



Minireview

The function of efference copy signals: Implications for symptoms of schizophrenia

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ABSTRACT

Efference copy signals are used to reduce cognitive load by decreasing sensory processing of reafferent information (those incoming sensory signals that are produced by an organism's own motor output). Attenuated sensory processing of self-generated afferents is seen across species and in multiple sensory systems involving many different neural structures and circuits including both cortical and subcortical structures with thalamic nuclei playing a particularly important role. It has been proposed that the failure to disambiguate self-induced from externally generated sensory input may cause some of the positive symptoms in schizophrenia such as auditory hallucinations and delusions of passivity. Here, we review the current data on the role of efference copy signals within different sensory modalities as well as the behavioral, structural and functional abnormalities in clinical groups that support this hypothesis.

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1. Introduction

Of the vast majority of sensory information with which our central nervous system is inundated, only a small portion reaches our attentional capacities and ever reaches conscious awareness. Sensory gating is a complex process whereby sensory information is processed with extraneous information being filtered out. The end result of this is an experience of the external world that is computed from a number of different sensory signals to allow for the understanding of environmental stimuli and the generation of an appropriate behavioral response. Thus, sensory information is not passively perceived but transformed in many stages of active processing. Failures in different types of sensory gating may play a causal role in symptoms of different psychopathologies. For instance, efficient sensory processing requires a comparator mechanism, ensuring actual sensory feedback matches expected feedback. To achieve this, sensorimotor systems are thought to make use of a 'forward model', whereby information about motor output is used to generate predicted reafferents that modulate the response of sensory systems (see Fig. 1). Without such a system various types of internally and externally generated stimuli, cannot be adequately processed and their features recognized by their origin with respect to the observer.

In some sensory systems, modulation of sensory responses can come from either proprioceptive information or efference copies of the motor command during the preparation for motor output. Efference copies are those neural representations of motor outputs that predict reafferent sensory feedback and modulate the response of the corresponding sensory cortex. Efference copies of the motor command travel to the appropriate sensory cortex preparing it for reafferent stimuli (Cullen, 2004). This system presumably increases the efficiency of attention and cognitive processing by preventing the central nervous system from wasting metabolic resources processing irrelevant sensory stimuli. This process ultimately allows sensory reafferents from motor outputs to be recognized as self-generated and therefore not requiring further sensory or cognitive processing of the feedback they produce (Frith, 1995). Some researchers make minor distinctions between the terms and prefer to use the term corollary discharge (CD) (Sperry, 1950) when discussing signals arising from any stage of motor output that can affect anywhere from the early stages to higher order sensory processing (Crapse & Sommer, 2008a; Sommer & Wurtz, 2002), while the term 'efference copy' (Von Holst & Mittelstaedt, 1950; see review of Cullen (2004)) is used in the same context by others (i.e. Blakemore, Oakley, & Frith, 2003; Ford et al., 2008). In this paper we use the terms interchangeably.

Not only humans are equipped with mechanisms to deal with sensory reafference. Efference copy signals are present across species to prevent allocation of attention to reafference or inhibit maladaptive reflexes. Corollary discharge signals have been studied at

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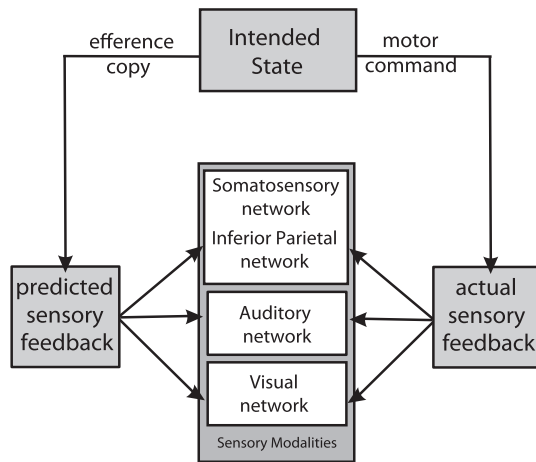


Fig. 1. The efference copy mechanism with sensory feedback to sensory modalities. This mechanism begins with a desired motor command (intended state) sending motor command signals to the motor system for movement execution. This same desired motor command (intended state) sends efference copies to prepare the related sensory modalities (visual, auditory and proprioception/somatosensory) for reafferent feedback.

the cellular level in crickets during chirping behavior. Crickets possess a specific neuron, called the corollary discharge interneuron (CDI), which has widespread connections to several CNS regions, indicating it could affect multiple sensory systems. Recordings from CDI indicate bursts of activity that correspond with sound production during chirping. Paired recordings from CDI and auditory afferent axonal arborizations demonstrate that spikes in CDI result in primary afferent depolarizations that cause presynaptic inhibition in auditory areas (Poulet & Hedwig, 2006). A similar signal has been observed in cockroaches, in giant fibers of the ventral nerve cord during leg movements (Delcomyn, 1977). Cockroaches normally display a running reflex in response to air puff stimuli, yet these extremely sensitive receptors are not activated by the air current generated during movement. This provides evidence at the cellular level that supports the necessity of discriminating between self-induced versus externally induced stimuli across species. This particular example represents a simple inhibition of the sensory and reflex response (which can be categorized as lower-order CD), whereas the effects of CD in many of the primate sensory systems that we will discuss is used by the CNS for more complex sensory analysis (higher-order CD) (Crapse & Sommer, 2008a). For instance, the auditory system in primates is hypothesized to monitor any potential mismatch to expected reafferents with increased sensitivity rather than presenting with an overall attenuated response to noise (Crapse & Sommer, 2008b; Eliades & Wang, 2008).

In both human and non-human primates, research has suggested efference copies have a role in a variety of modulatory functions according to the requirements of each of the sensory networks (Fig. 1). Within the visual system the constantly shifting image on the retina that results from eye, head or body movements must be accounted for when processing the visual image so that these movements do not cause illusory shifting the external environment (Haarmeier et al., 1997). Within the somatosensory system, the corollary discharge signal may inform somatosensory network when tactile stimulation is self-induced (Blakemore, Wolpert, & Frith, 2002). In the auditory cortex, the attenuated response to the sound of one's voice as compared with externally produced auditory stimuli is likely the result of corollary discharge signals (Ford & Mathalon, 2005).

Failures of the efference copy system to generate corollary discharge, or the failure of other CNS areas to receive and integrate

these signals has been proposed as a possible cause for symptoms commonly experienced by schizophrenia patients such as auditory hallucinations and delusions of passivity (Blakemore, Wolpert, & Frith, 2000; Blakemore et al., 2002; Feinberg, 1978; Ford & Mathalon, 2004, 2005; Frith, 1995). The inability to predict the sensory consequences of one's actions may result in the subjective experience of being under the control of external forces. Similarly, the failure to recognize one's voice or inner speech as self-generated might produce the subjective experience of an externally generated sound then interpreted as hearing voices. The following sections will review the literature on CD signals in vision, audition and somatosensation and their relation to symptoms experienced by patients with schizophrenia.

2. Efference copies in the visual system

Efference copies in the visual system ensure visual stability in spite of the displacement of the image on the retina during movements – for instance when watching a video taken with an unstabilized camera it is difficult to focus on the images in the scene, however our own movements resulting in the same visual perturbations as we make eye movements or walk down the street are never perceived. The idea that the brain informs and modulates the activity of sensory processing systems of eye position via an efference copy of the motor command was widely disseminated by Herman von Helmholtz and first demonstrated by von Graefe (1854) (Helmholtz, 1924; for review see Cullen, 2004). Eye position modulation has been found in multiple brain regions using a variety of techniques in animals (Andersen, Essick, & Siegel, 1985; Ferraina et al., 2001; Balan and Ferrera, 2003) and more recently in human neuroimaging studies, (Baker, Donoghue, & Sanes, 1999; DeSouza et al., 2000; DeSouza, Dukelow, & Vilis, 2002) indicating that information about eye position is likely important for many of sensorimotor and cognitive processes.

Although it has also been proposed that information about eye position with respect to the head and body comes from proprioceptors in the eye muscles (for more on this topic see Donaldson, 2000; Steinbach, 1987; Wang et al., 2007), it is widely accepted that corollary discharge for saccades provides the accurate information regarding eye position that is necessary for the ability to estimate correct saccade end-points (Guthrie, Porter, & Sparks, 1983; Sommer & Wurtz, 2004a, 2004b see reviews Sommer & Wurtz, 2006, 2008a, 2008b; Wurtz, 2008), and that proprioceptive information about eye position does not reach the cortex fast enough for the online processing of visual space (Wang et al., 2007; Sommer & Wurtz, 2008a; Xu et al., 2011). While many studies provide indirect evidence for a corollary discharge signal, Sommer and Wurtz have conclusively demonstrated a corollary discharge pathway for visual information that sends information pertaining to saccade direction from the superior colliculus through the MD (dorsal medial nucleus of the thalamus) in order to update the receptive fields in FEF (see Fig. 2A). Orthodromic activation of MD activates FEF, antidromic activation of these same neurons activates SC while antidromic activations of FEF activated MD (Sommer & Wurtz, 2004a, 2004b, 2006; Sommer & Wurtz, 2008b). Disruptions of the SC-MD-FEF pathway via muscimol injection to the MD results in inaccurate second saccade end-points in double step saccades, in which the corollary discharge signal relaying information regarding the position of the eyes after the first saccade is necessary in order to accurately make the second saccade. Corroborating evidence is found in patients with thalamic lesions who also show deficits in making the successive eye movements required for double-step saccades (Bellebaum et al., 2005; Ostendorf, Liebermann, & Ploner, 2010). This corollary discharge signal allows neurons in FEF to update their receptive field

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