# *The Reafference Principle and Control Theory*

By William T. Powers

When E. von Holst, with Horst Mittelstaedt, studied the subject of reflexes, he arrived at some conclusions that led to a new concept of how they work. The key insight came from observing that reflexes were not simple brief input-output processes, but arose from continuous activity in the nervous system. "A continuous stream of impulses links the higher and lower centers even when there is external motor inactivity." (all citations from Von Holst, 1950). Furthermore, he noticed a paradox. Postural reflexes were then thought to maintain "normal postures" by reflex actions that corrected deviations from normal. However, von Holst had observed that fish and other creatures could maintain not only normal postures, but abnormal ones, such as a fish orienting its body vertically or on its side rather than in the more usual horizontal configuration. Not only could they do that, but when disturbances caused deviations from the abnormal posture, the muscles acted reflexively to restore not the normal posture but the abnormal one. How a simple reflex could act this way was a mystery.

Through various experimental means, von Holst found that the corrective effects of reflexes depended on the presence of afferent signals caused by the motor activity of the reflex: "The 'voluntary movement' proves to be dependent on the afferent return stream which it evokes!" Interfering with those signals greatly altered the behavior. He called these sensory signals "reafferent" signals because they re-entered the system that carried out the reflex act. The writing of the seminal paper was clearly done after the advent of cybernetics (Wiener, 1948), for von Holst recognized that these were what the cyberneticists called "feedback" signals.

However, there was a key gap in von Holst's understanding of feedback, which was predictable from footnote 6 in the paper. It said "We owe our acquaintanceship with technological cybernetics to Dr. Boehm...". In short, von Holst himself was not acquainted with the properties of negative feedback control systems, or not with enough of them. When he tried to understand how these phenomena could be embodied in the nervous system, he attempted to devise a model that seemed to account for them. He came close to independently inventing control theory. That is what led to his ideas of efference copies, reafference and exafference, and a "residue" left over from the subtraction of a reafference signal from an efference copy. He assumed this residue would be sent upward toward higher systems.

In fact this residue is called an "error signal" in control theory, and it is sent not upward, but outward toward the muscles. The downgoing efferent signal, the "command" signal, corresponds to the reference signal in a control system. By changing the point of origin of just one signal in von Holst's basic diagram, and slightly rerouting the reafference signal, we can change his model into a negative feedback control system. In von Holst's diagram, a downgoing command signal splits into two branches. The long branch carries an efferent signal to the effector; a short branch, the "efference copy," goes laterally and meets the upgoing reeafference signal being caused by the effector. The reafference signal subtracts from the efference copy and the resulting difference- signal is shown as going upward toward higher centers.

If we just move the start of the main efferent signal to the point where the command signal has the reafference signal subtracted from it, the efferent signal becomes the error signal and is the input to the effector. The downgoing command signal, now a reference signal, stops where it meets the reafference signal. The upgoing afference signal can now be split with one branch continuing on upward toward higher centers, and a local branch carrying a copy of the afferent signal, via an interneuron that makes the signal subtractive, to meet the efference copy (now the only place where the efferent command signal

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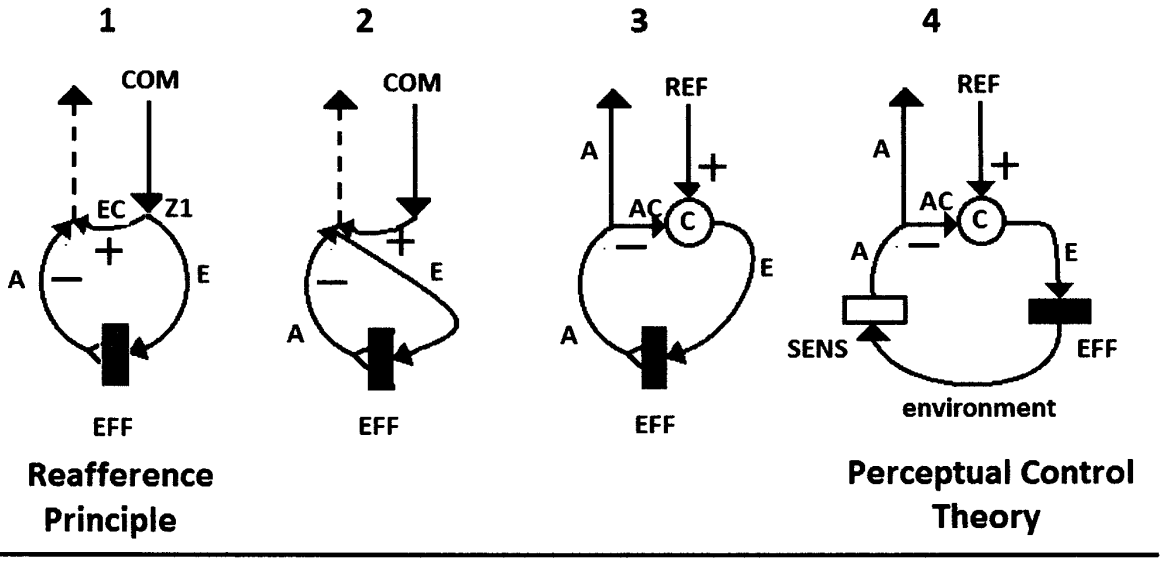
goes, so it is no longer a "copy"). In spinal reflexes, the division of the afferent signal into two pathways is called the "bifurcation of the dorsal roots" and is ubiquitous. The place where the reafference signal meets the command signal- now the reference signal of a control system — is a motor neuron in the spinal cord. The meeting place is called the comparator in a control-system diagram..

These small changes convert von Holst's model into a true negative feedback control system. lf we assume with von Holst that a similar architecture holds at higher levels in the nervous system, we have a hierarchy of control systems.




COM = Command; A := afferent signal; E = efferent signal / error signal; EC = efference copy; EFF = effector; AC = afference copy; C = Comparator; REF = Reference signal; SENS = sensor.

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