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Motor-sensory feedback formulations: are we asking the right questions?

Gyr and his colleagues would have us confront anew the evidence for assigning a critical role to motor activity in visual perception. While their discussion of "sensorimotor processes" suggests a tightly-coupled relationship between perception and action systems, we believe that the authors present a potentially misleading picture of the relationship between efference and afference. The thrust of this commentary will be to lay out some of the logical problems associated with a theory that utilizes the concept of efference copy. By and large, these supplement points already raised in this journal be a number of commentators on a paper by Roland (1978). The present position is that efference copy and its often synonymously used affiliates, corollary discharge and central monitoring of efference, are, with perhaps a single exception, low in theoretical power. This is the *general* claim to be made here. In addition, we wish specifically to point to an alternative account for the type of data that Gyr et al. seek to explain. This focuses on the concepts of information discordance and allocation of attention, which, when allied, seem to provide an adequate explanation of much of the adaptation literature without resorting to unique contributions from efference copy.

Gyr et al. present the classical data for the role of efference in visual perception. Many of the methodological problems in extending this approach to human behavior have been raised by Shebilske (1977) and will not be re-enumerated here. More damaging, however, is the elegant rationale by Turvey (1977a; see also this Commentary and elsewhere in this issue) that an explanation of visual perception, relying on a comparison of efferent signals to eye muscles and the retinal input provided by vision, falls sadly short when we move beyond the situation of a simple eye movement in a stationary head on a stationary body. When one considers the complexity of the visual array (when an individual performs locomotory activities, for example), a simple computational explanation no longer suffices.

It is clear that Gyr et al. wish to extend the efference-copy notion to movement coordination in general. They are, of course, not alone in this enterprise, in that the efference-copy concept is often used to explain, among other things: 1) the superiority of active over passive movement perception (e.g. Kelso 1977; Teuber 1964 *op. cit.*); 2) the ability of subjects to make rapid error corrections in step-tracking tasks well within the bounds of peripheral feedback loop times (e.g. Higgins & Angel 1970); and 3) the motor performance of de-afferented animals (e.g. Taub 1977). While such data require satisfactory explanation, we do not want to place our money on an all-encompassing efference-copy/reafference relationship. As long ago pointed out by Bernstein (1967), there is an equivocality between motor commands and the effects that they produce. There can therefore be no direct comparison between efference copy and reafference, because such a one-to-one mapping between the two sources of information cannot exist.

More important for a theory of coordination is the issue of how the multiple degrees of freedom of the motor apparatus are regulated. Powerful arguments can be generated against a view that efferent commands specify the states of individual muscles. This would result in an extraordinarily detailed efference copy that fails to take advantage of the intrinsic organization of the nervous system (for details see Grillner 1975). Rather, we wish to view efference not in an executive role, but as an *organizational* factor, in which the entities regulated are coordinative structures (Easton 1972; Turvey 1977b)—that is, functional groupings of muscles constrained to act as a single unit.

A specific operation of efference in this perspective is feed-forward in nature, such that the performer is prepared for the impending motor output and the afference arising from such activity. Thus, various experiments have illustrated postural adjustments and descending biasing influences on the segmental machinery in preparation for particular types of activity, such as lifting the arm or dorsiflexing the foot (see Kots 1977). Note that efference does not necessarily carry a central, motor-to-sensory corollary-discharge connotation (Teuber 1964 *op. cit.*). Such a view, while placing the motor commands in a sensory "code" readily available for comparison with reafference, is just as subject to the mapping-invariance and degrees-of-freedom criticisms outlined above. Rather, efference may be viewed in terms of feedforward, which, because of its particular biasing or tuning operations on the spinal cord, constrains the performer to a limited set of activities (Fowler 1977; Greene 1972).

Gyr et al. refer to deafferentation research as evidence for autoregulation of behavior at a central level. In agreement with Pew (1974), we would have to say that the argument is really one by default, taking the following form: 1) peripheral

feedback has been eliminated; 2) the animal can perform various motor activities; 3) therefore some internal monitoring mechanism is responsible. A variety of alternative conclusions have been offered (e.g. Adams 1976; Schmidt 1975). But it has never been clear in this formulation what is meant by *monitoring*, or the nature of the entity that is being monitored. Taub's more recent work on perinatal deafferentation (e.g. Taub 1977 for review) can be interpreted to mean that residues of past experiences, efference copies, and the like are unsuitable candidates for the monitored representation. These are likely to be very impoverished indeed and hardly able, even if one could image them to do so, to contain all the details of the action patterns, such as climbing, hanging, and grasping, that have been observed. But the stronger criticism here is that it is a conceptual error to pose the question: Is an efferent signal necessary or not for normal perception? The tight coupling between efference and afference demands that we not treat them as individual entities but rather seek to understand the nature of their interaction.

Some headway has already been made in this regard. There is neurophysiological evidence that, prior to and during voluntary movements in cats, afferent information in the dorsal-column medial lemniscus is modified (Ghez & Lenzi 1971; Coulter 1974). Similarly, anatomical evidence reveals that descending pyramidal fibers exert both pre- and postsynaptic influences on the transmission of sensory information in the spinal cord (Kostyuk & Vasilenko 1968). Furthermore, human psychophysical experiments on the perception of vibratory stimuli show that the sensory threshold becomes elevated during voluntary movement (Dyhr-Poulson 1975). This modulation is specific to the digit being moved and is not merely a general gating effect on sensory inputs. In sum, we have evidence from a variety of sources illustrating the efferent modulation of afference.

Just as interesting is the rather direct influence of afferent information on efferent activity. At a neurophysiological level, Easton (1972) has shown that stretching the vertical eye muscles leads to facilitation and inhibition of cat-forelimb flexor and extensor muscles. A downward-directed gaze results in facilitated forelimb extension while upward gaze facilitates flexion. More recently, Thoden, Dichgans, & Savidis (1977) have produced evidence that hindlimb flexor and extensor activity can be modulated by both vestibular and visual stimulation. Of particular note is the finding that direction-specific reflex excitability in extensor and flexor motoneurons can be induced by rotating a visual display about the cat's line of sight. Thus, counterclockwise rotation, indicating displacement to the right, leads to an enhancement of extensor motoneuronal activity and a depression in flexor motoneurons, while clockwise rotation has an equal but opposite effect. Analogous findings are available from the elegant "swinging room" experiments of Lee (1978) and his colleagues. Even though the subject is supplied with veridical kinesthetic receptor information that the floor is stable, posture and balance are shown to be under visual control, as evident in the excessive sway observed when the room is moved. Indeed, body sway can be visually driven by oscillations as small as 6 mm without the subject being aware of it. All this points to a tight coupling—a specification, as it were—of efference by afference.

The general claim here, then, is that the efference-copy construct cannot handle the vagaries of the motor system, nor does it provide a particularly useful explanatory device for visual perception. Neither do we want to approach the issue of adaptation via a framework that promotes a dichotomy between efference and afference, as Gyr et al. have done. In actuality there is no need to revert to a recorelation formulation for an explanation of perceptual adaptation. It is now well-documented, for example, that adaptation can occur without movement (Howard, Craske, & Templeton, 1965 *op. cit.*) in passive conditions (Melamed, Halay, & Gildow 1973) and in conditions where passive movement is induced by vibration (Mather & Lackner 1975). All that is needed for adaptation to occur is a discordance between two or more sources of information that are normally congruent with each other. The performer's attempt to nullify this discordance, and hence return the inputs to their previous correspondence, is seen to be representative of the adaptive process. Numerous studies support this viewpoint (see Kornheiser 1976 for a review) by showing that the degree to which adaptation takes place is a function of the information available to the subject regarding the altered state of the system.

While the notion of discordance is plausible as an account for the occurrence of adaptive change, it lacks predictive power with regard to the exact form that such change will take. The additional concept of attentional allocation provides a potential solution to this problem, in that the outcome of any noncorrespondence between two sources of information (say proprioceptive information detected visually and proprioceptive information detected by joint, muscle, and tendon receptors) can be predicted on the basis of the attentional demands of each

input. Thus Canon (1970), Kelso, Cook, Olson, & Epstein (1975), and more recently Warren & Schmitt (1978) have all shown that adaptation takes place in the modality that is not used during the exposure period. When allocation of attention is left uncontrolled, the dominant modality (in most cases, vision) will remain stable, while the paired source of information will undergo an adaptive shift.

We are accordingly left to explain, within this formulation, the consistent finding that self-produced movement facilitates the adaptive process more than passive movement. Viewed from the informational account, we would argue that under active conditions S is sensitized to pay attention to the discordance between the seen and felt positions of the limb, while under passive conditions, attention is more evenly distributed between the two sources of information. Given the dominance of vision and S's inherent bias to attend to it (Posner, Nissen, & Klein 1976), we would then expect greater adaptation under self-produced movement conditions. Hence, what matters for the adaptive process is information about discordance, which, when combined with attentional factors, seems adequate to explain the findings attributed to motor-sensory mechanisms.

In the present view there is, therefore, no urgent need to reopen this issue based on Gyr et al.'s failure to replicate H & R. Many of Held's predictions have been tested over and over again in an area already burgeoned with empirical data (e.g. see Kornheiser 1976; and Welch 1974 *op. cit.* for reviews). The real need is not for more experimentation, but rather for more *understanding* of the nature of the adaptive process, with particular reference to the interaction of efference and afference.

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A provisional sensory/motor "complementarity" model for adaptation effects. After an impressive amount of experimental research on the phenomenon of adaptation and re-adaptation, occasionally called recalibration, recombination, re-arrangement, re-adjustment, and so forth, the moment for a more rational pause had to come. The Gyr et al. study provides this in a very valuable way.

From the point of view of our earlier Innsbruck studies, we did not find any reason to deviate from a basic theory of direct visual perception in considering general adaptation and re-adaptation processes or the special cases of prism experiments, although in many cases motor activity was clearly coupled with the sensory effects in question. The "complexity" of re-adaptation, as we suggested, resides in the unusually long time that visual input remains "distorted" after prisms are removed. A variety of contextual contingencies are operative during re-adaptation to determine its speed and course. In our studies the pattern appeared to approach the classical conditioning story: After frequent prior presentation of a stimulus configuration to a sense organ under certain characteristic conditions, those particular conditions lost their "neutrality" and became cues for the adaptation effects, irrespective of whether the conditions were "motor" or "sensory." In the case of prism-induced color fringes, for instance, the cue for adaptation to color was the direction of the brightness gradient of the contours in the visual field itself (a predecessor of the well-known McCulloch effect). In the case of apparent movement, however, various types of locomotion, combined with head, trunk, and body movement, functioned as the special cues for stabilizing the initially-experienced "textural flow."

Conditional processes of this sort seem to serve as generalized descriptions of the phenomena in question rather than as explanations. Nevertheless, it may be fruitful to adopt an oversimplified "complementarity" model, for the moment, leaving it open as to whether a particular phenomenon should be explained by purely sensory effects (visual or kinesthetic) or by a kind of sensorimotor link. Let me pursue this a little further.

First of all, there exist some noncontingent adaptation (and re-adaptation) phenomena that seem to occur completely independently of any accompanying motor activity, neither active nor passive, other than keeping eyes open, being seated in a chair in the lab, looking through a hole at a target, and pressing a button at the right moment. I suspect that because the situation remains completely unchanged under such conditions, the phenomena obtained look purely "sensory," with no particular "cue" for the attendant adaptational process. In addition, the testing situation is kept identical to the training situation, a point of no small importance, as we shall see later on.

The added "complexity" in the Gyr et al. study may, at first glance, be thought of as the effect of the systematic introduction of motor activity (locomotion, eye, head, and body movements) into the training situation, resulting in the perceived visual gradient changes. The latter effect would have served as a critical one, not only in the case of the "frozen" environment of random spots on the wall of H & R's experimental cylinder, but even in a "living" environment consisting of, say, randomly-moving dots comparable to a swarm of flies, or the snow showers on the screen of a television set. What is true of all these cases when one is moving while viewing them through prisms is the peculiar change of the configurational flux, which diverges from a lifetime of pre-experimental experience. It is this superimposed change that seems to operate as the higher order "stimulus," not the kind or size of the configuration itself.

So far this only describes one aspect of the antecedent training situation. The most important variable in the work of Held and his associates is the question of self-induced versus imposed activity. This seemed to be the critical factor in determining adaptation effects in a variety of experiments.

It is my personal belief, derived from some of my own observations while wearing various experimental prisms, that a more thorough analysis of pre-experimental life situations may provide the key to a better understanding of adaptation. Consider that most organisms are self-locomoting; thus, in the case of active movement, they are the causal sources of a special group of stimulus transformations superimposed on their own sensory inputs. The condition of passive transportation, on the other hand, occurs rather rarely—indeed, even artificially. Although various types of vehicles now multiply the situations of passive transportation for human beings, nevertheless, a rolling pedestal (as in some of the Held studies) remains a very unusual situation for a healthy man. I should wonder whether experienced wheel-chair riders (especially passively-moved ones), or persons with extensive escalator experience, would have shown the same minimum effect of re-adaptation when wearing wedge prisms?

From such a naturalistic point of view one would expect a rather different result with up/down prisms. A distortion of distance and shape with respect to the ground we walk on causes a much more dangerous change than the deformation of vertical shapes. We have not used up/down prisms because of the highly attendant danger, especially when going downstairs. The same type of transformation from a mathematical point of view, due to the same optical device, may nevertheless be connected to very different "biological" effects, due, for example, to the asymmetry of the pull of gravity.

A personal observation by Taylor (1962) provides a further illustration. Crippled since the first years of his life, he was strongly handicapped in walking. He thus spent many hours a day in a chair, only occasionally standing up to get around his work table. While wearing wedge prisms (base-left), he soon became aware of a decrease in the bending effect and, especially, of the apparent incline of the surface of the table and of nearby areas on the floor. After one or two weeks of such training (four to seven hours a day) the effect became almost "regional," in the sense that it seemed to become linked to the accustomed life situation of sitting and writing at his table; in the case of walking about, the floor appeared almost completely horizontal, but only within the range of his walking cane. Outside this mysterious circle the surfaces continued to appear shifted, and the (vertical) edges bent. This observation and similar ones underscore the importance of equating the training and testing situation.

Some further observations strongly support the existence of motor effects in adaptation (or re-adaptation) (although not their necessity). Eyeglass wearers must often push their spectacles back in place when they slide down the nose. Associated with this active "correction" is a small perceptible jump of the visual array (in the case of myopic lenses, ipsiversive with the motion of the frame; in hypermetropics, contraversive). If habitual wearers instead move empty eyeglass frames up and down, they see clear-cut apparent motion of the visual array (in the direction opposite to the habitual one). But if another person performs exactly the same movement for them, no apparent movement occurs (see Figure 1). I think a

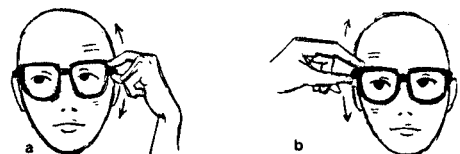


Figure 1 (Kohler). Eyeglass correction: a-active, b-passive. (Artwork by Judith Economos.)