistable stimulus pattern they used the so-called 'orthogonal alternating movement' (OAM, VON SCHILLER 1933): Two lights are presented on two diagonally opposed corners of an imaginary square or rectangle, and alternated with the two lights of the other corners (see figure 1c). In humans this produces perceptual switching between two points that apparently move vertically – though in opposite directions – and two points that move horizontally.

It is known from human studies of orthogonal apparent movement that changes in the aspect ratio of the configuration, i.e. the ratio of the horizontal to vertical distance of the dots, biases the perceptions in a specific way (HOETH 1968): If horizontal distance is increased subjects are more likely to see vertical motion and vice versa. This, too, could be demonstrated for pigeons (VETTER et al. 2000).

HOETH was especially interested in finding out whether the perceived directions of the apparent movement of the dots are weighted equally. Does observing a square OAM pattern lead to a balanced distribution of horizontal and vertical apparent movement or, rather, to the preferred perception of one of the two? The well-known horizontal-vertical illusion results in observers tending to judge a vertical line as being longer than a horizontal line of the same length. Because of that one should expect that the vertical distance of the dots is overestimated, i.e. seen longer than the horizontal distance. Taking into account the principle of proximity this should result in a dominance of the horizontal as compared to the vertical apparent movement direction.

On the other hand, RAUSCH showed in a series of experiments (1949, 1950, 1952), that for two-dimensional patterns the two dimensions have different roles in perception. One dimension is seen as *variable* and the other as *constant*. Seen as a variable dimension of a figure is perceived as the direction in which it is oriented and in which variations may possibly take place. That seen as a constant dimension on the other hand is perceived as given, unattended. Varying the figure in this direction is not taken into account. This is the so-called Variability-Constancy Principle (VC-Principle).

According to RAUSCH (1952), it is the *vertical* dimension which takes on the role of the seen variable whereas the horizontal is perceived as the constant. HOETH assumed this should cause perception to preferably place dynamic events (e.g., apparent movement) into the vertical dimension.

In this case one would expect that with a square OAM pattern it is the apparent vertical movement that is seen more often.

To correctly understand the dominance of verticality in these two apparently contradicting cases it must be considered, that with a horizontal-vertical arrangement of two lines it is not only the vertical line that grows isolated on the surrounding empty field which itself remains unchanged. Rather, both the (vertical) line and the surrounding field are being stretched into the vertical direction. And it is this distortion of the blank field that creates a tension in verticality, leading to a preference of apparent movement in this direction. That this vertical field tension really exists can be shown by the method of STADLER et.al. (1991). Thus, both the VC-principle and the H/V-illusion work in the same direction and lead to a dominance of verticality.

Now, the results of HOETH's experiments unequivocally showed that vertical apparent movement is seen significantly more often than motion in the other direction when elicited by a square OAM pattern.

HOETH found out that in order to compensate this dominance of verticality the horizontal to the vertical distance of the OAM dots has to be 5 to 8, which equals an aspect ratio of .626. In that case there is an even distribution of the two apparent movements. This value was later confirmed by KRUSE, STADLER & WEHNER (1986).

It was well known even earlier as KOFFKAS "Principles of Psychology" (1935) that the human visual field is anisotropic. The horizontal and the vertical dimension differ significantly. The environment expands primarily in the horizontal direction. The vertical dimension is always small compared with the length of the visible horizon (GIBSON 1979). The environmental effect of the primarily horizontal extension of the earth's surface is paralleled by the form of human visual field. Due to the fact that humans possess two eyes with a horizontal distance of approximately 6.5 cm their combined visual field is a horizontally oriented ellipse subtending about 200° versus 130° along the horizontal and vertical meridians, respectively. According to KÜNNAPAS (1957) this leads to a kind of framing effect insofar vertical lines will be closer to the boundary of the visual field than will horizontal lines, and hence vertical lines will appear longer, thus for instance causing the horizontal-vertical illusion. He also proved that this illusion is reduced by 30 % if it is measured in a completely dark room with no distinct boundaries of the visual field.

Since these factors causing an anisotropy of the visual field all work into the same direction, viz. cause a stretching of the vertical dimension, they may explain the observed dominance of verticality with square OAM patterns, demanding an aspect ratio of about .625 to ensure that the phase lengths between seen horizontal and vertical apparent movement are approximately equal.

Contrary to anisotropies in human vision, such factors are not found in pigeons. For pigeons the combined visual field is much smaller, viz. 22° (MARTIN 1993; NALBACH, WOLF-OBBERHOLLENZER & REMY 1993) and hence less asymmetric.

Furthermore, birds have an entirely different representation of the optical flow in the environment during flight. As GIBSON (1979) emphasized, there should be no anisotropy of the visual space, as the horizon equals a circle around the animal without any optical flow which forms a natural boundary of the visual space. The two dimensions - that corresponding to the direction of flight and the direction transverse to flight - are symmetric, so there should be no preference for one or the other.

Thus, for pigeons a comparable anisotropy of the visual field should not exist and one might assume that there is, at best, a reliably reduced dominance of verticality. If this is true they should not need an aspect ratio very much different from 1.0 in order to secure an even distribution of the two apparent motion percepts. The aim of the present study was to test this assumption.

Experiment

Method

Subjects. Five experimentally naive pigeons (*Columba livia*) served as subjects in the experiment. They were maintained at approximately 80 % of their free feeding weight, water and grit being freely available.

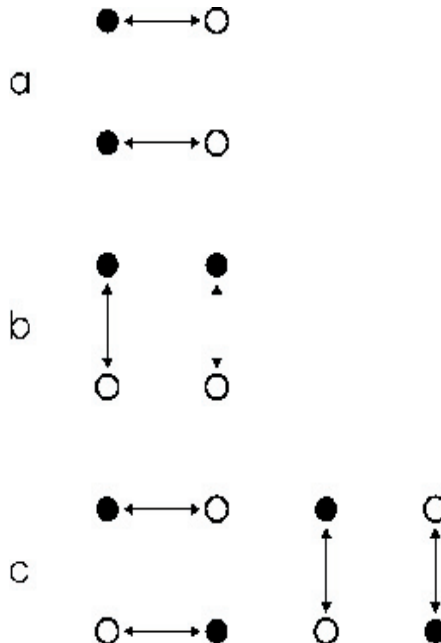


Figure 1: Orthogonal alternating movement (OAM). Four LEDs are positioned at the corners of the square. ● and ○ circles indicate two pairs of LEDs that are flashed together and in alternation with the other pair. The stable cases lead to (a) unambiguous horizontal and (b) vertical apparent motion. The bistable pattern (c) leads to perceptual switching between horizontal and vertical motion.

Apparatus. A conventional operant chamber with a transparent response key was used. The key was split in half to allow separate programming and recording for each

side. The stimulus display unit was mounted 1 cm behind the response key. It consisted of a matrix of 16 x 16 red light emitting diodes (LED, diameter 3 mm), allowing the presentation of the different stimulus patterns to be used in this experiment (see Fig. 2). Rewards (mixed grain) were delivered with a food hopper situated below the response key. The box was illuminated with a house light and all relevant events were computer controlled and registered. Two loudspeakers outside the box supplied white masking noise.

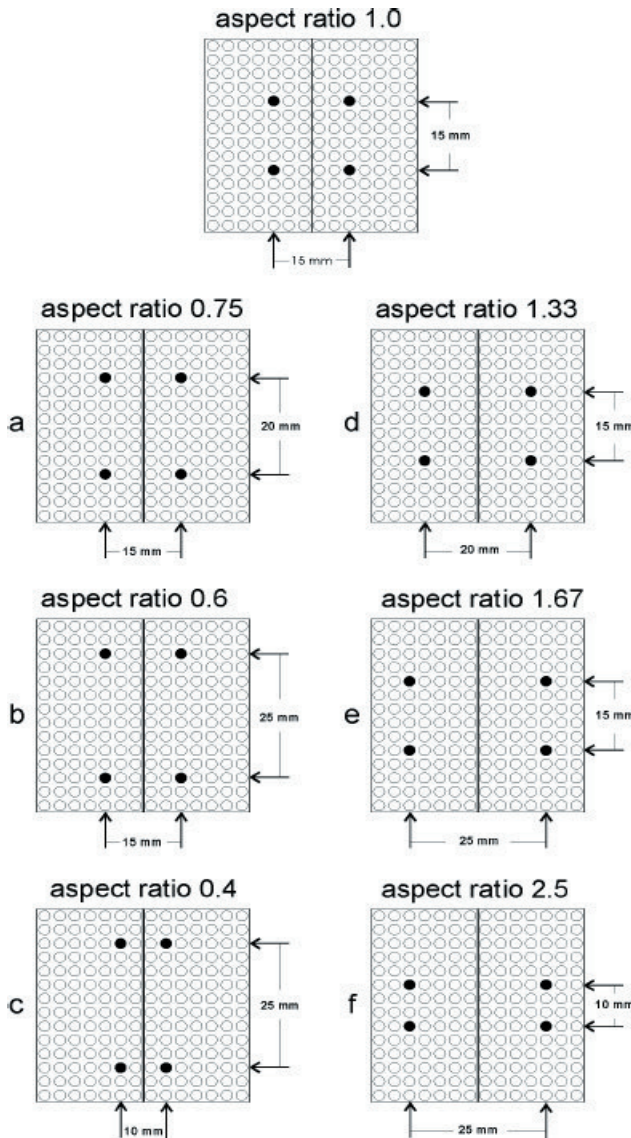


Figure 2: Matrix with the seven stimulus patterns used in the experiment and their aspect ratios. Black dots indicate the activated LEDs.

Stimuli. Stable and bistable sequences similar to those depicted in Figure 1, but varying in their aspect ratios, served as stimuli. The stable stimulus for horizontal motion consisted of two frames (Fig. 1a). The first showed the left two of the four display LEDs, the second the right two. These alternated with a frequency of 2 Hz (without interstimulus interval) which is known to produce a stable percept of horizontal apparent motion. In the same way the vertical motion stimulus alternately showed the top and the bottom two LEDs (Fig. 1b). The multistable stimulus was the orthogonal alternating movement (OAM) which consisted of two frames showing the diagonally opposite LEDs (Fig. 1c). This is known to produce alternations between horizontal and vertical motion percepts.

For discrimination training three different four-dot patterns with the aspect ratios 1.0; 0.6; 1.67; (see Fig. 2) and two three-dot patterns (aspect ratios 0.75 and 1.33) were used. The latter patterns were achieved by simply “turning off” one randomly chosen LED per trial as if it were covered. This resulted in a motion pattern which consisted of one LED as one frame and two LEDs as the second frame. In these cases human observers see apparent motion.

Altogether seven OAM four dot stimuli were being presented during test, viz. those with the aspect ratios of 2.5; 1.67; 1.33; 1.0; 0.75; 0.6; and 0.4 (see Fig. 2).

Procedure. After magazine training, pecking on the key was shaped using an autoshaping procedure. As soon as they had learned to associate key-pecking with food reward, discrimination training began. Now the birds were conditioned to discriminate between the unambiguous horizontal (S_H) and the unambiguous vertical (S_V) movement of the dot pairs. In a go/go discrimination task the pigeons were trained to peck either the right or the left side of the key depending on which of the two unambiguous movement directions was displayed¹. For half of the birds the left side was to be pecked in the presence of S_H , for the other half in the presence of S_V . At the beginning, correct responses were reinforced on a 3 s variable interval (VI) schedule, subsequently increasing this interval until VI 45 s was reached. The reinforcement schedules for both sides were identical, but operated independently. Pecks to the wrong side were slightly punished with a 5 s black out (both house light and stimulus display were turned off). The average stimulus duration was 3 s at the beginning of discrimination training and was stepwise increased up to 45 s. One daily session consisted of 8 presentations of each of the five discrimination stimuli, in a quasi-random sequence. Occasionally occurring side preferences were corrected when the pecking rate to one side was twice as much or more than to the other side. In this case the reinforcement rate for pecking to the less preferred side was changed from VI 45 s to VI 35 s until the side preference was extinguished.

The day after achieving the discrimination criterion of 90 % correct responses the test was started. It was a so-called steady-state procedure: The usual discrimination training was run with intermittent test phases of 120 s each, always spaced by 340 s of normal discrimination training. In each test phase, one of the seven OAM stimuli

¹ The term go/go discrimination task is used to distinguish it from go/no-go designs in which one of the trained responses is non-pecking.

was presented under conditions of extinction. The first test session was finished after 10 test phases. From the next day on the normal discrimination training (without test phases) was run as retraining until the original criterion of 90 % correct responses was reached again. Then the next test was run in the described manner, followed by retraining again, and so forth. This was done until every bird had been exposed to the seven test stimuli ten times.

Results

As in our previous study all the birds showed switching behavior during OAM-tests.

In order to compare the phase length changes between the seven different aspect ratio conditions on an individual bases an index was computed that gave the mean horizontal phase length divided by the mean vertical phase length (X_H/X_V) for each animal under each of the seven conditions.

Table 1: Ratios of mean horizontal to mean vertical phase lengths for all seven aspect ratios (X_H/X_V).

aspect ratio	OAM _V			OAM _{square}	OAM _H		
	2.5	1.67	1.33	1	0.75	0.6	0.4
Animal							
316	0.177	0.13	0.351	0.944	2.02	2.06	4.275
400	0.081	0.059	0.282	0.453	0.803	1.161	1.306
1522	0.098	0.093	0.464	1.238	0.814	1.796	1.982
1283	0.534	0.57	0.435	0.754	1.24	1.782	3.223
512	0.906	0.734	0.974	1.242	1.191	1.461	1.906

Table 1 shows that the results were as predicted: Increasing the aspect ratio to bias horizontal movement increases the corresponding phase length and increasing the bias for vertical movement leads to longer vertical phase lengths. (Friedman two-way analysis of variance; $\chi_r^2 = 27.9$; $df=6$; $p<.001$)

Now, our main interest was to find out at which aspect ratio the two phase lengths were about equal, i.e. $X_H/X_V = 1.0$.

Inspection of table 1 suggests two candidates: aspect ratio 1.0 and aspect ratio 0.75. As a matter of fact, these two values are not significantly different (Fisher-Pitman, $p=0.18$).

We then plotted the grand averages of the phase durations for horizontal and for vertical movement registered which each of the seven aspect ratios. Figure 3 shows,

that the resulting two curves intersect at an aspect ratio value between 1.0 (square) and 0.75 (slightly horizontally biased), but closer to 1.0. According to our data, this should be about the value at which we register an equal distribution of horizontal vs. vertical motion perception.

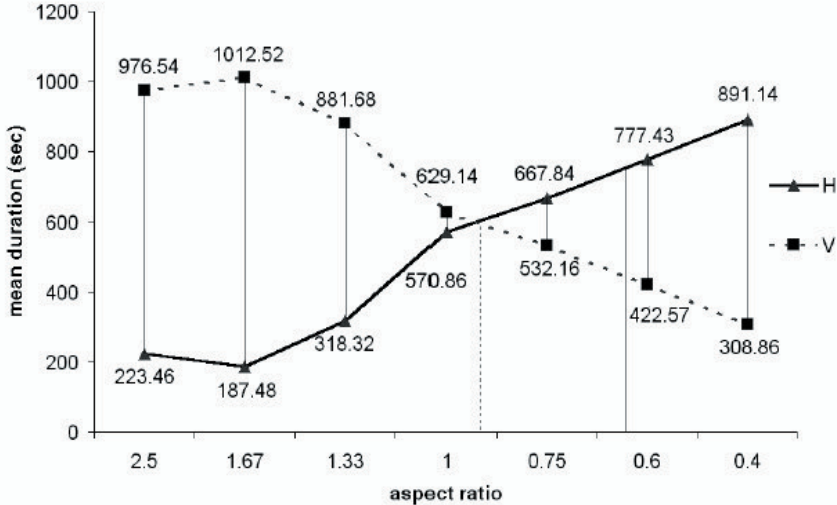


Figure 3: The grand averages of the phase durations for each of the seven different aspect ratios presented during the OAM-tests. H = perceived horizontal motion; V = perceived vertical motion. The solid straight down line indicates, where the curves should intersect were there a dominance of verticality similar to humans.

The solid vertical line in figure 1 indicates at which aspect ratio humans would have a comparable balance between the two percepts. It is obvious that with pigeons a similar bias leads to a clear dominance of horizontal as compared to vertical motion perception.

Discussion

The change of phase durations according to the bias introduced by the aspect ratios clearly indicates that we are dealing with a percept-driven process and can rule out random behavior as the cause for the behavioral switching.

Our data show that a balanced distribution of horizontal vs. vertical motion perception occurs with an aspect ratio close to 1.0 or only slightly horizontally biased. If one remembers that the corresponding aspect ratio for humans is 0.62 – a point, where pigeons clearly are far from such an equilibrium – it is safe to conclude that there is no dominance of verticality in pigeons that is directly comparable to that observed in humans.

In the introduction we referred to two factors that cause the anisotropy of the human visual field as possible explanations for this result, factors which contrary to humans are not found in pigeons.

There is, however, still another factor that causes such an anisotropy in humans and not in pigeons: Gravity. Gravity, which always acts in the vertical dimension may account for the dominance of verticality, because a greater sense of effort is associated with this direction. Contrary to that, with flying birds gravity acts evenly on the total visual field and there is no such dominance of one or the other direction.

HOETH himself did not spend much space to explanations for his reported preference of verticality. In a short note, however, it was gravity which he suggested might be the reason for perception to preferably place apparent motion (i.e. variability) into the vertical dimension.

Gravity was also considered to be a possible cause for another interesting observation. Experiments on rotational invariance have shown that pigeons perform differently in specific matching-to-sample tasks (HOLLARD & DELIUS 1982). A previously presented sample form had to be compared to one of two alternative visual forms: An identical one and a mirror image of the sample form. The two comparison forms were presented in various orientations with respect to the sample. Whereas with humans the reaction time (the time elapsed between appearance of comparison stimuli and the reaction of the subject) depended linearly on the angular disparities, those of the pigeons did not. HOLLARD & DELIUS speculated that this could be due to phylogenetic reasons. Pigeons, they argued, operate visually predominately on the horizontal plane where the orientation of objects is largely arbitrary, being relative to the position of the observer. "Humans primarily view the frontal plane where their orientation and that of objects are highly consistent, being dependent on gravity" (S. 806).

In various experiments it was shown, however, that at least the horizontal-vertical illusion is more likely a function of verticality in retinal space than in the gravitational field (MORINAGA, NOGUCHI & OHISHI 1962). LIPSHITS et al. (2001) also demonstrated that this illusion is independent of gravitation. They performed experiments in weightlessness during long orbital space flights on board the MIR station.

Since it is not clear whether this also holds for the V/C-principle, one should not exclude gravity as a possible contributor to our observed dominance of verticality. The two factors we presented in the introduction, however, surely should play an important role:

(1) The ecological environment. Particularly in this respect there is quite a difference between human observers looking toward the horizon as compared to flying birds who look to the ground, which extends as a fronto-parallel plane (see figures 7.3 and 7.4 in GIBSON 1979). Actually in Fig. 7.4 the strongest optical flow can be found in the vertical direction (the direction where the animal moves) while flow decreases the more it is seen horizontally. Similar as in the elliptical structure of the visual field in humans, in the GIBSONian environment, horizontal lines cover only a small part of the widely stretched horizon as compared with vertical lines of the same size. The latter are of importance for the control of locomotion of the animal even if it does not fixate the focal point. For the bird flying over the ground the situation is symmetric with respect to the length of the textural distribution before and behind the animal (see GIBSON 1979, figure 13.1.; see also CUTTING 2000).

As there is no asymmetry in the fronto-parallel view between the direction 0 degrees - 180 degrees and the direction 90 degrees - 270 degrees, there should be no dominance of the vertical direction, which is the direction of flight.

By the way, this could also explain the specific differences between humans and pigeons HOLLARD & DELIUS reported about in their above cited experiments on rotational invariance.

(2) The elliptical structure of human visual field seems to be a good explanation for at least a part of the vertical dominance effect. Vertical lines occupying a larger proportion of the visual field may be judged larger than horizontal lines of the same length occupying a smaller part. Due to the rather small binocular overlap integrating the input of both eyes of about 22° , this kind of visual field is not found in pigeons. Since the human monocular field is less asymmetric than the binocular one, KÜNNAPAS (1957) predicted that the magnitude of the horizontal-vertical illusion should be less with monocular viewing than with binocular viewing. This was later confirmed by PRINZMETAL & GETTLEMAN (1993). Bearing in mind that a pigeon's combined visual field is less asymmetric than that of humans, too, underlines the possible relevance of this factor in our context.

The relative contribution of either of these two factors of anisotropy to the dominance of verticality HOETH reported about should be clarified by further research. Since the human monocular visual field is less asymmetric than the binocular one (and thus closer to that of pigeons), one could, for instance, think of running an experiment in which a square OAM is presented monocularly to human observers. The effect of this condition upon the value of the aspect ratio needed to secure an even distribution of the two apparent movement directions should allow an estimation of the relative contribution of the anisotropy due to the elliptical structure of the human visual field.

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Abstract

Like humans, pigeons exhibit multistability of perception when they are confronted with a constant stimulus pattern like the so-called orthogonal alternative movement (OAM): Perception switches between two interpretations of the unchanging sensory stimulus. In the experiment we reported here, five pigeons were trained to discriminate horizontal and vertical apparent motion stimuli and were then tested with seven (multistable) OAM stimuli that differed in their aspect ratios. Because for humans there exists a dominance of verticality, the OAM pattern that leads to an equal distribution of the two perceptual interpretations has to be horizontally biased (aspect ratio 0.62). Contrary to that, the results we obtained suggest that for pigeons a comparable dominance of verticality does not exist. The possible contribution for an explanation of the preference of verticality by human observers of OAM patterns of other well-known factors of the visual field anisotropy that differ for humans and pigeons are discussed.

Zusammenfassung

Wie Menschen zeigen auch Tauben perzeptive Multistabilität gegenüber einem konstanten Reizmuster wie die sog. orthogonale Alternativbewegung (OAM): Die Wahrnehmung wechselt zwischen zwei Interpretationen der invarianten Reizvorlage. Im hier dargestellten Experiment wurden fünf Tauben trainiert, zwischen eindeutig horizontaler und eindeutig vertikaler Scheinbewegung zu unterscheiden. Daran anschließend erfolgte ein Test mit insgesamt sieben (multistabilen) OAM Mustern, die sich in ihrem aspect ratio unterschieden. Da für Menschen eine Bevorzugung der Vertikalität besteht, muss zum Erreichen eine Gleichverteilung beider perzeptiven Interpretationen der horizontale Punktabstand der Reizvorlage kürzer sein als der vertikale (aspect ratio 0,62). Im Gegensatz dazu legen unsere Ergebnisse die Annahme nahe, dass es für Tauben eine vergleichbare Dominanz der Vertikalität nicht gibt. Der Bezug zu anderen bekannten Faktoren der Sehfeldanisotropie, die für Menschen und Tauben unterschiedlich sind, wird aufgezeigt und deren Beitrag zu einer Erklärung der Bevorzugung der Vertikalität durch menschliche Beobachter bei OAM Reizmustern diskutiert.

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