Efference Copy – Did I Do That?
CMSC828D Report 3

Cody Buntain
Department of Computer Science
University of Maryland

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Efference copy is a neurological phenomenon first proposed in the early 19th century in which efferent signals from the motor cortex are copied as they exit the brain and are rerouted to other areas in the sensory cortices [5]. While originally proposed to explain the perception of stability in visual information despite constant eye movement, efference copy is now seen as essential in explaining a variety of experiences, from differentiating between exafferent and reafferent stimuli (stimulation from the environment or resulting from one's own movements respectively) to attenuating or filtering sensation resulting from willed movement to cognitive deficits in schizophrenic patients to one's inability to tickle one's self [5, 7].

As mentioned, early work on efference copy was performed in 1823 by Charles Bell and 1825 by Johannes E. Purkinje, which focused primarily on understanding stability in visual perception [2]. In general terms, the two scientists were trying to explain why active movement of the retina did not cause a perceived motion of the retinal image whereas introducing movement to the eye by pressing against it with a finger did result in a perceived motion. The theory of efference copy (though not strictly named) was introduced to explain this difference: as the eye is actively moved, a copy of the responsible signals are made (the efference copy); these copies are then used to cancel out displacement in the image; such signals are not present to copy when the eye is moved through external means (e.g., with a finger), so the image appears to move.

Following the works of Bell and Purkinje, Hermann von Helmholtz expanded this idea further in 1866 to include not only visual perception but also sensorimotor coordination. In his experiments, Helmholtz worked with patients who had suffered forms of paralysis in their ocular systems and asked them to observe an object beyond the point of their paralysis, called "past pointing" (e.g., if a subject cannot turn his/her eyes completely to the right, the subject is asked to observe an object at the far right of the field of vision). The subject perceives the target and concludes that the object lies in the direction of the intended gaze even though the ocular paralysis has ensured the gaze did not reach the intended direction. Helmholtz concluded that the internal inference made by the subject was therefore influenced only by the intended direction of the gaze. It is the efference copy of the non-existent eye movement in this scenario that augments the sensory information for the subject to conclude the object is in the intended direction. One should note that the previous three works are also very closely related to the Vestibular Occular Reflex (VOR), which is being covered in a separate report.

The next important work in efference copy did not appear until 1950 with E. von Holtz and H. Mittelstaedt's research into differentiating internal and external stimuli. It was this research that coined the term "efference copy," or "Efferenzkopie" in the original German as well as the terms "reafference" and "exafference." Holtz and Mittelstaedt performed their investigations by reversing a subject's reafferent signals by rotating a fly's head by 180 degrees. Such a modified fly would end up flying in a circle in a lit environment but normally in a darkened environment. Holts and Mittelstaedt concluded that an efference copy was being created within the fly's visual system, and in its attempts to stabilize its visual perception using the negative feedback of the copy, the fly would correct its locomotion in the direction *opposite* of the correct one (because of the visual inversion). Since the darkened environment did not offer the same inverted reafferent feedback, the circling behavior was absent because the correction stimulus was not present.

At approximately the same time as Holtz and Mittelstaedt, Roger Sperry was also performing similar research on fish. Similar to Holtz and Mittelstaedt, Sperry surgically inverted the eyes of fish and also observed normal behavior in darkened environments, which led him to exclude the possibility of circling behavior resulting from nerve damage. He also coined the very related (and sometimes interchangeable) term of "corollary discharge," which refers more specifically to inhibitors in the nervous system related to active movement but operates similarly to the notion of efference copy.

Almost thirty years after Holtz, Mittelstaedt, and Sperry, Irwin Feinberg published a paper in 1978 that drew a connection between efference copy and psychotic disorders like schizophrenia. The general idea of this paper is that, if the phenomenon of efference copy is essential in differentiating between exafferent and reafferent feedback, then disorders with the efference copy mechanism may explain a schizophrenic's inability to differentiate between internal thoughts as reafferent and external voices as exafferent. That is, if a person has a deficiency with the mechanisms of efference copy, that person would potentially perceive his own thoughts as external stimuli or an outside voice in his head, a prototypical symptom of schizophrenia [4].

More recent research into efference copy from the early 1990s has attempted to describe the mechanics of how efference copy affects perception. In 1992, Jordan and Rumelhart proposed that the brain creates a model of the body's physical motor system and how it responds to outgoing motor commands (cited in [6]). Such a representation is called a "forward model" and leverages efference copies as model inputs, and it is through this modeling that the brain attempts to predict the body's responses, which can lead to the circling behavior described above when the model's predictions do not match the external perceptions.

In fact, consistency or discrepancy between efference copy-based forward modeling and actual perception has been theorized to be the cause of several interesting phenomena. As stated early on, it is thought that the brain's efference copy mechanism and its ability to inhibit sensation as a result (i.e., corollary discharge) is the reason why one cannot tickle one's self. That is, the body uses efference copy and forward modeling to predict the sensations caused by one's attempt to tickle one's self, and corollary discharge suppresses the resulting sensation. In the works of Blakemore et al., they actually model this behavior by connecting a robotic arm to a subject to mimic arm movement. When the subject attempts to tickle himself with the robotic arm, the tickling sensation is suppressed. If, however, a delay is introduced between when the subject makes the tickling action and when the robotic arm actually repeats the action on the subject, the tickling sensation increases significantly. Blakemore et al. concluded from this experiment that the temporal discrepancy between what the brain predicts and what actually happens leads to an inability to cancel out the sensations (in a manner similar to the fly described previously) [1].

Current literature on this phenomenon, while still varied, has progressed significantly in demonstrating the presence and effects of efference copy and forward modeling in the brain. Within the past ten years, Ford et al. have developed a suite of electrophysiological mechanisms for tracking efference copy and how it relates to auditory hallucinations [5]. Furthermore, Miall and Wolpert have published work on forward models in understanding human internal modeling and its applicability neural networks and learning mechanisms [6]. This work has been further extended to help understand the physical and psychological processes in fast movement and how efference copy and forward models are continuously updating predictions on body response throughout an action instead of immediately prior to the action and right at its termination, which could potentially be useful in creating quick-reacting robotic systems [3].

References

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