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2.4 The Uses of Proprioception and the Detection of Propriospecific Information

The terms sensory and motor, when applied to the nervous system, are not precisely descriptive, for not all sensory impulses yield sensations and not all motor impulses yield movements. The physiologist speaks of afferent and efferent impulses instead, which are exact terms. The human engineer speaks of input and output, which are still more descriptive. Thus, when we want to talk about the input to the nervous system produced by its own output we can use the engineer's term *feedback*, or the physiologist's term *reafference* (Von Holst & Mittelstaedt, 1950). However, the available terms from psychology carry meanings that imply the theory of special conscious sensations and are weighted with history. The *muscle sense* dates from 1826 but the term is not very useful because it leaves out of account the return inputs from the joints.¹ *Kinesthesia* dates from 1880 but it implies sensitivity to movement whereas it ought also to imply information about the postures of the limbs and body.² The *vestibular sense* registers movements of the head, but only accelerations, and it also contributes to reflex postural equilibrium of the body, head, and eyes. *Somaesthesia* is a useful term, but too general. Boring (1942), of course, is the authority on all this.

*This paper was presented at an American Psychological Association symposium on the Role of Reafferent Stimulation in Perception, September 1964. It has not been published previously.

¹The idea of a muscle sense comes from the work of Thomas Brown and Charles Bell. (See Bastian (1880, appendix) and Sherrington (1900).) (Eds.).

²The term "kinesthesia" was coined by Bastian (1880). Bastian (1887) includes a debate on the concept of kinesthesia with commentary by Hughlings Jackson, David Ferrier and others. For a recent review of work on kinesthesia, see McCloskey (1978). (Eds.).

From behavior theory there comes the old term *circular reflex*, which implies part of what we want to talk about. It was used, for example, by G. H. Mead and E. B. Holt in theories of the development of speech in the child and of social imitation. There is also Hull's term *response-produced stimulation* which is useful but implies acceptance of Hullian theory. Finally, there is available the term *proprioception*.

This word is practically synonymous with kinesthesia in modern usage. It is so used by the other contributors to this symposium. But, with apologies, I want to have it mean general self-sensitivity, that is, the fact that an animal stimulates itself in many different ways by nearly all of its activities, from the lowest to the highest, including the activities of looking, listening, touching, smelling, and tasting.

Sherrington, when he distinguished between proprioception and exteroception, in 1906, had a great insight. He suggested, and should have made us realize more fully, that an individual animal needs information about its own activities as well as information about the environment in order to function in the environment. It must have both to get along.³ But Sherrington was so much influenced by the classical theory of mutually exclusive senses, each with its sensory nerve, that he could only ascribe proprioception to a class of proprioceptors and exteroception to a class of exteroceptors. In 1906 no one could doubt Johannes Müller's law of the special sensory qualities of the receptors and their nerves, nor that the resulting sensations were the sole basis for the getting of information. The notion that proprioception is a general function, not a special sense even now may sound strange after a half a century. But the modern concept of feedback or reafference is not that of a special sense. Return inputs to the nervous system, we now realize, may come through any of the sensory channels, not just through the receptors in the muscles, the joints, and the inner ear. The control of locomotion depends on the eyes; the control of manipulation on the eyes, joints, and skin; the control of speech on the ears, and so on. But this is proprioception in the exact meaning of the term.

A recurrent and unsolved puzzle now becomes obvious. How does an individual tell the difference between an input caused by its own activity and one caused by an external event if both come over the same nerve? If proprioception is not confined to a distinct anatomical class of proprioceptors separate from another class of exteroceptors, how is an input that is propriospecific distinguished from one that is exterospecific? For example, in the case of the eye, how is a shift of the retinal image over the retina when it is caused by a rotation of the eye any different from one that would be caused by a rotation of the world? This is the old problem of why we do not see the world move when the eyes move. There are many other examples, although they are less well known. The skin can be moved over a stationary object or an object can be moved over the stationary

³Thinès (1977, Ch. 3) reviews this aspect of Sherrington's work in considerable detail. (Eds.).

skin; the cutaneous stimulation may then be identical but the two cases are not confused in perception, and the question is why?

This puzzle, it seems to me, is even deeper and more far reaching than these examples suggest. In driving an automobile, in wielding a hammer, or in exploring the shape of an unfamiliar object in the dark, there is a complex concurrent *mixture* of response-produced stimulation and environment-produced stimulation. Consider the visual stimulation. One component of the visual flux is specific to the individual while another is constrained by the external arrangement of things or by external events. The same is true of the cutaneous flux of stimulation, for part of it is self-produced and another part is object-produced. It is even true of the flow of vestibular stimulation, for some of the forces on the little weighted hair-cells are initiated by the individual, some by external pushes, and some underlying component is due to the incessant pull of gravity. At cocktail parties, the sound of one's own voice is mixed with the sound of other voices. How can the individual sort out the mishmash of sensations and perceive their causes? If Müller was right about the specificity of sensations to receptors and only to receptors, and if Locke was right about sensations being the only ultimate source of perception, how does any person or animal distinguish between the feedback to the nervous system and the feed-in to it? What is the difference between the propriospecific information and the exterospecific information? In the terms of Von Holst (1954) what is the difference between reafferent and exafferent nervous impulses over the same nerve?

Von Holst's solution to the puzzle, as I understand him, is to imagine a central neural hookup that can distinguish the sensation following a motor command from the same sensation *not* following a motor command. To do this, the brain needs to keep a "copy" of each output, and determine whether or not an input matches it. If there is a match the input is given a proprioceptive quality; if not an exteroceptive quality. Von Holst's theory need not involve consciousness, but the explanation is in the same tradition as the hypothesis that a *feeling of innervation* always accompanies the arousal of a motor pathway—a hypothesis that carried the theory of sensations to its ultimate extreme.⁴

It seems to me that a more radical solution to the puzzle is called for. If proprioception is a general function of the overall perceptual system; cutting across the classical senses, then the subjective sensation-qualities have nothing to do with it. I make a sharp distinction between the input of information and the input of conscious sensation. The puzzle disappears if one simply postulates that the neural input is different when it is propriospecific than when it is exterospecific. The input that specifies its source, to be sure, comes in larger chunks than the one that specifies only its anatomical point of origin, but it is truly

⁴The controversy over innervation sensations was quite vigorous towards the end of the 19th century. James' (1890) chapter on the will is a good introduction to the debate. (Eds.).

informative and does not have to be corrected or supplemented as the bare sensory data would have to be.⁵

On this theory, proprioception utilizes whatever anatomical equipment is available for the pickup of information, just as exteroception does. The changing pattern of nervous input contains invariants that specify what is constant and variations that specify what is varying. We can now begin to study proprio-sensitivity and extero-sensitivity as such. We can afford to recognize that the state of the body and the state of the world are interdependent, and that both must be detected in perception. We can take account of the phenomenal fact that our experience usually has both subjective reference and objective reference at the same time.

It is true that, for this approach a number of cherished assumptions have to be thrown overboard. We have to suppose that sensations as conscious contents are neither the causes of perception nor the components of perception, but are merely incidental. If perception is based on the pickup of information, it may or may not be accompanied by sense-data. We have to suppose that the classical senses, the conveyers of bare sense-data, are in large part mere artifacts of human analytic introspection. We shall have to define a new set of perceptual systems, recognizing that they are not mutually exclusive. We must suppose that organs of perception exist, incorporating the receptor-cells and receptive fields of single afferent neurons, but these organs have to be defined in functional not anatomical terms. The organ of sight, for example, consists of two eyes, not one. The organ of touch consists of the limbs and trunk, not just the skin. We can then suppose that the sensory qualities, intensities, extensities, and protensities celebrated by Titchener may reflect the receptors excited but not the organs at work. The great Cornell program of a complete inventory of the possible sensations becomes irrelevant for the study of perception. The study of the energy thresholds for sensation in measured amounts of intensity or frequency is relevant only to the receptors, not the perceptual organs. We must suppose that the psychophysics of intensity and frequency, however elegant a discipline, will not lead to a psychophysics based on the *information* in light, sound and mechanical energy, that is, information about the environment and the body of the observer.

The hypothesis being entertained is that there exists information for proprioception and that it can be registered. The sensations resulting from refference are a matter of no consequence. This is a very disruptive hypothesis but it frees us to think in other ways. We have long wanted to acknowledge that the senses are active, exploratory, and search-oriented but the very term *sense* prevented this. We have failed to distinguish between active perceptual organs and passive

⁵The same idea seems to be behind Granit's (1973) theory that coactivation vitiates the need for refference in muscle and articular proprioception (see Miles and Evarts, 1979, for discussion). (Eds.).

receptors. Consequently the study of the *orienting* capacities of the eyes, ears, nose, and hands has proceeded in a theoretical vacuum, and they had to be lumped together with behavior. The *adjusting* of perceptual organs, the overt acts of attention in looking, listening, smelling, tasting, and touching, can now be understood as an activity of extracting the invariants from potential stimulation, that is, the act of optimizing the pickup of external information. This suggests that the adjustments of the eyes, ears, nose, mouth, and hands are skills capable of development, but skills in their own right, not subordinate to motor performances.

The remarkable thing about this new concept of active exteroception, as contrasted with the old one of passive exteroception, is that we can no longer consider the stimulation of the retina (for example) apart from the ocular adjustments of accommodation, of intensity modulation, of stabilization, fixation, and exploration, that determine what the retinal image will be. The normal everyday retinal image is a truly *obtained* stimulus, not an *imposed* one as we have so long assumed.⁶ The ocular adjustments are continually producing new retinal images so as to pick up the potential information in light. Note the implication. The ocular system has to be sensitive to the imperfections of a retinal image in order to make these adjustments. The system has to be *propriosensitive* in order to work. But the *sensations* incidental to focussing, fixating, exploring, and pursuing have nothing to do with their function, which is to achieve clear perception. When the eye shifts its fovea from one item of interest to another and the retina moves relative to the retinal image the input simply reflects and controls the shift of attention, and it is beginning at the wrong end to ask why the world does not seem to move. A pure transposition of total pattern, with gain of new detail on one side and loss of old detail on the other *specifies* an eye-movement, and this information is normally registered as such.

The feedback of the retina from ocular adjustment and ocular exploration is very much worth study, but we should not forget its perceptual purpose in considering what kind of sensation, if any, accompanies this feedback. Its modality or quality may be that of the retina if it is experimentally brought into consciousness but its meaning is that of an adjustment; it is information about the state of the ocular system. Reafference is part and parcel of the perceptual process inasmuch as it controls the activity of the perceptual organs in their search for external stimulus information. If there were time, I would try to show that this rule works just as well for the ear-head system in active auditory localization, for the hand-body system in active touching, and for the nasal-respiratory system in active smelling or sniffing, and in what we call "following our nose."⁷ The perceptual systems all include what Pavlov termed orienting

⁶Gibson (1962a) applied this theory to touch and later (Gibson, 1966b) to all the perceptual systems. Cf. Wall's (1970) application of this idea to touch and kinesthesia. (Eds.).

⁷These are all discussed at greater length in Gibson (1966b). (Eds.).

responses, and they are all neatly hooked up with the basic system of postural orientation to gravity and the surrounding environment. That system is notoriously one which operates in a continuously circular fashion to achieve an equilibrium state. So do the higher perceptual systems.

Here is a role, then, for reafference or proprioceptions to play in perception. What about its role in overt behavior? We are fairly familiar with the latter from the rise of what is called cybernetics. And we may be tempted to assume that reafference is all one thing, working the same way in perception as it does in performance. But this, I think, would be a mistake. Performance modifies both the environment *and* the perception of the observer, whereas perception can modify only the stimulus information obtained from the environment. That is, by the education of attention the observer can isolate invariants, extract the critical features of things, and enhance his ability to detect small differences. I do not want to depreciate learning by doing; I only want to assert the possibility of learning by looking.

Motor learning cannot go to its limit unless it is accompanied by perceptual learning, but perceptual learning can proceed with very little muscular action except for the exploratory adjustments of the eyes, ears, and hands. The fallacy of the theory of *response-produced cues* as an explanation of perceptual learning lies in the assumption that the motor responses *as such* improve the discrimination of things. Hidden in the gross motor responses are more subtle activities of the perceptual organs that fix on and clarify the relevant stimuli. Along with this goes a "tuning" of the nervous centers that filters out irrelevancies. This is not an obvious kind of behavior. It is an activity but it deserves the name of perceptual activity and it cannot simply be thrown into the pot of motor responses.⁸

The perceptual systems include muscles, to be sure, but some of them like the eye muscles cannot do much to change the environment. They are exploratory, not performatory. The input is optimized, not the output. Eye and ear movements tend toward an equilibrium state of clarity, not of need-reduction. In exploratory activity the observer has to *move*, that is, move his eyes, his head, his hands, or even move to a new point of view. He has to do so in order to find out what is lawful, regular, recurrent in the world. He can only do this by isolating what remains invariant in a self-produced flow of changing stimulation. The permanent objects and their layout then emerge from the flow of perspectives. But the observer does not *necessarily* have to perform a task or achieve a purpose during this exploration.

If what I call proprioception is a general function instead of a special sense, and if it is normally a component of all the active exteroceptive systems, what sort of classification of the perceptual systems is possible and what sort of

⁸Most modern theories of reafference still hold that the motor output or feedback provides the information for discrimination, as opposed to Gibson's idea of action as adjustment to perceptual information. (Eds.).

terminology do we use? This is a fair question. I am sorry to be a troublemaker but the only answer is a flexible terminology until a new consensus is reached. (Actually the classification of the special senses themselves, much as we might hope it to be clear, is a thorough muddle).

A new classification of the perceptual systems will have to start out with the information they register, and we now know that there is a great deal of redundancy in perception, that is, multiple cues for the same thing, or multiple equivalent information. The perceptual systems therefore have overlapping functions for getting external information although, of course, they do not overlap completely. Only the eyes can register the color of a surface, and only the skin can register its temperature, but the eye and the hand both can register its roughness or texture, its size, its inclination to gravity, and both systems can register its distance within about three feet. Beyond that, the eyes have to take over. Each perceptual system has some special virtue but none seems to neglect available information just because another system gets it too. Detection organs seem to relish redundancy, and a fire that is simultaneously seen, heard, felt, and smelled is experienced as one fire, not as four sensations. Consequently a classification of perceptual systems cannot be made as a mutually exclusive list in the way that it was hoped the senses could be listed.

Efforts to account for the "unity of the senses" in exteroception have not succeeded, and perhaps it is now clear why. As conveyers of sensation they cannot be unified, and their cooperation remains a puzzle. As detectors of information, however, their unity is just what they have in common and their diversity is what they do not.

If this is true the adaptation that occurs when the input of one perceptual system is put in conflict with the input of another is a problem in the resolution of information, and the question of the change in one sensation modality relative to the other is secondary. The ancient puzzle, going back to Bishop Berkeley, of whether we should *believe in vision* on the one hand or touch on the other, of which sense we should *trust*, is actually a problem of information pickup but it was thought to be a problem of sensory modalities because the modes of sensation were the only recognized channels of information.

The experimental evidence suggests to me that, in cases of discrepancy of information, the individual learns what is invariant. The learning is not, therefore, a matter of one sense modality altering another, or correcting it. No one is intrinsically more trustworthy than another. It is a matter of discovering what specifies the real layout of the world. And adaptation in this sense could occur in either the visual system or the haptic system independently or both together.⁹

Adaptation to prismatic distortion of the visual input, and to the resulting instability of the phenomenal world when the head moves, seem to be facilitated by exploratory activity. But this does not mean that behavior determines perception; it only implies that perception, like behavior, is an activity of the individual.

⁹See Pick (1980) for a recent review of work on haptic perception. (Eds.).