Vestibular System Part 2: Psychophysics, Applied Aspects and General Interpretations

By

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Preface

The function of the vestibular system is not as obvious as those of vision, hearing, touch or smell. Vestibular dysfunction, however, is clearly apparent where lesions are present. It is probably for this reason that the vestibular sense was not discovered until the nineteenth century and that clinicians have continued to play a major role in basic vestibular research right up to the present. The relationship between basic and clinical research is certainly stronger in the vestibular field than in that of tactile sensation, for instance, as testified by the work of clinicians as MENIÈRE, BREUER, BÁRÁNY, DEKLEIJN and FRENZEL. In this respect the situation is similar in vestibular physiology and in endocrinology, and for the same reason.

This second part of the vestibular volume of the Handbook of Sensory Physiology will be of interest to neurologists, otologists, neurosurgeons, ophthalmologists and physiotherapists on the one hand, and psychologists, physiologists, engineers and aviation specialists on the other. For a full understanding of Part 2, it is necessary to have assimilated the basic anatomy, physiology, and biochemistry of Part 1.

Each sensory system has some motor aspects. Nociceptors, for instance, have a special relation to the spinal flexion reflex and to flexion spasticity after spinal cord lesions. Tactile afferents are strongly engaged in the regulation of voluntary finger, hand, lip, and tongue movements. However, there is no other sensory system where the motor aspects are as important as in the vestibular. The cerebellum has evolved out of the vestibular system; the cerebellar nuclei are analogous (in function and in their connections to the cerebellar cortex) to the vestibular nuclei. The study of the role of vestibular mechanisms in body posture and eye movements has made a substantial contribution to the theory of the motor system. The simpler organization of active eye movements as compared to limb movements has facilitated understanding. This book takes these facts into account.

It is hoped that this volume may represent a small step toward an understanding of this part of Nature's secrets and at the same time facilitate clinical knowledge about the vestibular system.

Ulm, June 1974 HANS HELMUT KORNHUBER

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E. Psychophysics

Chapter II.

Optic-Vestibular Orientation to the Vertical

By

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With 12 Figures

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I. Introduction: On Orientation

By "orientation" we mean the proper arrangement of an object within a frame of reference.

Using the term "proper" takes account of a connotation of value attached to the concept of orientation in common language. It may be understood either in a merely *formal* sense, referring to aspects of symmetry, equilibrium, and the like, or *functionally*: we may call an animal "well" or "poorly" oriented if it is able or unable to find its way home after having been displaced; or, generally speaking, if its "arrangement within a frame of reference" is such as to optimize the animal's (or its species') chances of survival.

In humans, the "arrangement" may be understood to occur in the realm either of body activity or of perceptual organization, the "object" and the "frame of reference" beeing defined physically in the former case, and psychophysically in the latter. We therefore distinguish between *body orientation* and *perceptual orientation*.

We speak of *spatial orientation* if the frame of reference is a spatial one. Within spatial orientation two general groups can be distinguished, with the frame of reference being the essentially horizontal *map of life space*, on one hand, and the vertical *pull of gravity*, on the other. The former group, including, for instance, the problem of homing and route perception, will not be discussed here, although both the eye (as in sun-orientation, cf. BRAEMER, 1960) and the vestibular organ (BERITOFF, 1962, 1963) seem to play an important part in these performances, too. Instead, we shall restrict discussion to orientation to the vertical where, as we shall see, optic and vestibular sense are substantially involved.

Applying the dichotomy of "body" and "perceptual" orientation to this case, we may distinguish between

(1) *postural equilibrium responses*, i.e., motor activity serving to stabilize the intended posture of the body in the field of gravity (e.g., vestibular righting responses), and

(2) *perceptual space transformations*, i.e., physiological processes monitoring the constancy of space perception in the presence of factors changing the position of sense organs.

Perceptual space transformations will be called "*external*" if non-nervous processes like muscular mechanics are involved (as in the case of eye-movements), and "*internal*" if they are confined to pure nervous system activity (for further detail, see below, pp. 159 f.).

Postural equilibrium responses and perceptual space transformations are by no means independent of each other; instead, it is commonly felt that there is one and the same system producing both. In man, to be sure, much more sophistication has been invested in the study of the latter, at least in healthy subjects. The following chapter will therefore deal mostly with problems of perceptual orientation.

This report shall be organized with a *functional* viewpoint. In a field of research where the data available are clustered on two widely different levels of complexity — reports of perceptual phenomena on one hand, and records of neuronal discharges on the other — a functional approach seems to be most promising to bridge the gap. It might, moreover, provide us with heuristic strategies for further research both in neurophysiology and in psychophysics.

Three functional principles, i.e. three major types of information processing involved in orientational achievements, shall be distinguished below under the names of "compensation", "reconstruction", and "correction". Each of these principles has been introduced and discussed by a different group of authors: Compensation processes were first postulated by K. BÜHLER (1922) and form the core of the famous, though originally not quite consistently defined "reafference principle" of VON HOLST and MITTELSTAEDT (1950); the importance of reconstruction processes has been stressed by GIBSON (1950, 1966) and MACKAY (1966); correction processes play an outstanding role in the perceptual theory of E. BRUNS-

WIK (1934, 1956). A synopsis of these three principles has, connected with partial re-formulation, first been attempted by BISCHOF (1966b, p. 357–399). They will serve as a frame of classification of the following report.

II. Directional Constancy and the Compensation Principle

A. On Vertical Constancy

When exposed to a laterally tiltable, fronto-parallel luminous line in a dark room, a normal subject is able to estimate the slope of the line with quite satisfactory approximation: the inclination of the perceived contour to the apparent vertical nearly corresponds to the inclination of the physical contour with respect to the field of gravity. The sensory datum referred to by the brain in this estimation apparently consists in the slant of the line's retinal image or, more precisely, in the angle between the retinal projection of the line and a given reference axis fixed to the retina. This retinal image (the so-called *proximal stimulus*) serves, as it were, as the causal bridge connecting the object of interest, namely the luminous line outside in the dark room (the *distal stimulus*), and the perceived inclination (the *phenomenon*). Moreover, unless the subject contacts the distal object via an additional sensory channel (e.g., by touching), it is the *only* causal bridge of this kind.

Considering the latter we ought to be surprised that the relation between the retinal image and the distal object is by no means unique. Any particular inclination of the proximal stimulus contour within the retinal frame of reference may occur in the presence of a given slope of the distal stimulus line, because of the interference of a further independent variable, namely, the head tilt. When, for instance, the head is laterally inclined, the picture of a vertical line will appear on a retinal meridian different from the one upon which it is projected with upright head position. If the brain, in anthropomorphic terms, were to "rely" solely upon the information conveyed to it via the optic channel, it would be entirely unable to distinguish this situation from one in which the body remained upright but the line was tilted. The fact is, however, that the central-nervous perceptive mechanism is quite capable of making this distinction. This performance is usually referred to as "vertical constancy". The analysis of vertical constancy, then, has to start from the fundamental biological problem common to all constancy performances (others being, e.g., color, brightness, size and shape constancy): How can a veridical correspondence between the perceptual phenomenon and the distal object be established despite the fact that the only causal bridge intervening between them, i.e., the proximal stimulus, is disturbed unpredictably by the interference of a further variable?

B. The Compensation Principle

The solution of this general constancy problem was found, after preparatory work by HELMHOLTZ, HERING, MACH, and others, by K. BÜHLER and L. KARDOS (BÜHLER, 1922; KARDOS, 1928, 1929; BRUNSWIK and KARDOS, 1929) and later restated by von Holst and Mittelstaedt (1950). The basic idea is this: the organism neutralizes the interference *by repeating it with reversed sign.* Since a process of this kind may aptly be called "compensatory", Bischof (1966b) has proposed the term *compensation principle* to characterize this form of biological information processing.

The compensation principle is illustrated by the flow diagram Fig. 1a. The sensory channel S (generally the eye) is affected by a proximal stimulus, the latter

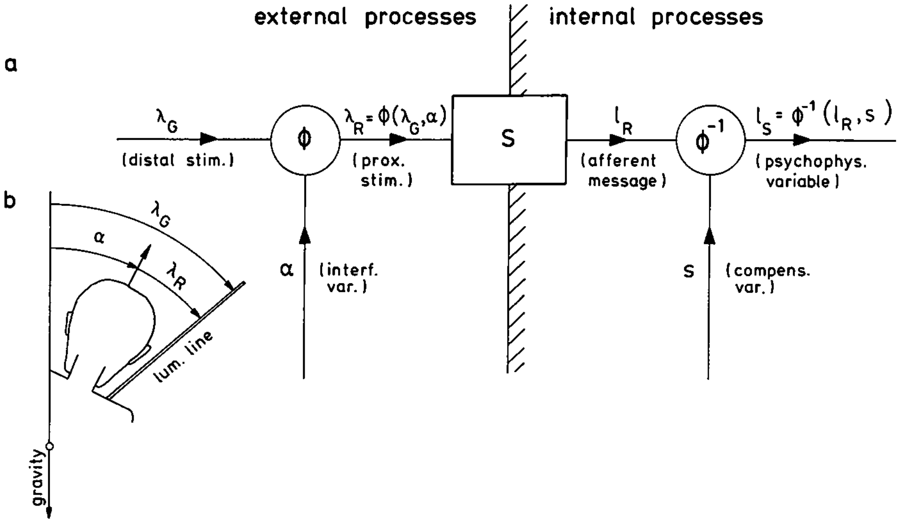

Fig. 1. a) Control diagram of the compensation principle. Here and in all subsequent block diagrams arrows represent variables, and boxes represent operators. Orientation of arrows denotes direction of causal influence. Φ = interference function, Φ^{-1} = compensatory function, S = mapping function of sensory channel. b) Interference function in the perception of verticality. Distal stimulus (λ_G) equals the *sum* of interfering variable (a) and proximal stimulus (λ_R), if orientation of angles is uniformly defined (here: clockwise inclinations positive, when viewed from Subject)

depending upon a distal stimulus and an "interfering variable", according to an "interference function" Φ. In our case, the interfering variable is the angle of head tilt (a), while the inclination λ of the luminous line relative to *gravity* (subscript G) is the distal stimulus. The slant of the line measured within the *retinal* coordinate system (subscript R) can serve as a representative of the proximal stimulus. The interference function has the form of a simple subtraction, as shown in Fig. 1b:

$$\lambda_R = \lambda_G - a.$$

The proximal stimulus is reported to higher central-nervous centers by means of afferent messages (l_R). Making use of this information, now, the organism has to arrive at a psychophysical variable[1] (l_S) representing veridically the distal

---

[1] By the expression "a psychophysical variable" we denote a hypothetical central-nervous process thought directly to underly a consciously experienced phenomenon (cf. also Bischof, 1966a).

stimulus. This is done by means of a compensatory process consisting of the following two operations:

(1) The organism ascertains in a suitable way a representation of the interfering variable, the "compensatory variable" (s).

(2) This compensatory variable is fed into the afferent information flow in such a way as to compensate for the influence of the interfering variable ("compensatory function").

In Fig. 1a the compensatory function is denoted by Φ^{-1}, since it can easily be seen that *in the ideal case* it would have to be exactly the inverse of the interference function. In our case, consequently, the ideal compensatory function would be an addition:

$$l_S = l_R + s.$$

In connection with the compensation principle three main questions arise: (1) Where is the compensatory process performed? (2) How should the flow diagram be modified to take account of the compensatory errors recorded under experimental conditions and in every-day life? (3) Where does the organism obtain the information about the interfering variable needed to determine the compensatory variable? These problems will be discussed successively in the following sections, with respect to the special case of vertical constancy.

C. External and Internal Compensation

As far as localization is concerned, two possible types of compensation are conceivable: (1) "external" compensation outside the boundary of neurophysiological processes, and (2) "internal" compensation within the central nervous system. Only the second possibility is taken into account in Fig. 1. The first is more obvious and easier to analyse. It consists in the so-called *ocular countertorsion* (rolling of the eyeballs around their sagittal axes). In the ideal case the amount of countertorsion should exactly equal the degree of lateral head tilt, thus leading to complete constancy of the retinal stimulus pattern. This, however, is never attained in any vertebrate species. In man, particularly, the countertorsion response can only be called vestigial (FISCHER, 1927, 1930a; WOELLNER and GRAYBIEL, 1959; SCHÖNE, 1962; MILLER, 1962; MILLER and GRAYBIEL, 1963; COLENBRANDER, 1964; KELLOGG, 1965; BRANDT and FLUUR, 1966, 1967; UDO DE HAES, 1970; BISCHOF and SCHEERER, 1970). When plotted against head tilt, ocular countertorsion shows a sinusoidal curve with extreme values ocurring at tilts of about 60°. Even at its extremes, the response seldom exceeds values of 6–8°, being, therefore, far too small to account for the compensatory achievements actually observed.

Consequently, there remains only the alternative of assuming an "internal" compensation, i.e., a central-nervous processing of the optical afference according to Fig. 1. Formally, such a process could be conceived as a rotatory transformation of a functional coordinate system, the latter being the physiological correlate of phenomenal space. The anatomical localization of these processes is still open to speculation, although recent neurophysiological findings (cf. chapter FREDRICKSON, KORNHUBER and SCHWARZ, this volume), contradicting the earlier opinion that no vestibular afferences reach the cerebral cortex, may turn out to be a first step towards answering this obscure question.

D. Allowance for Compensatory Errors

The argumentation in favor of the compensation principle (see above pp. 158 f.) may sound somewhat artificial, as it starts from the fictitious presupposition of exact veridicality of directional perception. This presupposition is, indeed, only approximately fulfilled in every-day life, and even larger deviations occur under experimental conditions.

If the optical stimulus field is reduced to a single luminous rod in a dark room, a subject's apparent vertical (as indicated by his setting of the rod) will exhibit systematic deviations from the physical plumbline, especially if the body is in a tilted position (cf. Fig. 2). Large amounts of lateral body tilt are undercompensated (AUBERT, 1861), i.e., the apparent vertical deviates towards body axis, whereas moderate amounts of tilt are sometimes overcompensated (MÜLLER, 1916), i.e., the apparent vertical deviates in the opposite direction (A and E phenomenon, respectively: UDO DE HAES, 1970; SCHÖNE and UDO DE HAES, 1971; for a review of earlier investigations, see BISCHOF, 1966c, pp. 474f.). Errors of the same order of magnitude occur with forward-backward body tilt (BRECHER and SCHUBERT, 1934; SCHÖNE, 1962, 1964; CORREIA et al., 1965). Considerable deviations are also observed when the subject is presented with an optical stimulus pattern containing one or more distinct main axes besides the luminous rod, provided that none of the main axes coincides with the pull of gravity. This phenomenon has been called "Richtungsinduktion" (directional induction) by KLEINT (1936). It obtains with such stimulus configurations as a field of parallel stripes (HOFMANN and BIELSCHOWSKY, 1909; GIBSON and RADNER, 1937; BISCHOF and SCHEERER, 1970), a grid pattern (BORING, 1952; MANN, 1952), or a luminous frame (WITKIN and ASCH, 1948; WITKIN, 1949b; PASSEY, 1950; YOUNG, 1959; NAYLOR, 1963, 1965; BERTINI, 1964; MORANT and ARONOFF, 1966). Under such conditions the subject's apparent vertical, as shown by his settings of the luminous rod, is "attracted" to a certain degree by the axes of the stimulus pattern. Directional induction effects are strongest with stimulus patterns that are closely similar to natural environments except for their slanted bearing. Such situations are created when the subject observes a natural scene through a suitable mirror system (WERTHEIMER, 1912; GIBSON and MOWRER, 1938; ASCH and WITKIN, 1948a) or through prism spectacles (KOHLER, 1951; OHWAKI, 1961; WITKIN and ASCH, 1948b; WITKIN, 1949a), or if the natural scene is tilted as a whole, e.g., in a rotatable dummy room ("haunted swing", WOOD, 1895; KLEINT, 1936; ASCH and WITKIN, 1948b; MANN, 1952); see also HOWARD and TEMPLETON (1966).

In the flow diagram (Fig. 1), three possible sources for deviations of this kind are conceivable: (i) the afference l_R may be a distorted image of the proximal stimulus configuration λ_R. (ii) The compensatory variable s may be an inaccurate representation of the interfering variable a. (iii) The compensatory function Φ^{-1} may differ from a mathematically exact summation process.

In this connection the three variables l_R, l_S, and s merit further consideration[2]. First, these quantities are to be regarded as "hypothetical constructs" in the sense of the terminological differentiation proposed by MCCORQUODALE and MEEHL (1948); i.e., they are meant to be not directly observable, but nevertheless physically existing, links of an innerorganismic causal chain. Simultaneously, however, they are "intervening variables" in the stricter sense defined by the authors — viz., they are conceived as products of a mere mental abstraction drawn out of (unknown) physiological entities likely to be in fact much more complex. The same holds for the above-mentioned compensatory operation Φ^{-1}.

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[2] For more detailed discussion, see BISCHOF and SCHEERER (1970).

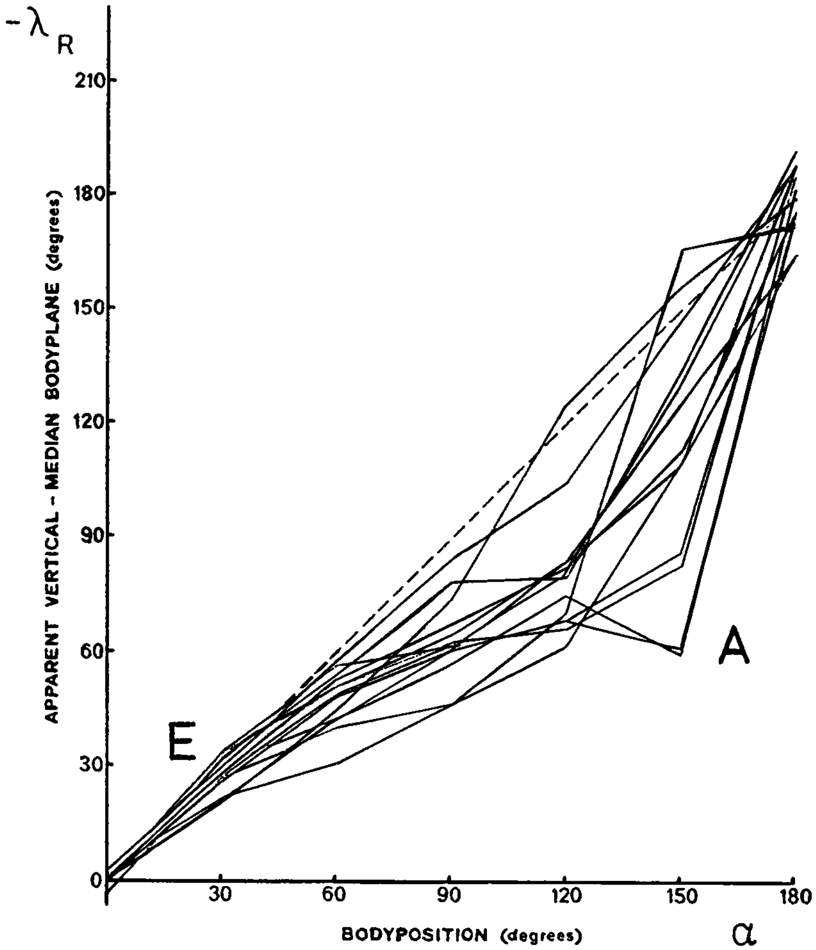

Fig. 2. Apparent vertical as a function of lateral body tilt for 13 Ss (according to Udo de Haes 1970). Abscissa: Clockwise body tilt. Ordinate: Inclination of a luminous rod, set to Ss apparent vertical, measured in retinal coordinates with inverted sign (for explanation, see below, p. 162). Dotted line indicates ideal veridicality of directional perception. E- (Müller) Phenomenon: measured value *above* dotted line (as shown in some Ss with body tilt of 30°), A- (Aubert) phenomenon: measured value *below* dotted line (most marked in the majority of Ss under body tilt of 150°)

With regard to the three alternatives listed above, Bischof and Scheerer (1970) arrive at the following proposition: If deviations from ideal veridicality in directional perception consist merely in rigid orthogonal rotations of phenomenal space without angular distortions occurring, they can be due solely to inaccuracy of the compensatory variable (alternative ii accepted), whereas the input-output characteristics of the optic channel and the compensatory summation process must be linear (i and iii rejected).

In this case, an indirect measure for the compensatory variable s could be derived from the setting of a luminous rod to the apparent vertical: If (i) $\lambda_R = l_R$, and (iii) $l_S = l_R + s$, and if further the apparent inclination l_S of the rod is zero (= vertical), then we should arrive at $\lambda_R = l_R = l_S - s = -s$. Thus the proximal stimulus λ_R with reversed sign, as plotted in Fig. 2, could serve as an operational measure for s.

As to the premise of this proposition, Gibson and Radner (1937, p. 464) state that the apparent vertical and horizontal "behave as if they were aspects of a single system for visual orientation"; the authors add, however, that both axes nevertheless "are not rigidly linked together; there is, as it were, a certain amount of 'play' or 'lost motion' between them". This angular distortion phenomenon was observed as an after-effect of prolonged exposure of an optical stimulus pattern containing (or consisting of) one predominating axis. Under these conditions, two factors seem to be involved in direction perception. They generate, respectively, (a) a so-called "*normalization effect*", which amounts to a rigid transformation of the phenomenal frame of reference as a whole (Gibson, 1937a, b; Gibson and Radner, 1937), and (b) a "*satiation effect*", which only occurs in the vicinity of the stimulus axis, thus indeed impairing the orthogonality of space perception (Köhler and Wallach, 1944). The latter phenomenon can probably be accounted for in terms of adaptation or inhibition of orientation detectors in the visual channel S of Fig. 1 (Sutherland, 1961; Coltheart, 1971; cf. also Carpenter and Blakemore, 1974). Thus, possibility (i), as listed above, cannot be ruled out entirely. However, satiation seems to be a second order effect. By factoring out the normalization effect be means of a "split-field technique", a magnitude of maximally 1.5° has been found for the satiation phenomenon (Morant and Mistovich, 1960; Morant and Harris, 1965).

These studies, to be sure, have only been performed with upright body posture. In a survey of the literature, unfortunately, no investigation dealing with the influence of body *tilt* on the orthogonality of space perception could be found. This leaves alternative (iii) undecided. Actually, some authors did record the apparent vertical and horizontal alternately in the same subjects as a function of head tilt, body tilt, or centrifuging, both with and without optical direction cues presented (Gibson and Mowrer, 1938; Asch and Witkin, 1948a, b; Witkin and Asch, 1948a, b; Bitterman and Worchel, 1953, Graybiel and Clark, 1962). However, these experiments yield no answer to our problem since they are not sufficiently precise for that aim or, as in the studies of the Witkin group, because of some peculiarities in the data analysis performed by the investigators. Nevertheless, the authors do not seem to have encountered a conspicuous decay of perceptual space orthogonality. Generally, one may presume that if body tilt and the like did produce startling angular distortions, this would have attracted the attention of some of the numerous investigators of vertical constancy during the past century, especially since under *pathological* conditions (cerebral lesions) or with *inadequate stimulation* (e.g., by electric currents) considerable distortions of the space coordinates have been repeatedly observed and reported under the name of *metamorphosia* or *dysmorphosia* by Gelb (1926), Bender and Jung (1948), Halpern (1949), Derwort (1953) and others.

E. Postural Direction Cues

For the time being we may therefore assume that the errors of directional perception observed under physiological conditions are due virtually alone to the compensatory quantity s not precisely coinciding with the head inclination a. Thus the third problem stated above (see p. 159), namely, where the organism obtains a representation of a, becomes crucial. Clearly, the sources of pertinent information have to be looked for in the realm of stimulus parameters that are correlated with head and/or body tilt. Such parameters are hereafter referred to as "direction cues".

The sensory systems thought to be capable of providing direction cues are usually classified into (1) *optical* and (2) *postural* groups. The postural group may be subdivided into (a) *tactile*, (b) *kinesthetic*, and (c) *vestibular* cues.

(a) The *distribution of pressure* on the body surface may well be taken into account as a direction cue, as its maximum corresponds to the physical "down" unless, to be sure, the support at the surface of contact is in a slanted position (GIBSON, 1966). The functional effectiveness of this factor at least for the "posture reflexes" has been demonstrated by MAGNUS (1924), its relevance for verticality perception follows from experiments of SCHÖNE and UDO DE HAES (1968, 1971).

(b) Coping with gravitation necessitates a continuous tonic innervation of the whole skeletal musculature, the pattern of which has to reflect in fine gradations the distribution of forces acting upon the body. Therefore the combined messages of *tension* and *position receptors* in muscles, tendons and joints (see BISCHOF, 1966c) may well be used as a source of information about the arrangement of trunk, head, and limbs with respect to gravity. The importance of these factors is underlined by the fact that asymmetric body tonus brought about, for example, by means of additional weights is accompanied by changes of the apparent vertical (KLEINT, 1937; SCHNEIDER and BARTLEY, 1962; KLIX, 1962; WERNER et al., 1951).

(c) Whereas the two aforementioned sensory systems are primarily concerned with tasks apart from the perception of body posture in the gravito-inertial field, the vestibular apparatus appears to be constructed directly to serve this purpose.

Among the vestibular cues, both *ampullar* and *macular* messages can be shown to contribute to human perception of verticality. In the maculae, *phasic* and *tonic* responses may be distinguished, according to LOWENSTEIN and ROBERTS (1950). There are few pertinent investigations deliberately involving stimulation of all vestibular portions mentioned (e.g., VON HOLST and GRIESEBACH, 1951; UDO DE HAES and SCHÖNE, 1970). In experiments with parallel swings (JONGKEES, 1952; WALSH, 1960, 1961; SCHÖNE et al., 1967) the semicircular canals remain essentially unexcited. Devices providing steady-state head tilt, as employed by most investigators, additionally rule out phasic receptor activity in the maculae. This restricts stimulation to the tonic (non-adaptive) receptor system in the otolith apparatus, which may be considered the basic issue in postural control of vertical constancy, at least as far as the *external* compensatory mechanism (eye countertorsion, see above, p. 159) is concerned (FISCHER, 1930a; MILLER, 1962; SCHÖNE, 1962; FLUUR and MELLSTRÖM, 1970a, b).

F. The Significance of Vestibular Direction Cues

The question as to whether vestibular afference has a direct access also to the *internal* mechanisms of perceptual space transformation is comparatively more intricate.

The significance and even preponderance of the vestibular apparatus in this respect has been maintained by investigators like JONGKEES (1952), but denied by some earlier authors (ALEXANDER and BARANY, 1904; BECK, 1912; STIGLER, 1912; GARTEN, 1920); partly, perhaps, since the latter expected (and failed) to encounter particular "postural sensations", reported by their subjects. These authors did not realize that a sense organ might well have the function of solely controlling perceptual *coordinate systems* rather than contributing new *qualities* to the perceptual world.

There is, of course, great difficulty in assessing the relative importance of each of the three postural systems mentioned above, since they convey information about one and the same stimulus parameter and may mutually substitute for each other. Thus, it is in no way conclusive if, in the case of deficiency of one of them, the performance in question does not substantially decrease — especially if the subjects have been allowed to adapt to the loss.

When, e.g., GARTEN (1920) and ARNDTS (1924) could demonstrate that the ability of subjects to judge the vertical position of their bodies remains unimpaired with *tactile information* being cut off by local anaesthesia, this finding nevertheless cannot disprove the possible participation of tactile direction cues in the same performance under normal conditions or after labyrinth loss.

On the other hand the same holds true for findings according to which patients with bilateral loss of *labyrinth function*, when tilted laterally, are still able to set a luminous rod in a dark surround in rather good alignment with the physical vertical, or even surpass the achievement of subjects without labyrinth malfunction (cf. FISCHER, 1930b; GIROTTI and BORDOGNA, 1963; GIROTTI, 1963; MILLER and GRAYBIEL, 1966; CLARK and GRAYBIEL, 1966a; GRAYBIEL et al., 1968). These experiments show that the activity of the vestibular apparatus may be substituted by other postural factors, if necessary. But they do not tell us anything about the error one is likely to commit if, as a first approximation, one ignores the latter when working with healthy subjects, and interprets the results obtained in the absence of optical cues as attributable mainly to the vestibular apparatus.

There seems to be only one consistent method for determining whether in the postural system vestibular cues are of prior importance in the perception of verticality: one has to play the vestibular information off against other conflicting postural direction cues. Experiments with this particular aim show that there is little extra-otolith postural influence on verticality perception with body tilt up to 90°, whereas in body positions unlikely to occur in normal life, somesthetic factors do play a role which is, however, not very marked (SCHÖNE, 1962; SCHÖNE and UDO DE HAES, 1968, 1971; CORREIA et al., 1965).

Unfortunately, it is still an open question as to how the organism gathers information about the direction of gravitational force from the excitation patterns of *utricle* and *saccule*, separately.

Within the framework of his "bicomponent theory", MITTELSTAEDT (1964, 1966) has called attention to the fact that the formula for rotatory transformation of a Cartesian coordinate system requires information about the sine and the cosine of the angle of rotation, and that the utricle and saccule, respectively, could well be understood to supply this information.

Actually, there is evidence that earlier views, according to which only the utricle, but not the saccule, has a static function at all (e.g., Maxwell, 1923; Versteegh, 1927; McNally, 1929; Tait, 1932) are untenable at least for birds and mammals and also for some fishes (Benjamins and Huizinga, 1927; Hasegawa, 1935; Perlman, 1940; Adrian, 1942; Jongkees, 1950; Lowenstein, 1950; Szentágothai, 1952; Huizinga, 1955; Meyer zum Gottesberge and Plester, 1965; Fluur and Mellström, 1970b). Whether, however, in the perception of verticality saccular and utricular information is computed in the elegant way proposed by the bicomponent theory, remains to be investigated. (For pertinent theoretical considerations, see Schöne, 1962; Correia et al., 1965; Young and Meiry, 1968; Schöne and Udo de Haes, 1970). The main difficulty with a bicomponent transformation of perceptual-space coordinates is that it could in principle be independent of otolith weight. When, however, the amount of gravito-inertial force is actually changed by means of applying *centrifugal forces* (Schöne, 1962, 1964; Correia et al., 1965; Miller and Graybiel, 1966; Schöne et al., 1967; Schöne and Parker, 1967; Schöne and Udo de Haes, 1970) marked changes of the apparent vertical do occur, showing that the aforementioned independence does not exist[3].

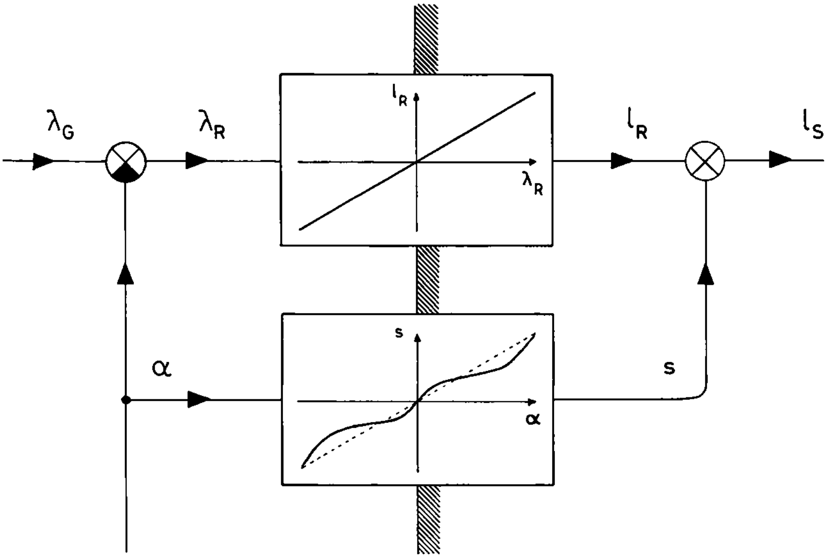

Fig. 3. Vestibular heterocompensation. Crossed circles: Operational symbols for addition. If a quadrant is black, the respective input variable is subtracted rather than added. Upper box: Visual system with linear input-output characteristics. Lower box: Otolith system with nonlinear characteristics according to Fig. 2

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[3] We are, of course, not referring here to changes of the apparent vertical due to changes in the *direction* (rather than the amount) of mechanical force during centrifugation. This effect is a physical triviality which never needed to be authenticated by psychophysicists, and which certainly did not deserve any pretentious labelling ("oculogravic illusion"). For a criticism of pertinent experiments designed by the Graybiel and Witkin groups, see Howard and Templeton (1966, pp. 197ff.) and Bischof (1966c, p. 481).

While leaving this question to further analysis, we are free to characterize the function of the otolith apparatus in vertical constancy by the control diagram Fig. 3. In this diagram the A and E deviations result from the input-output characteristics of a single black-box labeled "otolith system", leaving aside intravestibular differentiations for the time being.

The particular type of network presented in Fig. 3, in which the compensatory variable is provided via a sensory channel separate from the one conveying information about the proximal stimulus, will be referred to hereafter as "heterocompensation" (BISCHOF, 1966b). A possible alternative, called "autocompensation" of the optic message, shall be introduced in the next section.

III. Visual Direction Cues and the Reconstruction Principle

A. The Concept of Perceptual Reconstruction

The idea that the eye itself should be able to mediate perceptual information about the position of the head with respect to gravity not only seems to contradict our statements above, concerning the independence of retinal and distal coordinates (see p. 157); it also does not fit into the theoretical framework of classical sensory psychology. For the latter it was a matter of trivial self-evidence that a distal object could be immediately perceived (rather than inferred by logical reasoning) only in the presence of a proximal stimulus-pattern which to a sufficient degree "looks like" the distal object or, as GIBSON (1950) characterized this view, which can serve as a "facsimile" of the object. Since, now, neither the subject's own head nor the field of gravity is portrayed on the retina, perceptual information about these features cannot be conveyed via the optic system, according to classical understanding.

Modern perceptional psychology (cf. GIBSON, 1950, 1966; ATTNEAVE, 1954; KOHLER, 1961; METZGER, 1968) has abandoned this unreflected conception and arrived at the following principle: Although it makes sense to conceive of the perceptual phenomena as "images" of *distal* objects, it is entirely misleading to expect them to portray the *proximal* stimulus-configurations as well; a particular percept may be established on the basis of any sensory process whatsoever, provided only that the proximal stimulus concerned is at least *correlated* to the distal object. In terms of information theory, the principle maintains that the perceptual system takes advantage of the *redundancy* within its physical surroundings in a manner that could be compared to the way one reconstructs the text of an abbreviated or distorted telegram. Therefore, BISCHOF (1966b) has proposed the term "*reconstruction processes*" for this kind of stimulus elaboration.

B. Visual Direction Cues

Put in anthropomorphic terms the reconstruction principle states, in essence, that the organismic perceptual system "relies" on certain regularities "expected" in its physical surroundings (LORENZ, 1959).

Such "redundancy expectations" may be very concrete. It can be expected, for instance, that cigarette smoke rises opposite to the pull of gravity. One can show that such data, accumulated apparently in the course of individual life-experience, influence spatial perception without any noticeable intervention of higher cognitive processes (cf. KOHLER, 1951, 1953; KLOPP, 1956).

In addition to these, however, there are redundancy expectations of a far more generalized and abstract nature. For these is would be difficult to determine whether they have been acquired in an individual learning process or whether they are part of the phylogenetically preadapted organization of the perceptual system. This question, to be sure, is rather irrelevant in the present connection. With regard to vertical constancy two general redundancy expectations are of particular significance.

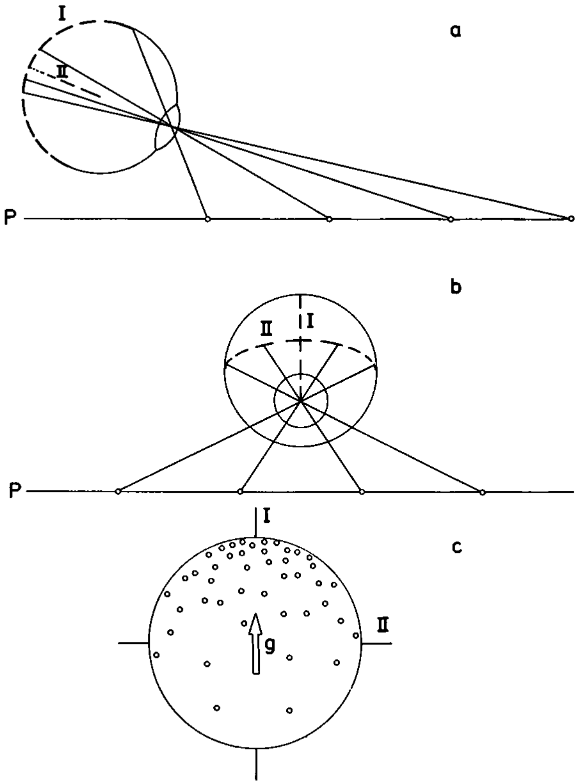


Fig. 4. Natural redundancy: Texture gradients. Equidistant marks on a plane surface (P) project on the retina in such a way that (a) the pairwise distance between proximal stimuli decreases monotonically in a retinal meridian (I) perpendicular to P, but (b) decreases symmetrically in a meridian (II) orthogonal to the former. If the marks are not equidistant but distributed in random fashion, as they are in most of the natural surface textures, the above statements would still hold true for the local average density of proximal stimulus distribution (Fig. 4c). Thus the *gradient* (g) of proximal-stimulus texture (i.e., the vector defining maximal change of stimulus density) should coincide with the physical vertical, providing that the surface regarded is horizontal

(1) The clarification of the first one has been pioneered by Gibson (1950). It consists of two mutually independent assumptions: (a) in a natural environment the texture of large surfaces is generally homogeneous, and (b) an approximately plain surface, filling large portions of the visual field, is likely to be of horizontal extension. From these two premises the following conclusion can be drawn: the mean gradient of retinal texture density, i.e., the direction in which retinal stimulation exhibits maximal average compression of its microstructure, will usually correspond to the projection of the physical vertical upon the frontal head plane (for explanation, see Fig. 4).

(2) The second redundancy expectation, the biological utilization of which has been substantiated by many authors (like, e.g., Koffka, 1935), assumes that under natural conditions equilibrium-states are encountered with a probability higher than that of any other comparable states. Consequently, objects of elongated shape should be likely either to stand upright (labile equilibrium), to hang down (stable equilibrium), or to lie horizontally on the ground (indifferent equilibrium), rather than to have any other *preferential* bearing. It can be shown by means of projective geometry that the outlines of such objects, when projected on the retina, form a stimulus pattern containing two prominent figural axes perpendicular to each other, and that one of these axes again corresponds to the projection of the physical vertical upon the fronto-parallel plane (see Fig. 5).

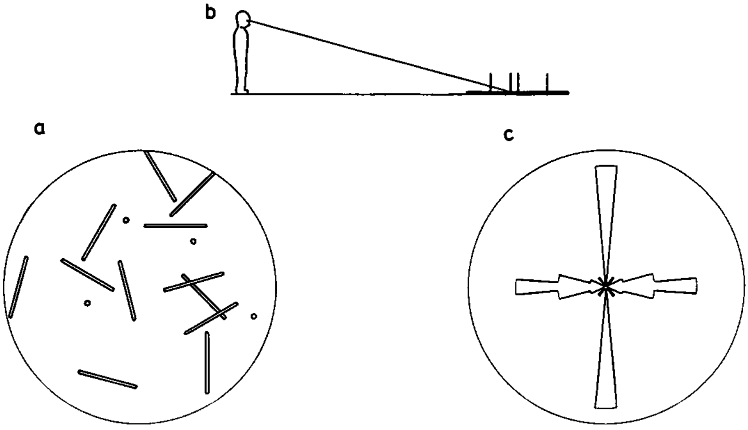


Fig. 5. Natural redundancy: Prominent figural axes. Sixteen contours of equal length, arbitrarily distributed on a horizontal surface, viewed from above (Fig. 5a). Among the contours, 4 stand upright (indicated by little circles), and the remaining 12 lie horizontally, oriented in such a way as to provide uniform angular distribution. When this arrangement is viewed from an angle of 15 degr. (Fig. 5b), the angular distribution of the retinal stimulus contours, taken in steps of 10 degr., appears as shown in Fig. 5c. Note that, although the number of horizontal contours exceed that of vertical contours by a factor of three, in the proximal stimulus distribution the peak resulting from originally vertical contours is still dominant

Whenever, therefore, the stimulus pattern impinging upon the retina contains a marked figural axis (particularly if the prominence of this axis is due to many single contours being parallel to each other), this axis tends to be accepted as a cue for either verticality or horizontality. It should be noted that the directional cue thus provided may be ambiguous. At least it can easily be rendered so by proper experimental device. If exposed, for instance, to a striped field or a square frame, the optical system is left in absolute doubt as to (a) which of the two prominent axes is vertical, and (b) which end of the vertical axis is the upper.

Experiments carried out by BISCHOF and SCHEERER (1970) illustrate how the organism copes with this fourfold ambiguity. The authors investigated three (female) subjects who were tilted by means of a chair rotatable around the sagittal head axis. The subjects looked towards a stimulus pattern consisting of a circular field of twenty-five parallel stripes on a dark ground. Shining on to the surface of the striped field from a pivot at its center, was a narrow light beam, which was to be set continuously to the subject's apparent vertical. The striped field was automatically rotated with a constant angular velocity of no more than 0.5 degrees per second either clockwise or counterclockwise. In each trial, the field made one full revolution of 360 degrees (taking a time of 12 min), while body-tilt was held constant at one of seven values (0, 30, 60, 90, 120, 150, 180 degrees clockwise). The subject's settings of the luminous beam were automatically recorded on a time scale.

The responses of one of the subjects are plotted in Fig. 6; they show that the apparent vertical is indeed entrained by both the direction of the stripes (referred to as the "primary axis" by the authors) and the axis perpendicular to the stripes ("secondary axis"). Each end of both axes, alternately, behaves as the upper one. Incidently, it can be seen that the "attractive power" of the primary axis exceeds that of the secondary axis to a noticeable degree. Applying a FOURIER-analysis to the curves shows that the primary axis is also dominant for body inclinations of $a = 150$ and 180 degrees, although this is not easily recognizable in the raw material, due to noise.

These results are in substantial agreement with earlier findings of GIBSON (1937a, b) and GIBSON and RADNER (1937), who observed that in the presence of a single tilted line the apparent vertical deviates towards the line if the latter's tilt is moderate, but away from it if its inclination is nearing the horizontal (cf. also CULBERT, 1954; MORANT and BELLER, 1965).

C. Visual Auto-Compensation

When outlining in his 1966 publication what is basically the reconstruction principle, GIBSON contrasts this idea with the compensation principle in the form proposed by VON HOLST and MITTELSTAEDT (1950). According to GIBSON, the optical feed-back produced by displacement of the body is substantially different from an optical stimulation caused by changes in the distal environment. Thus the visual afference is not really "disturbed" by the body activity (a), and consequently no compensatory process is required. This consideration is felt to dispense with the concept of "a brain that copies, stores, compares, matches, and decides" (*loc.cit.*, p. 39). This remark, however, is misleading. What really turns out to be dispensable from this point of view is what we have called "hetero-compensation" (see p. 166). The need for a compensatory process as such still

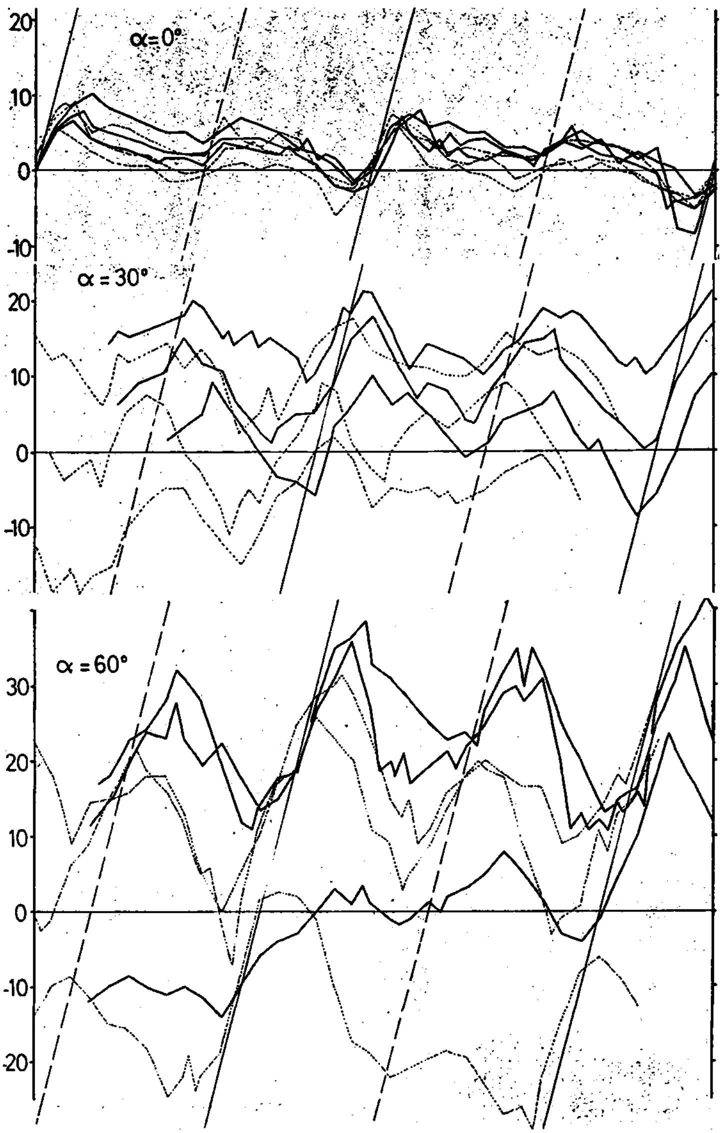
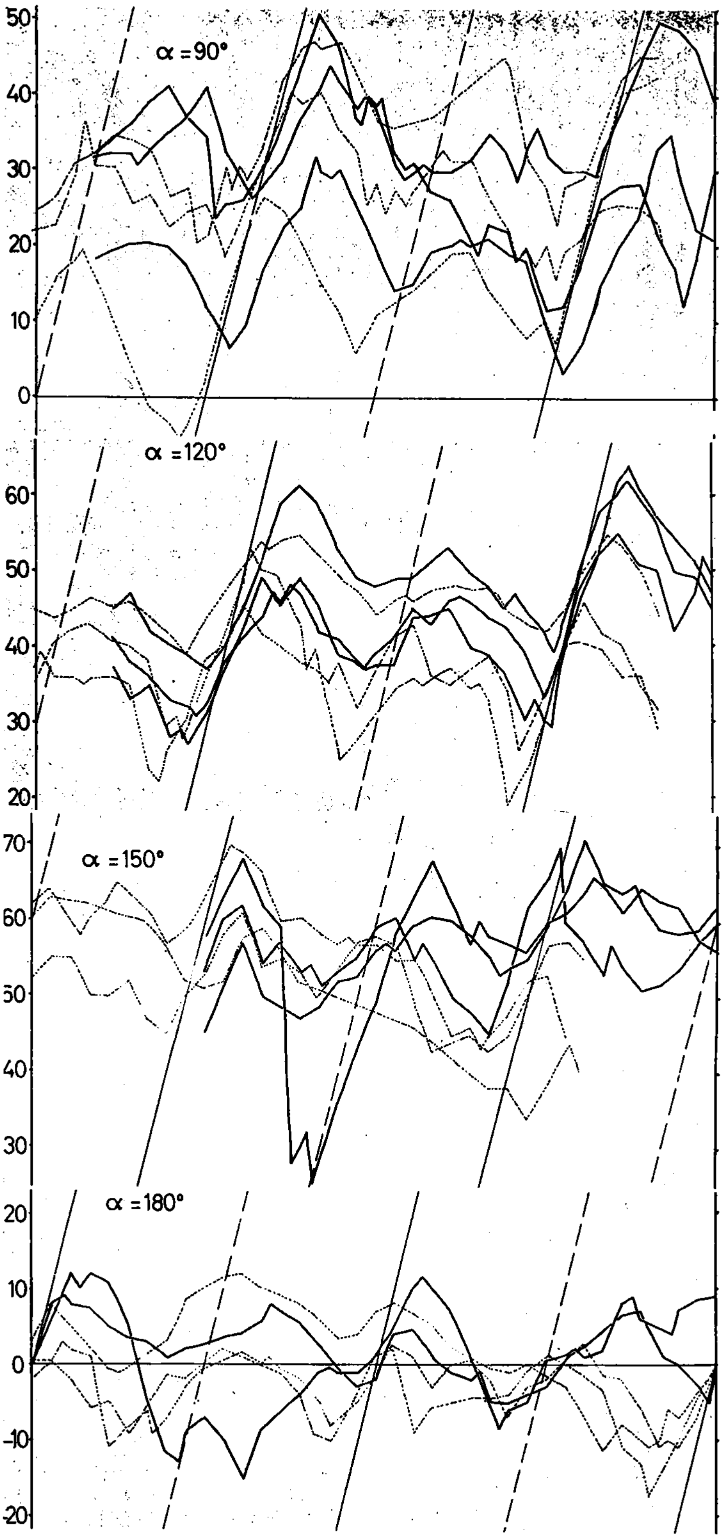


Fig. 6. Raw data of one S in the experiments of Bischof and Scheerer (1970). Each single diagram (a–g) comprises about 6 measurements of the apparent vertical in one particular body position (α), the latter being specified in the upper left corners. Half of the curves are from clockwise (solid lines), half from counter-clockwise rotation of the striped field (dotted lines). *Ordinate:* Angle (λ_G) between gravity and light beam set contineously to S's apparent vertical. *Abscissa:* Angle (β_G) between gravity and primary axis of background striped field. Full length of abscissa = 360 degrees = one revolution of the striped field. Since the latter rotates with constant velocity, the abscissa may also be understood as a time scale (full length = 12 min). In this case, the abscissa reads from left to right for the solid curves, but from right to left for the dotted ones. Recordings in most cases begin about 1 min after the striped field starts to rotate, in order to eliminate onset transients. *Diagonals* indicate the position of the striped field's primary axis (solid diagonals) or secondary axis (broken diagonals). The underlying white curves are simulations computed from the model Fig. 12 (see below, p. 184)


α = 90°
50
40
30
20
10
0
α = 120°
60
50
40
30
20
α = 150°
70
60
50
40
30
α = 180°
20
10
0
-10
-20

remains. It may now be, however, of a different type, namely, what could be termed "auto-compensation".

The essentials of auto-compensation are most easily understood in the case of *motion constancy*. Looking down at an ant-heap, e.g., causes a great deal of stimulus movement on the retina. Suppose, now, that the central nervous system would simply average the messages of all the retinal motion detectors, thus computing the vector sum of the velocities of all proximal stimulus elements. Since these elementary vectors are virtually independent of each other, the outcome of the calculation would more or less equal zero. If, however, the reafferent stimulation of smooth eye movement — caused, e.g., by pursuing one particular ant — were superimposed on the retinal stimulus-processes, then the average taken would equal with considerable exactness the eye velocity (with reversed sign, to be sure) and thus be fit to function as a compensatory variable for motion constancy. This procedure evidently is followed, erroneously, in cases of so-called "induced movement" (swimming up-stream with the bridge, etc).

Speaking generally, in auto-compensation the compensatory variable is derived directly from the afferent (in our case visual) message contaminated by the interfering variable. It presupposes the existence of a *filter mechanism* that selects, utilizing redundancy-expectations, the reafferent component (a) out of the retinal message itself (cf. Fig. 7).

How the filtering process is performed in the case of vertical constancy remains unknown. Presumably contour detection as described by HUBEL and WIESEL (1959) is involved, with subsequent averaging to compute the predominant

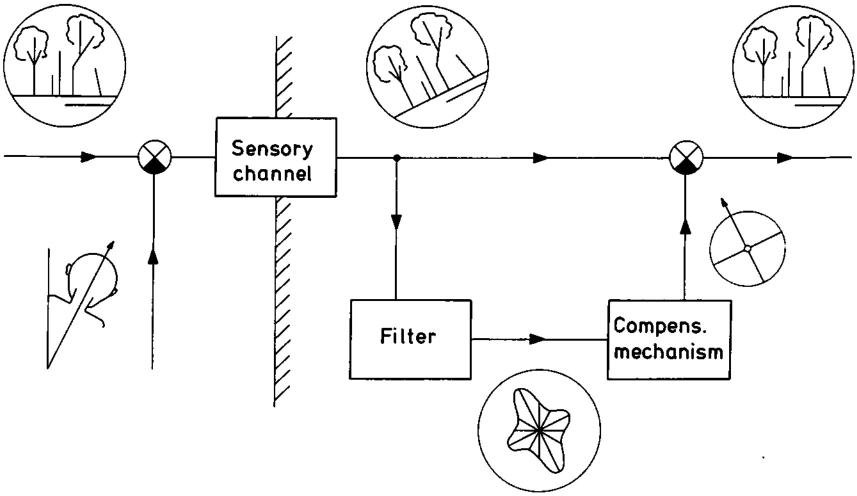


Fig. 7. Feed-forward autocompensation. A variety of distal-stimulus contours (left input variable, corresponding to λ_G in Fig. 1) when regarded with tilted head (lower left input variable, a) impinges on the retina in oblique orientation. When the resulting afferent message (l_R) is "filtered" in such a way as to compute the angular distribution of contour directions (according to Fig. 5c), the resulting main axis of retinal contour elements should, with sufficiently high probability, equal head inclination (with reversed sign). Consequently, it could be used as a compensatory variable (s, symbolized by a coordinate frame). When referred to these coordinates, the retinal afference should indeed be transformed in such a way as to render a sufficiently veridical perceptive representation (right output, l_S) of distal stimuli

proximal-stimulus axis, but for a definitive answer one must await further neurophysiological evidence. In this connection, moreover, neurophysiologists should also look for detectors sensitive to Gibson texture-gradients (cf. p. 168).

Auto-compensation by a filter-mechanism can in some degree be compared to an *adaptive* process. The crucial difference between it and a genuine local adaptation is, however, that in the latter every site of the sensory field tends independently of the others to approach the zero-level of excitation; whereas in auto-compensation the zero-level of the entire stimulus field shifts uniquely, which has the important consequence that the differences appearing within the proximal stimulus pattern are preserved (cf. also Metzger, 1968, p. 167ff.). In the special case of verticality perception, adaptation and auto-compensation are exemplified, respectively, by the "satiation" and "normalization" effects mentioned earlier (see p. 162).

D. Feed-Forward and Feed-Back Compensation

In all cases of auto-compensation two fundamentally different ways of feeding the compensatory variable into the optic afference are available: the compensatory variable may enter *after* the branching point to the filter (*feed-forward compensation*, Fig. 7), or *before* it (*feed-back compensation*, Fig. 8). In terms of control theory the first model has been called a "mesh", the second one a "loop" (Mittelstaedt, 1960).

In feed-forward compensation, provided that the filter can reconstruct the head inclination without error, the compensatory variable has to equal the filter output in order to establish ideal space constancy. In feed-back compensation, on the other hand, veridicality requires that the compensatory variable

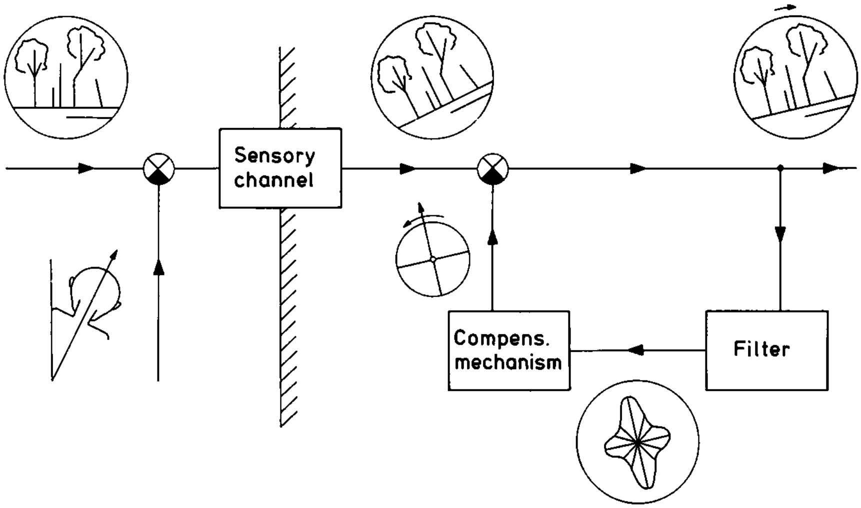


Fig. 8. Feed-back autocompensation. Differing from the system of Fig. 7 in that the perceptual output (l_S) itself undergoes the "filtering" procedure, and that the compensatory coordinate frame (s) is *rotated* as long as the inclination of the main axis of apparent contour distribution differs from zero

equal the time integral of the filter output. In the latter case, the magnitude of the compensatory variable will *change* as long as the filter output is different from zero; obviously, this process cannot come to rest with a steady value of s until the filter output has vanished, i.e., until the main axis of the perceptual field has turned *apparently* vertical. For a broader discussion see BISCHOF and SCHEERER (1970).

Which of the two possibilities is actually realized in the organism can be readily answered in the case of "external" compensation (cf. p. 159). Here, by definition, the compensation takes place outside the boundary of neurophysiological processes, whereas the compensatory variable comes from the filter that lies within this boundary. Thus, the ocular countertorsion and, incidentally, also all optokinetic reactions including nystagm, are examples for feed-back autocompensation.

Much more difficulty arises when we try to answer the same question in the field of "internal" compensation, since here the entire network is hidden within the brain, inaccessible to direct analysis. However, BISCHOF and SCHEERER (1970) could develop a method that allowed them to solve the problem in an indirect way. We can only outline their argumentation here; for a more thorough presentation, see the publication cited.

Regarding the oscillations in Fig. 6, which are schematized in Fig. 9, it is easy to see that for each particular curve the abscissa could be partitioned into sections extending, respectively, between two successive extreme values of the oscillation of the apparent vertical. In Fig. 9a, one half of such a section is labeled as B. Each of these sections would then mark a range of stripe inclinations which have in common a particular dominance relation between the four main directions of the striped field. The abscissa of each extreme value denotes the critical inclination of the field at which one of its main directions starts or ceases to predominate over the other three in determining the apparent vertical. What, now, causes the dominance to shift from one main direction to the next? Evidently, in the course of field rotation each particular main direction is alternately perceived to be more and more, and then less and less, likely to be a valid representative of the physical vertical. This, however, presupposes a *standard* reference with which the perceptual system may decide about accepting a given optical main direction as a cue for verticality (cf. also DAY and WADE, 1969). Presumably, the additional information required for this decision is supplied by the postural senses. However, this information appears in crucially different forms in feed-forward and feed-back compensation, respectively.

(1) *In feed-forward compensation* (Fig. 7) the standard determining the dominance relations within the set of optical main directions would consist essentially[4] of the vestibular compensatory variable (the "vestibular vertical") established according to Fig. 3. Thus, the inclination of a particular optical main direction with respect to the *vestibular vertical* decides about the acceptance of this direction as an optic cue for verticality. The vestibular vertical, however, depending as it does upon postural stimuli that are kept constant during each trial, should be expected to show limited systematic shifting at most, even when one allows for

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[4] Possible other postural cues (non-vestibular, non-optic) are being neglected here; this, however, is not relevant in the line of argument.

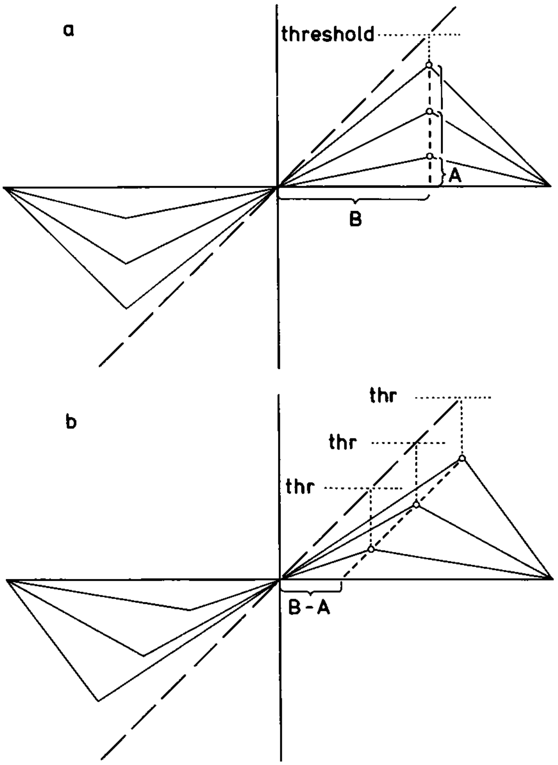

Fig. 9. Comparison of alternative compensatory mechanisms. Oscillations of an apparently vertical light beam. Ordinate: Angular inclination of light beam with respect to the DC component of oscillation (the latter representing the vestibular standard). Abscissa: Time; solid lines: settings of light beam for different body inclinations. Broken diagonals: Position of one particular main axis of the striped field. a) *Feed-forward compensation.* When the striped field axis has deviated far enough from the vestibular standard and reached a threshold (horizontal dotted line), the dominance will be taken over by the next axis. Hence the light beam would cease following the first axis and turn back to meet the next one. The curves should therefore show extreme values at this point. Since this process ought to be independent of body tilt, the maxima should all occur at the same time (B) in the cycle, irrespective of the amount (A) of oscillation. b) *Feed-back compensation.* If, however, the dominance of the striped field axis depends upon its deviation from the apparent vertical, i.e., from the respective light-beam curves, the threshold (dotted lines) *will* vary with the amplitude of oscillation. Thus all extreme values should now have a position such that their distance to the broken diagonal is constant. This distance ought to be the difference between the abscissa value (B) and the ordinate value (A) for every extremum

moderate changes due to system dynamics (transfer characteristics and the like) of the sensory systems concerned (cf. MÜLLER, 1916; MILLER and GRAYBIEL, 1963; GEISSLER, 1965; MCFARLAND and CLARKSON, 1966; CLARK and GRAYBIEL, 1966b; SCHÖNE and UDO DE HAES, 1968; UDO DE HAES and SCHÖNE, 1969). Hence the ranges of influence of the four main directions in the striped field are distributed according to a standard reference direction that remains virtually fixed during any given trial. To be sure, the reference direction will change from trial to trial, owing to there being different head inclinations, but within each of these it will remain essentially constant. This means, however, that we should find the sections of the abscissa apportioned by one and the same ratio regardless of head inclination, as indicated in Fig. 9a.

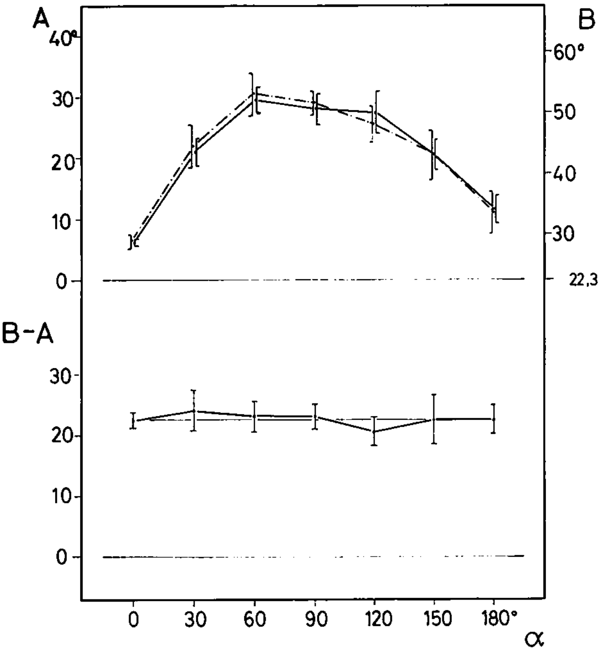

Fig. 10. Experimental support of feed-back autocompensation hypothesis in the perception of verticality (from Bischof and Scheerer, 1970). Comparison of ordinate (A: solid lines) and abscissa (B: broken lines) for extreme values of apparent vertical (cf. Fig. 9). Mean values of three subjects, with average variance of means shown by bars. B scale shifted so as to accomplish maximal coincidence of curves. Evidently, B is dependent on head inclination (abscissa), whereas B–A is not

(2) Hypothesizing *feed-back compensation* (Fig. 8) yields quite different predictions. In this case the optic messages do not reach the filter mechanism before having undergone the (combined optic-vestibular) compensatory process that transforms them into the final coordinate system of apparent space. It is thus the *apparent* inclination of the four optical main directions (rather than their inclination with respect to a postural standard) that determines the partitioning of their spheres of influence. In other words, with feed-back compensation the apparent vertical, as represented by the luminous beam controlled by the subject, serves as the reference required for the validation of the optical main directions. Defined in this fashion, however, the reference is no longer invariant during a trial, and it varies, moreover, in a different way with different head inclinations. With feed-

back compensation, consequently, the abscissa sections between extreme values in Fig. 6 would not be apportioned independent of head inclination. Only if we refer the stripe inclination at every moment to the position of the apparent vertical, i.e., if we project the extreme values, as in Fig. 9b, parallel to the diagonal broken lines, rather than perpendicularly, should we obtain an invariant partitioning of the abscissa.

Bischof and Scheerer (*loc.cit.*) could show, that, with this latter transformation carried out, the partitioning of ranges of influence among the four optical main directions in fact becomes invariant relative to head inclination (see Fig. 10). This indicates that the internal auto-compensatory system of visual perception of verticality is of the feed-back type.

IV. Optic-Vestibular Interaction and the Correction Principle

A. The Utilization of "Convergent Detection"

The simultaneous occurrence of both (optical) auto- and (vestibular) hetero-compensation in human vertical constancy sheds light on another peculiarity of perceptual information processing. Apparently, compensatory achievments are confined within the limits of precision of the mechanisms that provide the compensatory variable s. When, owing to possible shortcomings in information conveyance or computation, the compensatory variable does not exactly correspond to the interfering variable a, then s is unable to balance the effect of a exactly, and the interference is under- or overcompensated. The A and E phenomena described above (see Fig. 2) are examples of this.

In order to minimize such errors, the organism often seeks to provide information about an interesting distal item by using, in parallel, a plurality of sensory channels which are susceptible to different kinds of disturbing effects. Thus, the probability of error can be reduced by "convergent detection", as it were, a possibility that has been repeatedly discussed in psychological literature (cf. especially Brunswik, 1934, 1940, 1956). For reasons that will be explained later (see p. 180), Bischof (1966b) has proposed the term "correction principle" for this method of perceptual information processing.

B. Optic-Vestibular Equivalence

Separate sensory data which provide information about one and the same distal issue, and which are, accordingly, exchangeable with respect to their biological significance to the organism, will be referred to in the following as "*equivalent signals*". In this respect, a remarkably close relationship exists between optical and vestibular messages: for every particular output of the vestibular organs there exists an equivalent optical signal-parameter; likewise, every motor or perceptual effect known to be controlled by vestibular inputs can also be elicited by proper optical excitation.

More particularly, stimulation of the *semi-circular canals* is equivalent to visual excitation produced by uniform movement of the entire stimulus field. The perceptual results of the latter are usually referred to as "*induced movement*"

(Duncker, 1929; Linschoten, 1952; cf. also Gibson, 1950, 1954); the corresponding motor reactions are known under the name of "*optokinetic responses*". The optical counterparts of stimulation of the *otolith organs* have been discussed in an earlier section (see pp. 166 ff.); their perceptual effect, viz., their influence on the apparent vertical, has been termed "*directional induction*" by Kleint (1936), with obvious reference to Duncker. In labeling the corresponding motor reactions, it might be convenient to speak of "*optostatic responses*" in analogy to "optokinetics". The impairment of body balance while observing a slightly but uniformly slanted mountain meadow is an optostatic effect, as is the "dorsal light reaction" in fishes (von Holst, 1950). The occurrence of optostatic eye countertorsion in man has been reported by Greenberg (1960) (cf. however Howard and Templeton, 1964 b).

Note that optic and vestibular signals are *not* equivalent with respect to information concerning straight body movements. Here only the eye is able to convey reliable information (Gibson, 1954), and not the vestibular apparatus, contrary to repeated speculations (e.g., by Magnus, 1924). Whether and how messages of the latter may yet play some role in this connection, will not be discussed here (cf. Bischof, 1966 c, p. 483 f).

C. Incongruity of Equivalent Signals

Like reconstruction processes, the method of convergent detection is also based on the utilization of redundancy — not, to be sure, within the domain of distal objects, but rather on the level of sensory messages referring to these objects: the organism tries to keep on the safe side by seeking information from different "warrantors". But what if those warrantors are at odds with each other; i.e., what if equivalent messages exhibit *incongruity*? In general there are three possible organismic reactions in such a situation; all three do also appear in the special case of optic-vestibular incongruity.

1. "Compromise" Solution

The most usual organic reaction encountered with optic-vestibular incongruity is the calculation of a weighted average of the competing messages. The weight factors involved in this type of information processing will be discussed below (see pp. 180ff.). Evidently, the results of the experiments of Bischof and Scheerer (1970), as depicted in Fig. 6, can be understood as compromise solutions of this type. Von Holst (1950) and Braemer (1957) obtained comparable results with fishes.

2. "Alternative" Solution

A second possibility is that the organism takes account of only one of the competing signals while entirely blocking the others. The dominance may or may not flip-flop between the signals concerned. Here, again, weight factors are likely to play a role. Effects of this kind may be encountered if very suggestive optic direction cues, for instance a (tilted) dummy room, are viewed in upright body position. Some subjects of Kleint (1936) reported that under these circumstances the dummy room appeared to them alternately tilted and upright.

3. "Simultaneity" Solution

Whereas the two previous solutions to the incongruity problem will always provide an unequivocal basis of orientation, there are cases in which the incompatible signals reach conscious perception simultaneously, without mutual suppression. It may be questioned, of course, whether we can speak of a "solution" here, as the resulting perceptual phenomenon is over-determined in a paradoxical way, unfit for being reacted to. If, for example, a subject remains stationary, surrounded by a dummy room that rotates slowly around a horizontal axis, he generally experiences his body at first to be somewhat tilted in the opposite direction; subsequently he feels that his body keeps rotating, yet that its position no longer changes: the experience of motion ("I am rotating with constant angular velocity") and the experience of position ("I never reach the head-down posture") break apart (KLEINT, 1937; cf. also DUNCKER, 1929; OPPENHEIMER, 1935; METZGER, 1940, 1954, p. 150). — Even in the absence of visual information, some subjects experience two possibilities of setting a luminous line to apparent verticality simultaneously under body tilt of about 150°. This would indicate a conflict within the postural cue system (FISCHER, 1930; UDO DE HAES and SCHÖNE, 1969; GRAYBIEL and CLARK, 1962; MILLER and GRAYBIEL, 1966; cf. also below, p. 182).

D. Error Detection and Error Correction

The practice of obtaining information about the same item through parallel channels is in some measure analogous to that of modern communication technique, which uses, for conveying a message over a single channel, a number of symbols that exceeds the theoretically required minimum. Both methods utilize signal redundancy, and both do so for the sake of the advantage that in case of error the receiver is supplied with at least (1) a warning that an error is present, but perhaps also (2) with cues for its correction.

1. Error Detection

The receiving system can tell from certain irregularities in the signals received — in the case in point, from the incongruity of equivalent messages — at least *that* an error has occurred, although it may have no idea at which particular place. There is indication that the sensory systems react to this kind of "alarm" by forwarding only in a restricted form (with a proviso, as it were) the message likely to be erroneous. The corresponding phenomenal quality is often referred to by the subject with terms like "uncertain", "vague", "feeble", "faint", "unconvincing", "unreal", and the like (cf. METZGER, 1954, pp. 109f.). From experiments with the "haunted swing", for example, it is known that under conditions of strong optic-vestibular ambiguity a weakening, even a loss, of phenomenal verticality may result; in the extreme case, the subject may become unable to assign the terms "up" and "down" to *any* direction of his phenomenal space (KLEINT, 1936, 1940).

A particularly vigorous reaction of the organism to error warnings due to incongruities within the optic-vestibular domain consists, according to many authors, in the phenomenon of *vertigo*. Indeed, certain distinct features of this response, like anxiety and release of primitive security reflexes (clinging), may well be understood as emergency measures in the face of threatening decomposition of space orientation. For more details, see the chapters F.VIII; IX; G.I. in this volume.

2. Error Correction

In certain communication systems the receiver may not only be informed, by inconsistencies in the message, that an error has occurred, but also where it is probably sited and what the original text most likely was. We have reason to believe that the method of convergent ascertainment in the perceptual system also works as an error-correcting routine in this sense. That is why we have proposed the term "correction principle" here.

Above (see p. 178) we introduced the notion of "*weight factors*" that control the relative power available to equivalent sensory messages when they compete with each other in the case of incongruity (cf. Kleint, 1936). The evidence obtained up to now allows us to conjecture that those weight factors tend to be computed according to the following rule: The less a signal is likely to convey an erroneous message (i.e., the more and the better cues speak in favor of its reliability) the higher is it weighted in competition with contradicting equivalent signals (Brunswik, 1956; Klix, 1962). Thus we may tentatively summarize the *correction principle* as follows: The organism reduces the probability of error in the perceptual processes by providing for equivalent messages through different sensory channels and then "relying" exclusively or preferably upon those whose validity is supported by the better cues.

E. Determinants of the Optic-Vestibular Weight Ratio

In his classical investigations on the equilibrium responses of fish during conflicting optic and vestibular stimulation, von Holst (1950) coined the term "statisch-optische Verhältniszahl" (translatable as "vestibular-optic weight ratio") to refer to a specific parameter that expresses the degree to which the vestibular righting-response prevails over a conflicting dorsal light reaction (cf. also Braemer, 1957). Von Holst defined this coefficient as the cotangent of the angle between the dorso-ventral axis of the fish and the plumb line, recorded under conditions of horizontal light incidence. For the results to be interpretable the angle had to be measured when the fish was in a state of physiological equilibrium, i.e., after possible postural reflexes had ceased. Because of the latter condition von Holst's definition of the "vestibular-optic weight ratio" is suitable only for experimental situations in which the subject senses his body to be vertical. For perceptual experiments in which, by body fixation, every possible feed-back of the apparent vertical on body posture is blocked and in which, therefore, body inclination and apparent vertical do not necessarily correspond, a different way of defining the weight ratio is advisable. For reasons to be elucidated below (see p. 182), Bischof and Scheerer (1970) suggest taking the *average range of oscillation* of the apparent vertical, under conditions of steady rotation of the optical pattern around the visual axis, as an index of the weight ratio discussed.

In distinction to von Holst's term, we feel it would be better to speak of an "*optic-vestibular* weight ratio" here, since the value of the coefficient — the mean amplitude of oscillation in Fig. 6 — increases monotonically with optic predominance.

The factors governing the optic-vestibular weight ratio (however defined) have not yet been thoroughly investigated, partly because for years authors have engaged in a fruitless debate as to which of the two sensory channels, the optical or the vestibular, is "prior" or "more basic" to the perception of the vertical, instead of taking for granted that *both* are important and simply asking how they interact (for a critical review of this discussion, see GIBSON, 1952).

1. As far as the *optical* determinants of the optic-vestibular weight ratio are concerned, we know this much: with labyrinthine stimulation constant, the induction of the apparent vertical by a striped field rises with the size of the latter and with the number of parallel contours within it; when patterns of higher complexity are used, the induction effect is enhanced according to the degree of their similarity to natural scenes (for references, see above, p. 160). These findings harmonize well with the correction principle, since each of the factors mentioned apparently makes it more probable — outside the laboratory situation — that the main direction of the retinal stimulus field coincides with the direction of gravity.

2. Less transparent is the biological advantage of certain *intra-organismic* factors influencing optic-vestibular competition. Between different fish species, for instance, considerable variation in the vestibular-optic weight ratio has been found by VON HOLST (1950) and BRAEMER (1957). In man, typological differences are asserted to occur: women and children give comparably more weight to visual stimuli than adult males, according to WITKIN et al. (1954). It is difficult to see what all this should have to do with the "reliability" of optical or vestibular cues. Actual needs, moods, attention and the like can also influence the perceptual response in optic-vestibular conflict situations. VON HOLST (1948) could demonstrate that the body inclination of laterally illuminated fishes is markedly enhanced when objects of high motivational valence (e.g., food) are presented. The animal, as it were, becomes "all eyes" and consequently rates the light source as a directional cue comparatively higher than he otherwise would, although the light source is not his object of attention at all and certainly has not become any more "reliable." The effect of light intensity upon the weight of optical directional cues (CURRAN and LANE, 1962) may be mentioned in this connection. Findings like these suggest that the correction principle should not be understood as a general postulate, but rather as a heuristic principle.

3. The *vestibular-somesthetic* influences upon the optic-vestibular weight ratio are, again, interpretable in "reliability" terms. According to observations of VON HOLST (1950), shaking the water in an aquarium, simulating surf, is apt to enhance considerably the optical component with some fish species. In this experiment, the laterally illuminated animals inclined their bodies more and more towards the light source, only gradually returning to the previous position after the water movement had stopped. VON HOLST also noted that an increase in hydrostatic pressure tends to augment the weight of the vestibular component. This, too, can be understood teleonomically, since water pressure normally rises with depth and is thus positively correlated with the calmness of the water layer and, consequently, with the reliability of the vestibular positional messages.

The most important problem concerning vestibular control of the optic-vestibular weight ratio is the dependence of the latter upon *body inclination.*

Information about this dependence has been provided for head tilts up to 40° by earlier authors (Hofmann, 1910; Vernon, 1935; Witkin and Asch, 1948; Witkin, 1949) and extended to 180° by Bischof and Scheerer (1970) and Schöne and Udo de Haes (1971). According to the correction principle, the visual induction of the apparent vertical should be minimum in upright position, since with slight or no body tilt the precision of the statolith apparatus is maximal. This expectation was confirmed in all investigations cited. Additionally, however, one would predict a maximal visual induction effect in a body position of 150–180°, since in this range the A-deviation, the variance of the apparent vertical, the subjective uncertainty, and also the influence of various other directional cues, are all known to be maximal (cf. Quix and Eijsvogel, 1929; Brown, 1961; Correia and Guedry, 1964; Schöne, 1964; Guedry, 1965; Benson and Bodin, 1966; Schöne and Udo de Haes, 1968, 1971; Udo de Haes and Schöne, 1969; Udo de Haes, 1970).

Actually, the results of Schöne and Udo de Haes (1971) seem to confirm this expectancy. They exposed to their subjects a stimulus pattern consisting of a single line and a striped field, both rigidly connected so that the stripes formed a fixed angle of either plus or minus 15 degrees with the line. The subject, that is, when adjusting the single line to his apparent vertical, had to move the striped field as well, which therefore kept appearing to him inclined by 15 degrees in clockwise, or counterclockwise direction. In both conditions, the settings for the apparent vertical differed, due to directional induction, and the angle between both settings turned out to be greatest with a body tilt of 150 degrees.

However, the authors call attention to their method being rather susceptible to the well-known effect (cf. p. 179) that the vestibular vertical can be equivocal with extreme body tilt. If, say, with $\alpha = 150°$ the vestibular vertical has two different possible positions, it is difficult to tell from the data obtained by Schöne and Udo de Haes whether the visual induction of the apparent vertical was due to a flip-flop kind of effect, or to a greater tolerance of any *one* of both possible states against continuous deflection. This distinction can easier be made using the method of Bischof and Scheerer (1970). Actually, Fig. 6f (cf. p. 171) shows one case (lowest unbroken line) in which a temporary shift between two possible DC-states of the apparent-vertical might have occurred. Normally, however, there were no such shifts, and the optic-vestibular weight ratio, defined as the average range of oscillation, was most marked with body inclinations between 60 and 90 degrees (cf. Fig. 6). Surprisingly enough, the optic-vestibular weight ratio, when plotted against body tilt, rendered a curve that was highly correlated with the counter-torsion characteristic of the subject's eye (cf. Fig. 11).

Fig. 11. Mean range of oscillation of luminous beam setting (ψ = filled dots and solid lines) and ocular countertorsion (ρ = empty dots and broken lines), plotted against body tilt (α) for three Ss. Raw data and mean values (from Bischof and Scheerer, 1970). Ordinate scale ratio $\psi : \rho = 1.48$ calculated such as to minimize square difference of means over all three Ss. Note that there is not only a satisfactory proportionality between ψ and ρ but that even the factor of proportionality can be taken to be the same in all three subjects: the S with the highest amount of eye countertorsion (Vp H) also shows the widest oscillations of the apparent vertical in the presence of a rotating striped field. Considering the small number of Ss, the latter effect, of course, should not be generalized at the moment

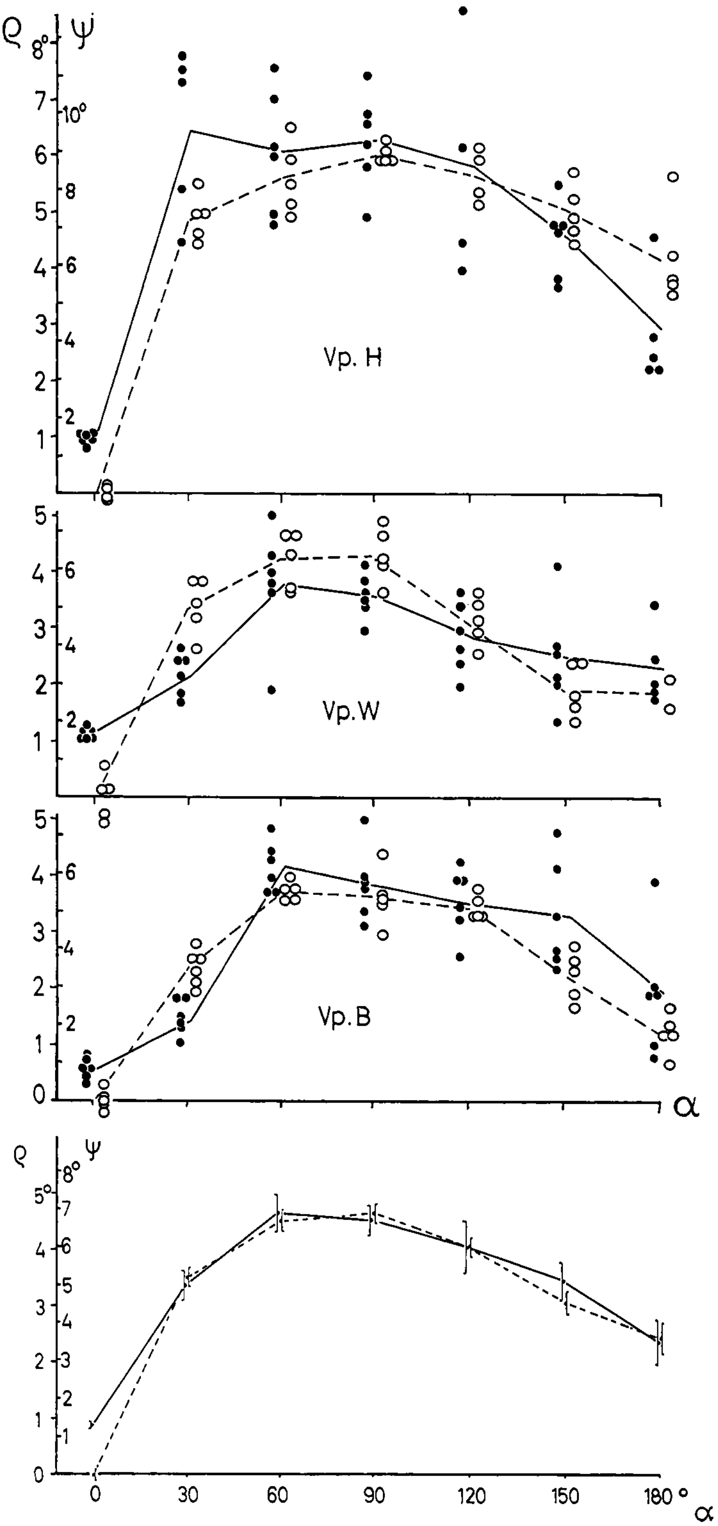

Fig. 11

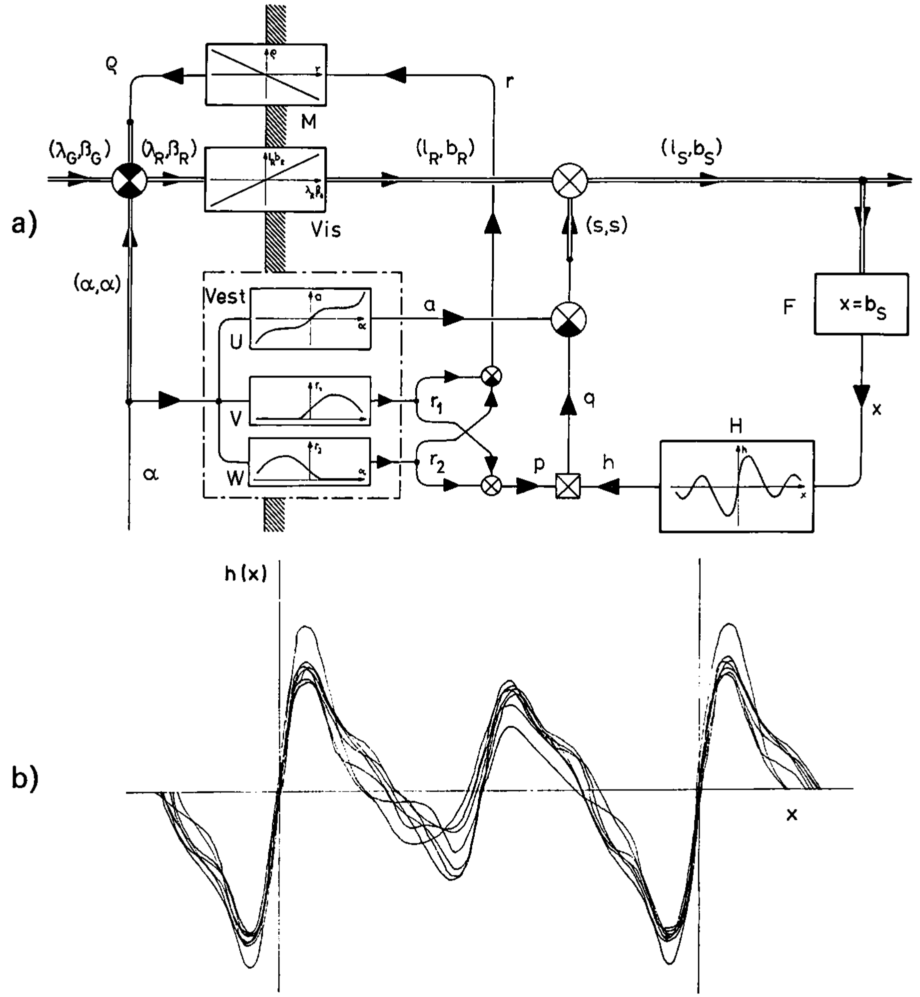

Fig. 12. a) Model of optic-vestibular orientation to the vertical. From BISCHOF and SCHERER (1970). Double arrows represent two-component variables. Crossed square is multiplication symbol. For the remaining graphic symbols see the legends of Figs. 1 and 3. M: oculomotor system; Vis: visual system; Vest: vestibular system, split up into three subsystems U, V and W, which can be distinguished functionally but must not necessarily be anatomically different. (λ_G, β_G): distal stimulus field, described by the inclination of light beam (λ) and of primary axis of the striped field (β) with respect to gravity (subscript G). (λ_R, β_R): corresponding proximal stimulus field in retinal coordinates (subscript R), resulting from (λ_G, β_G) by componentwise subtraction of head inclination (α) and eye countertorsion (ρ). (l_R, b_R): corresponding visual afference, operationally defined as a linear mapping of (λ_R, β_R). (l_S, b_S): apparent inclination of light beam and striped field, issuing from (l_R, b_R) by componentwise addition of a compensatory variable (s, s). The latter can also be understood to act like a subjective frame of reference (subscript S) into which (l_R, b_R) is mapped to yield apparent contour inclinations. According to the model, s results from *arithmetic* averaging of vestibular and optic direction cues, i.e., from a linear superposition of the vestibular tilt signal a (equivalent to s in Fig. 3) and a quantity q which itself is a product of a vestibular weight factor p and an optical induction component h. The factor p is operationally measured by the average range of oscillation ψ as plotted in Fig. 11. It derives from the *addition* of two vestibular outputs r_1 and r_2, each of which reacts sinusoidally to head tilt to one side. The *difference* of r_1 and r_2 results in a command (r) for eye countertorsion (ρ). The apparent inclinations (l_S, b_S) of the contours in the optic field are "filtered" by a mechanism F producing a quantity x which

The authors take this correlation as an indication that the optic-vestibular weight ratio as defined by them might be more than an arbitrary construction, and might refer to an actually existing physiological variable.[5]

Only in the upright position ($\alpha = 0^\circ$) is there a significant difference between the two curves in Fig. 11, the countertorsion being zero in this case (and changing sign for negative abscissa values), whereas the mean range of oscillation does not vanish entirely (and remains positive when the body is inclined counterclockwise). This discrepancy is accounted for by Bischof and Scheerer (*loc. cit.*) as being the effect of the subtraction or addition, respectively, of two separate otolith output components, one of which signals clockwise, the other counterclockwise head inclinations (for this distinction, cf. also Miller, 1962, 1966, 1970; Terins, 1971).

Relying upon these assumptions and on systems-analytic elaborations previously cited, Bischof and Scheerer summarize their theory about optic-vestibular interaction in human perception of verticality in the flow diagram of Fig. 12. Because obtained from the investigation of only a limited number of subjects, this model can only claim the status of a preliminary hypothesis, the confirmation or refinement of which must be left to further research.

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[5] Interpretable perhaps as the output of the utricles, which, due to their anatomical site, should yield afferent messages roughly proportional to the sine of head tilt (cf. von Holst, 1950).

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equals the apparent inclination of the striped field's primary axis. The optical induction quantity h, then, is a periodic function of x. b) The model predicts that *one single* function $h(x)$ may be calculated from *any* given curve in Fig. 6 (see p. 170—171) by: 1. reassigning the ordinate values to the oblique co-ordinate system consisting of the diagonals and the abscissa in Fig. 6; 2. normalizing the transformed curve to the mean oscillation level; 3. dividing the resulting curve through its mean range of oscillation. Fig. 12b shows that this prediction is valid. Drawn are 6 curves calculated as described above from the mean-value curves for one Subject at 6 different body tilts. As is apparent, one single empirical curve $h(x)$ results. When $h(x)$ is inserted in block H in Fig. 12a, theoretical λ_G-values yielding a permanent $l_S = 0$ can be computed; they are shown in white in Fig. 6

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