CONTENTS

ment; the other exteroceptive, orienting the observer with respect to his own position in space. This latter does not seem to be based on direct tectovestibular connections but could potentially use connections via the nucleus of the optic tract of the pretectum (Collewijn, 1975; Hoffmann and Schoppmann, 1975), the inferior olive, and the cerebellar flocculus (Maekawa and Simpson, 1973).

Compensation in the Perception of Verticality: Some Remarks on Exploring Causal Relationships in the Central Nervous System: N. Bischof

Some neurophysiologists consider psychophysics somewhat dull (see the Introduction). In certain areas of psychophysics, this attitude is understandable; indeed, the results of some investigations are often little more than a subsequent illustration of facts already established by neurophysiology: investigations on contrast, after-images, thresholds, flicker fusion, local adaptation, and the like. Such results add little or no substance to the neurophysiologist's fund of information; he can examine the structures concerned by his own methods, and better, too. So why use a roundabout route?

There are, however, psychological phenomena that cannot be so easily assigned to elementary physiological processes. To explain these, one would have to conceive models of neuronal interaction. Such models are no longer dull, but they are speculative, which is even worse. The neurophysiologist is hard to convince that he might, one day, find models useful as heuristic aids. Admittedly, the use made of the available empirical data in models offered by the behavioral sciences does not always comply with the standard of thoroughness set by neurophysiologists even, and particularly, when these models are garbed as systems-theoretical formalisms. Moreover, however painstakingly the psychologist may proceed in substantiating his conclusions with empirical arguments, those phenomena promising access to somewhat deeper insights are based, as a rule, on such complex physiological structures that any attempt to interpret them can be made only at the cost of an extreme generalization of the physiological data. But here one comes up against the distaste for generalizations peculiar to many scientists.

Thus, it is not yet clear whether one can trust to this path and confidently develop physiological models from behavior analysis. One hesitates, waiting for a breakthrough to show that the method works. That the method does work was established, for example, by the elegant

experiment of von Holst (1950) to determine whether the sensory hairs of the utriculus macula in fish are stimulated by shearing or pressure. Von Holst succeeded in solving this problem without even touching the fish, let alone implanting electrodes. The shearing hypothesis has since been borne out directly by neurophysiological recordings in accordance with von Holst's prediction. This is a clear indication of the heuristic validity of behavior experiments for neurophysiology. The theme of von Holst's experiments was admittedly a question of receptor physiology, posing the electrophysiologists' technical, but not fundamental, problems. In principle, the question of the adequate stimulus of the utriculus receptors should be open to direct electrophysiological examination, and if a few years had been allowed to elapse, no behavior experiment would have been needed in this case. But it is a different matter when the analysis of structural connections within the central nervous system is concerned. For here one lacks sufficiently clear neuroanatomical landmarks showing where the system begins and ends and how it is structured.

This would be less tragic if these structures were less complex. Those system connections directly discoverable by neurophysiological methods, that is, through single-cell recordings, must for methodological reasons be of a rather simple nature. If the neurophysiologist hits, in his examinations, upon a complicated system in which many neurons interact meaningfully over all sorts of cross-connections, then he will be very likely to pass over these, simply because neurophysiological methodology gives him no handle to get at what these interactions *mean*. One can hardly analyze complex systems without having an idea about their functional meaning. For only when one knows how a system functions can one set about thinking why a given connection is linked in a certain way and not otherwise or why two variables have no influence on each other although they "should" have. Then one can postulate that a certain connection exists and look for just that, and so on.

Thinking in terms of biological functioning has a definite heuristic value for neurophysiologists. The whole fruitful area of receptive fields, for example, was at least in part opened up by the attempt to expose stimulus patterns having a biological significance for the organism being studied (Lettvin et al., 1959; Hubel and Wiesel, 1959), instead of the usual point-of-light or homogeneous-field stimuli, which seem to come so close to the ideal of "simplicity."

One cannot, of course, overlook the fact that, after an initial success, the course since taken by neurophysiology has not added much

to the understanding of the higher perceptive functions. Characteristically, the direction taken is more and more definitely toward neuroanatomy, showing, therefore, a downhill tendency to the level of a still more microscopic analysis rather than a climb toward the more abstract level of the analysis of behavioral systems. And in these circumstances, no one will be surprised that psychophysical results, corresponding directly with this kind of neurophysiology, seem somewhat boring.

But there are other fields of psychophysical research. Some of them yield results not trivial but well quantifiable and reproducible, pointing unmistakably to central nervous system connections worthy of investigation. This is especially true of perceptual constancy, and here the area of space perception provides particular examples.

The perceptual constancy of the vertical has been investigated by psychophysicists over roughly the last 100 years. Whenever the head is tilted sideways, the retinal image of the environment is of necessity subjected to a counterrotation. This counterrotation must be compensated for in some way in the central nervous system, because our experience is that we do not normally notice it in our daily lives. Even if our environment is reduced to a single luminous line in an otherwise dark field, then at least two-thirds of the head tilt, and usually much more of it, is still compensated for in perception. This can be demonstrated by asking subjects to adjust the luminous line to their apparent vertical.

The problem posed by such experiments cannot be solved by applying the well-known theory proposed by MacKay (e.g., 1970e) to account for visual stability during voluntary eye movements. MacKay's theory would be applicable only in cases of *voluntary* head tilt in a *structured* visual environment. In Bischof's experiments, where the subject is tilted passively in the presence of a single luminous line, the need for a compensatory operation in the CNS becomes undeniable. It must, therefore, be assumed that the brain obtains information about head tilt by some other, nonvisual means and then does something with the visual afference that might functionally be termed a "rotatory transformation of a frame of reference." This other source of information is presumably the statolith apparatus. From physiological and anatomical information on this apparatus and from the type of error made by the system under given experimental conditions, one can try to deduce the principle on which this compensatory "coordinate rotation" operates.

The system doubtless functions much more efficiently and effects practically 100% compensation for head tilt if, instead of being artificially reduced, the optical stimulus consists of a naturally structured

environment. Apparently the visual system is so constructed that it is capable of inferring, from a moderately structured scene, what in this scene is up and what is down.

It is known from many experiments that the orientation of contours has much to do with this. As all objects in our natural environment have to come to terms with the ubiquitous pull of gravity, the orientation of object contours can be expected to preferably reflect states of equilibrium (stable, labile, or indifferent). If, that is, a number of contours on the retinal image are parallel to one another, then the brain can be fairly sure that these contours *also* run either vertically or horizontally. The eye offers the brain, so to speak, four different orthogonally arranged "suggestions" regarding the direction of gravity, which does not eliminate uncertainty altogether but reduces it to precisely two bits.

This can be tested by exposing the subject to a field of parallel lines in slow frontoparallel rotation and, additionally, to a single luminous line that is continuously adjusted to the subject's apparent vertical. The luminous line is entrained for some time by the stripes, then swings back gradually until it stands at right angles to them. In this position the luminous line is again dragged along, then again swings back, and the game is repeated. Under such experimental conditions, then, the subjective vertical performs an oscillatory movement, the mean amplitude of which depends, among other things, upon the degree of head tilt. This amplitude is, surprisingly, highly correlated with the magnitude of eye counter-rolling characteristic for the given head position (for this finding and its theoretical significance, see Bischof and Scheerer, 1970; Bischof, 1975).

The oscillation of the apparent vertical in the presence of a continuously rotating striped field shows that, apart from the retinal image, a further, nonvisual source of information about head tilt is heeded, apparently deriving from the postural senses. Oscillation could not occur unless the four visual "suggestions" of the vertical were considered *one at a time,* i.e., unless they were *weighted* according to a schedule that varies systematically with the position of the stripes. This schedule, however complicated it may be, ought to imply that each of the four "suggested" directions has a greater chance of influencing the subjective vertical the nearer it approaches a standard direction, which the central nervous system procures from other, nonvisual sources. It is possible to assess this standard direction.

At a first attempt, we may assume that the apparent vertical, experienced in the *absence* of visual cues such as a striped field, serves directly as the standard in question. Under striped-field conditions, this

"postural vertical" should be represented in sufficient approximation by the level of oscillation, i.e., the first, nonperiodic Fourier component of the apparent vertical. When determining which one of the four visual "suggestions" of the vertical direction ought to be taken most seriously, the central nervous system would, according to this idea, always choose the one that comes closest to the "postural vertical." The subjective experience of verticality would then result from a compromise between the postural vertical and the preferred figural axis of the visual pattern. If this hypothesis were valid, the data obtained in the rotating striped-field experiment should be expected to comply with the schematic drawing of Figure 37a.

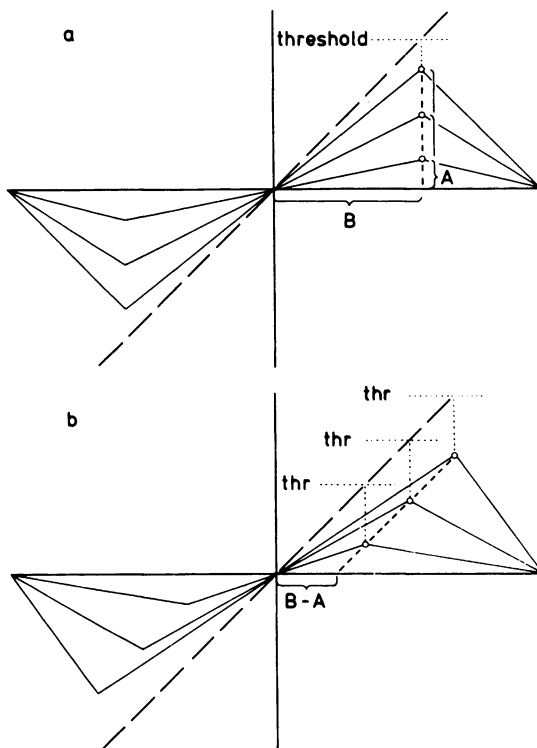Figure 37 shows the inclination of the subjective vertical (solid

Figure 37. Comparison of alternative compensatory mechanism; theoretical data of oscillations of an apparently vertical light beam. *Ordinate:* Angular inclination of luminous line with respect to the nonperiodic Fourier component of oscillation (the latter representing the vestibular standard). *Abscissa:* time. Solid lines: settings of luminous line for different body inclinations. Broken diagonals: position of main axis of striped field. (a) Expectation for feedforward compensation; (b) Expectation for feedback compensation. [Bischof, 1975]

lines) and of the striped field (broken diagonals) both plotted against time, with the "postural vertical" as reference (zero in the ordinate). In different head positions the oscillation of the subjective vertical varies in amplitude, as mentioned earlier.

The peaks of oscillation of the apparent vertical indicate the point where a given axis of the rotating visual pattern hands the role of being a dominant cue of verticality over to the subsequent axis. In Figure 37a these peaks (A) are assumed to occur for all head inclinations at the same time (B), namely, when the inclination of the striped field against the postural vertical reaches a critical threshold. This follows from the hypothesis outlined above, according to which the postural vertical serves as the standard for weighting the cue validity of the four figural main directions of the striped field.

The data actually obtained do not substantiate this hypothesis. Figure 38 shows what really happens. The upper part of this figure presents the mean values of three subjects for A (solid line) and B (broken line) depending on body tilt (α). As can be seen, the expecta-
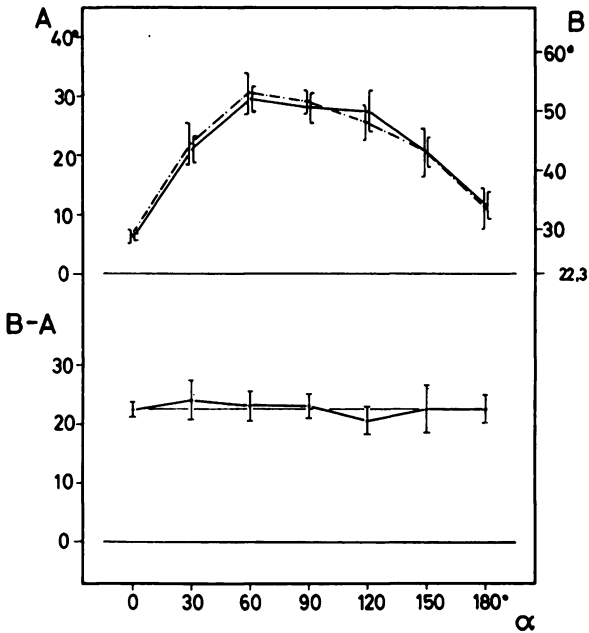

Figure 38. Experimental support of feedback autocompensation hypothesis in the perception of verticality. Comparison of *ordinate* (A: solid lines) and *abscissa* (B: broken lines) for extreme values of apparent vertical (compare Figure 37). Mean values of three subjects, with average variance of means 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. [Bischof]

tion that B is constant for all body positions is not fulfilled. Instead, the difference, B – A, turns out to be constant.

Figure 37b illustrates what this means: the peaks of oscillation of the apparent vertical occur when the striped field has moved by a certain threshold (thr)—not away from the postural vertical (the level of oscillation of the luminous line) but away from the *subjective vertical,* that is, from the luminous line itself. Decisive for the weighting of the visual axes is, therefore, their *perceived tilt.*

This seems at first to be a very peculiar finding. The subjective vertical itself is the result of a compromise between the postural vertical and one of the directional suggestions made by the visual system. Our data indicate that this result then reacts upon the processing of the optical stimulus and decides, so to speak in retrospect, which particular visual axis should be chosen to compete with the postural vertical. This seems to be a vicious circle. In actual fact, it is merely a feedback loop.

The results given elucidate an interesting structural alternative, which, at first glance, would not at all be expected to be resolved by means of a purely psychophysical experiment. There are two possible methods by which an engineer could go about solving the problem of the visual compensation of reafferent head tilt effects. Figure 39 depicts one of them. The first input arrow (left) symbolizes the physical stimulus situation, in particular the frontoparallel inclination of all perceivable object contours against gravity. As normally many contours are visible
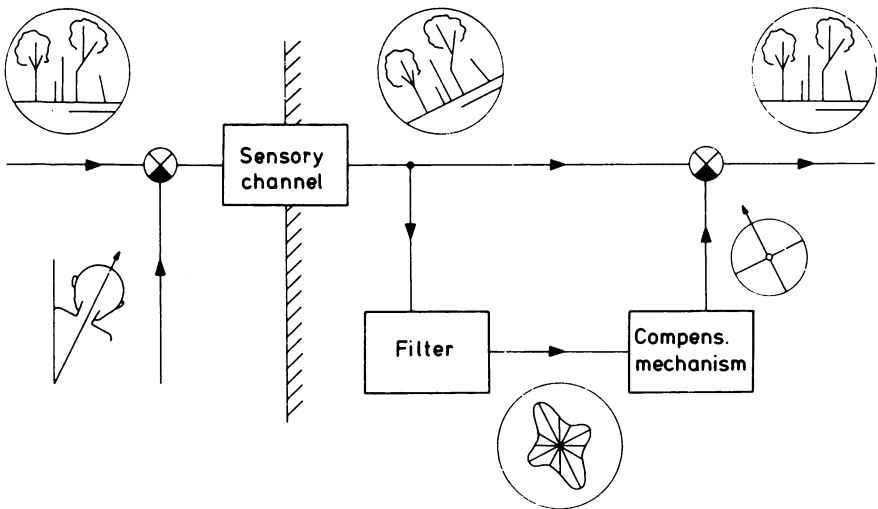

Figure 39. Feedforward autocompensation. [Bischof]

simultaneously, the arrow represents a multidimensional variable. The message about this variable is systematically interfered with by the superposition of another variable, namely, head tilt (arrow from below). This interference has the form of a subtraction. It occurs, of course, identically for all stimulus contours; that is, in retinal coordinates, the whole object field is rotated, by the amount of head tilt, in the opposite direction. In order to compensate for this rotation, the brain should be provided with a mechanism (Filter) that can ascertain the angular distribution of contours within the retinal stimulus pattern. For reasons discussed above, this distribution will be four-peaked under natural conditions (compare output of Filter). With the help of postural indicators not shown in the chart, the compensatory mechanism must now determine one of these four peaks as the most likely indicator of the vertical, and hence as a frame of reference for the directional information contained in the visual afference. Only if the counterbalance has been effected correctly will the subject experience the panorama as upright (arrow, extreme right).

The model just described has, on the same level of complexity, exactly one structural alternative, which is shown in Figure 40. This second model differs essentially from the first in that compensation occurs not "downstream" but "upstream" from the filter mechanism assessing the figural axes of the visual stimulus pattern. Here we are dealing with a feedback compensation as opposed to the feedforward
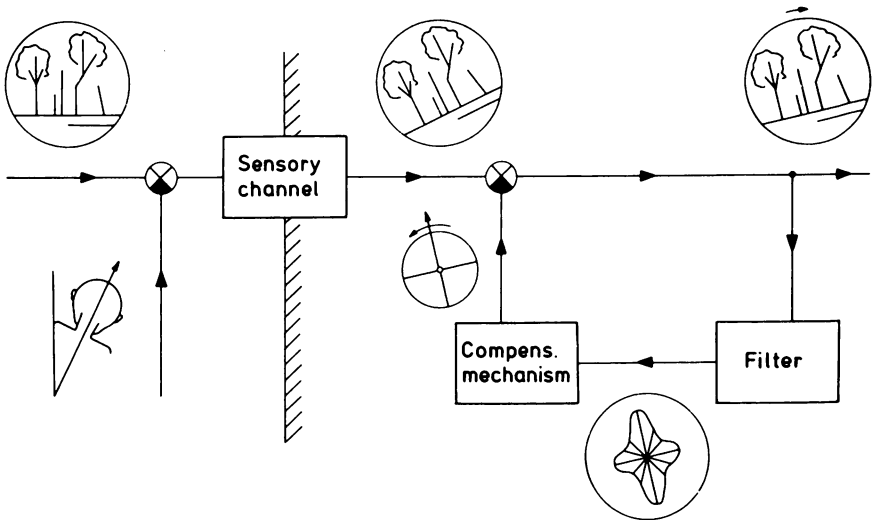

Figure 40. Feedback autocompensation. [Bischof, 1975]

compensation represented in Figure 39. This system can also produce ideal space constancy, provided that the feedback contains a temporal integrator.

It can be demonstrated, although unfortunately in a rather abstract mathematical derivation (Bischof and Scheerer, 1970), that each of the alternatives shown in Figure 37 belongs precisely to one of the two systems just described; the findings shown in Figure 37a being compatible only with a system of the Figure 38 type, while systems in Figures 37b and 40 are similarly connected. We might have had the misfortune to have had quite different results, or indecisive ones, lying somewhere in between the ideal cases represented in Figures 37a and b. The interpretation would then have been more difficult, or even impossible. Fortunately the results are unequivocally in favor of the feedback hypothesis. We therefore venture to predict that in future neurophysiological investigations on the mechanisms underlying space perception, the feedback loop outlined in Figure 40 will actually be found. This leads back to the question asked at the start: Can such preparatory work undertaken by psychophysics be of use to neurophysiology?

There is no substitute for direct neurophysiological evidence. The psychophysical experiment is legitimized by the claim that psychophysics is able to prestructure the field of neurophysiological research and therefore to render heuristic help. Nobody at present is able to assess just how indispensable this help is, for until now neurophysiology has not attempted to investigate the systems under discussion.

A variable appearing as a single arrow in a chart like Figure 40 can, when being translated into neurophysiological reality, disintegrate into a heap of splinter variables scattered over tens of thousands of nerve paths. It is difficult to predict what this will mean in structural terms. For example, something that has been identified as a feedback loop, using our methods of examination, may still be a feedback loop on the much more complex neuronal level; but it might also become some matted entity from which one can no longer perceive that a loop can be abstracted. If the latter is the case, then it does not help the neurophysiologist much, if it helps at all.

There are more "ifs" and "buts" of this kind. They may, or may not, render the whole approach useless. Until this has been clarified, psychophysicists might as well keep trying. And it would not hurt their critics to give them a fair chance.