

REAFFERENCE

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ReaffERENCE

Primary Disciplinary Field(s): Neuroscience, Motor Control, Sensory Psychology

1. Core Definition

ReaffERENCE refers specifically to the sensory signals that are generated and received by the nervous system as a direct consequence of an organism's own motor activity. This concept distinguishes internally generated sensory input from input arising externally from the environment. Essentially, when a muscle contracts or a sensory organ moves according to a voluntary command, the resulting sensory feedback--whether visual, auditory, or somatosensory--is classified as reaffERENCE. This mechanism is crucial for enabling the brain to interpret sensory information accurately, filtering out self-generated noise to maintain a stable and coherent perception of the external world.

A classic illustration of reaffERENCE involves eye movements, particularly during the tracking of an object or a rapid shift of gaze known as a saccade. As the eyeball rotates within its socket, the visual field moves across the retina. If the brain interpreted this retinal image shift as genuine movement in the external environment, the world would appear to jump wildly with every eye movement. However, because this sensory change is predictable and internally caused by the motor command to the eye muscles, the resulting visual signal is categorized as reaffERENCE and effectively suppressed or cancelled, leading to the subjective experience of **visual stability**.

The physiological significance of reaffERENCE lies in providing necessary feedback loops for motor refinement. While the immediate goal of the system is often to cancel the sensation to stabilize perception, the precise timing and pattern of reaffERENCE are simultaneously used by motor planning centers, such as the cerebellum, to learn and correct future movements. This dual function--cancellation for perception and utilization for learning--highlights the complexity of the sensorimotor integration necessary for effective interaction with the environment.

2. Etymology and Historical Development

The concept of reaffERENCE was formally established and detailed in the mid-20th century, primarily through the pioneering work of German scientists Erich von Holst and Horst Mittelstaedt. Their 1950 publication laid the foundation for the "ReaffERENCE Principle," a revolutionary framework for understanding how the nervous system achieves perceptual constancy despite continuous self-movement. Prior to their work, explanations for perceptual stability often struggled to account for the difference between a moving object and a moving observer.

Von Holst and Mittelstaedt studied movement in simple organisms, particularly flies and fish, developing models that demonstrated the necessity of comparing motor commands with sensory

feedback. They proposed that when a motor command is issued (the efference), a simultaneous internal copy of this command--known as the **corollary discharge** or **efference copy**--is sent to the sensory processing centers. This efference copy essentially acts as a prediction of the expected reafferent signal. By comparing the efference copy (prediction) with the actual reafference (sensory consequence), the organism could accurately determine if a perceived change was due to its own actions or external changes.

This historical development marked a significant shift from purely reflex-based models of behavior to models emphasizing predictive coding and internal simulation. The ReaffERENCE Principle provided the crucial neurobiological mechanism explaining phenomena like the inability to surprise oneself and laid the groundwork for modern theories of motor control, sensory gating, and self-recognition in neuroscience. Its profound implications extended beyond simple reflexes, influencing research into complex cognitive functions and even certain neurological disorders.

3. ReaffERENCE vs. Exafference

The nervous system must constantly distinguish between sensory input generated by the body (reafference) and sensory input arising from changes in the external world (exafference). This distinction is fundamental to survival and accurate perception. **Exafference** refers to the sensory input resulting from external stimuli, such as a ball moving across the visual field or a sound emanating from a source outside the body. The goal of the sensory system is typically to process and react to exafference, as it represents relevant changes in the environment.

Conversely, reaffERENCE represents internally generated sensory noise that, if not managed, would overwhelm the perceptual system. The process of sensory gating or cancellation is applied specifically to reafferent signals. When the efference copy matches the subsequent reafferent signal, the brain knows this input is self-generated and often filters it out. This active suppression allows the organism to focus its attentional resources on the unpredictable and potentially threatening changes represented by exafference.

The ability to flawlessly differentiate between these two types of input is the bedrock of stable perception and effective motor control. For instance, when an individual walks, the complex proprioceptive, vestibular, and visual inputs generated by the movement are mostly reaffERENCE. These signals are predicted and largely cancelled, allowing the nervous system to remain acutely sensitive to exafference, such as the unexpected texture of the ground underfoot or the sudden appearance of an obstacle. A failure in this mechanism results in perceptual instability and difficulties in coordinating movement, demonstrating the absolute necessity of this real-time distinction.

4. The Efference Copy and Sensory Cancellation

The mechanism underlying the processing of refference hinges entirely on the existence and reliable function of the efference copy. When the motor cortex initiates an action, the command (the efference) travels down to the muscles. Simultaneously, a parallel signal--the efference copy (or corollary discharge)--is relayed to various sensory and cerebellar processing nuclei. This internal signal serves as a feed-forward prediction of the sensory consequences of the impending action.

Upon receiving the actual refferent sensory feedback, specialized neural circuits compare it against the efference copy. If the two signals align closely--meaning the sensory input is exactly what was predicted by the motor command--the system concludes the input is self-generated. This match triggers a **sensory cancellation** or attenuation mechanism, often referred to as gating. The refferent signal is thus suppressed before it reaches consciousness or high-level perceptual areas.

This cancellation mechanism is observable across multiple sensory modalities. Perhaps the most famous non-visual example is the inability to effectively tickle oneself. When one attempts self-tickling, the motor command perfectly predicts the sensation, and the resulting refferent input is strongly attenuated, rendering the experience bland or non-ticklish. However, if the same sensory input is delivered externally by another person, it is classified as exafference, the prediction fails, and the full, intense sensory experience of ticklishness is registered.

5. Physiological Mechanisms and Neural Pathways

The integration and comparison of efference copy and refference involve distributed neural networks spanning several critical brain structures. Key areas involved include the cerebellum, the superior colliculus, and specific pathways within the thalamus and primary sensory cortices. The cerebellum is widely regarded as central to this process, acting as a crucial predictive engine. It utilizes internal models of the body and the environment to predict the sensory state resulting from any given motor command.

In the visual system, structures like the superior colliculus and dedicated pathways linking the oculomotor nucleus to the visual cortex are essential for processing eye movement refference. The efference copy related to saccades is relayed along these pathways, allowing the visual system to shift its processing window or suppress activity in a manner synchronized with the eye movement. This complex interaction ensures that, despite the retinal image sweeping wildly across photoreceptors, the perceived visual scene remains stable.

Furthermore, in the somatosensory domain, sensory gating occurs rapidly in the brainstem and spinal cord. Studies have shown that when a movement is initiated, the sensitivity of relevant

sensory receptors and relay neurons is momentarily reduced. This feed-forward suppression ensures that the heavy burst of reafferent proprioceptive and tactile information generated by the movement does not interfere with the perception of external tactile events. This highly refined neural pathway allows for continuous, precise motor adjustments without sensory overload.

6. Significance in Motor Learning and Adaptation

While sensory cancellation is vital for perceptual stability, the reafference mechanism is equally critical for **motor learning** and adaptation. Learning a new skill--whether riding a bicycle or playing a musical instrument--is fundamentally a process of calibrating the internal motor commands with the external sensory consequences. Reafference provides the error signal necessary for this calibration.

During initial skill acquisition, the motor command (efference copy) often fails to accurately predict the sensory consequence (reafference). This mismatch constitutes a sensory prediction error. The brain uses the magnitude and direction of this error to refine the internal model of the motor system. Over time, through repeated practice, the efference copy becomes increasingly accurate, predicting the reafference perfectly, thus reducing the prediction error and leading to smoother, more efficient, and seemingly automatic movements.

This mechanism is also central to rapid motor adaptation. If, for example, a person wears prism goggles that shift the visual field, their initial movements will produce a large visual reafference error. The discrepancy between the predicted visual input and the actual visual input (reafference) rapidly drives recalibration of the motor commands until the error signal diminishes. This adaptation relies entirely on the continuous comparison of predicted sensory outcome (efference copy) against the actual sensory outcome (reafference).

7. Clinical Implications and Disorders

Dysfunctions in the reafference system are implicated in several debilitating neurological and psychiatric conditions, highlighting the fragility of the brain's ability to distinguish self from non-self. One of the most studied areas is schizophrenia. Patients suffering from positive symptoms, such as auditory hallucinations and delusions of control (e.g., believing their thoughts or actions are being controlled by an external force), are hypothesized to have a faulty reafference mechanism.

Specifically, it is theorized that the generation or relay of the efference copy is impaired in these individuals. Consequently, when the patient performs an action--say, generating a thought or speaking--the resulting sensory feedback (reafference) arrives, but the predicted signal (efference copy) is either missing or severely attenuated. The brain, therefore, misinterprets the self-generated sensation as novel, unpredictable, or external (exafference), leading to the perception that their voice or actions are originating from a source outside of their control.

Furthermore, conditions involving motor incoordination, such as cerebellar ataxia, often demonstrate deficits in using refference for real-time error correction. Since the cerebellum is crucial for integrating predictive signals, damage to this structure impairs the ability to generate accurate internal models and compare them effectively with incoming sensory feedback. This results in clumsy, oscillating movements because the motor system cannot precisely anticipate or react to the sensory consequences of its own ongoing actions.

Further Reading

Efference copy (Corollary Discharge)

Reafference Principle

Sensory Gating

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