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Review

# Electrical induction of vision

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ABSTRACT

We assess what monkeys see during electrical stimulation of primary visual cortex (area V1) and relate the findings to visual percepts evoked electrically from human V1. Discussed are: (1) the electrical, cytoarchitectonic, and visuo-behavioural factors that affect the ability of monkeys to detect currents in V1; (2) the methods used to ascertain what monkeys see when electrical stimulation is delivered to V1; (3) a corticofugal mechanism for the induction of visual percepts; and (4) the quantity of information transferred to V1 by electrical stimulation. Experiments are proposed that should advance our understanding of how electrical stimulation affects macaque and human V1. This work contributes to the development of a cortical visual prosthesis for the blind. We dedicate this work to the late Robert W. Doty.



**Contents**



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## 1. Introduction

The question of how we see the world continues to elude us despite the wonderful electrophysiological experiments of Hubel and Wiesel (1977) showing that the striate cortex (i.e., area V1) is the primary recipient of retinal inputs for processing luminance, colour, motion, and stereopsis. Most of their experiments were performed in non-human primates, which have a visual system comparable to that of humans (Tootell et al., 2003). It is therefore understandable why investigators have devoted much effort to determining what monkeys see when electrical stimulation is delivered to V1 (Tehovnik et al., 2009). A person who committed a large part of his scientific career to this effort is the late Robert W. Doty (e.g., Bartlett et al., 2005; Bartlett and Doty, 1980; Bartlett et al., 1977; DeYoe et al., 2005; Doty, 1965, 1969; Doty and Bartlett, 1981; Doty et al., 1980; Doty and Rutledge, 1959). He was primarily interested in three issues: (1) the psychophysical properties of electrically inducing a phosphene which is a punctuate spot of light generated from V1, (2) the stability of eliciting a phosphene from V1, and (3) the neural pathways that subserve this process. Studies by Doty started almost a decade before the seminal experiments of Brindley and Lewin (1968) on the evocation of phosphenes from V1 of the blind. The purpose of our paper is to highlight many of the forgotten discoveries of Doty and colleagues and to relate them to recent findings by us and others. Effort is also made to relate these findings to studies that have evoked percepts by electrical stimulation of human V1. Our report has implications for investigators interested in developing a visual prosthesis for the blind.

## 2. Detection of current delivered to V1

It has been known for over half a century that animals can learn to respond to electrical currents delivered to the brain (Doty, 1969). Robert Doty showed that monkeys can detect electricity delivered to cortical and subcortical regions of the brain as evidenced by having them press a plate with the tongue or a lever with the hand in exchange for food reward or shock avoidance (Doty, 1965). The cortical regions that were conditioned included V1, V2, parietal lobe, temporal lobe, motor cortex, premotor cortex, and prefrontal cortex, and the subcortical regions included the optic tract, the lateral and medial geniculate nuclei, the pulvinar, the lateral posterior thalamus, the hypothalamus, the tegmentum, the superior colliculus, and the periaqueductal gray. The lowest current threshold for evoking a detection response occurred in the foveal representation of V1, in the hand area of the somatosensory cortex, and in the face/mouth region of the motor cortex. The threshold for evoking a detection response was always lower than it was for evoking a motor response. Even though eye movements stopped being evoked from V1 and prefrontal cortex after many bouts of electrical stimulation, a monkey could still respond to stimulations of these regions as long as a reward was forthcoming.

One of the most remarkable findings of Robert Doty is that brain regions could be functionally segregated according to whether additional behavioural training was necessary for transferring the detection response to a new site (Bartlett et al., 2005; Doty, 1965, 1969; Doty et al., 1980; Doty and Rutledge, 1959). Monkeys readily generalized the detection signal to any region within the V1 map, but failed to do so if stimulations were delivered between V1 and the extrastriate cortex, the lateral geniculate nucleus, or the optic nerve (Bartlett et al., 2005; Doty et al., 1980). Also if a monkey was blinded in one hemifield by lesioning the optic tract, stimulation effects were not generalized from intact V1 to blinded V1, but after bilateral retinal lesions stimulation was readily generalized between V1 and extrastriate cortex (Bartlett et al., 2005; Doty et al., 1980). The latter suggests that visual input is necessary to preserve the functional specificity of different visual areas in cortex. Indeed it has been reported that phosphenes evoked from striate and extrastriate cortex are comparable following blindness that commenced during childhood (Brindley, 1972). Doty and colleagues have interpreted their results to mean that stimulations that elicit similar percepts are generalized, while those that induce different percepts are not and therefore require extra behavioural training (DeYoe et al., 2005; Doty et al., 1980; Doty and Rutledge, 1959).

Murphey et al. (2009) found that sighted human subjects could more readily detect currents delivered to V1, V2, and V3 than to regions about the fusiform face area. The probability of eliciting a detection response was maximal for V1 (i.e., 100% of sites were effective) and minimal for the fusiform face area (i.e., 11% of sites were effective). The probability declined systematically as the site of stimulation changed from the occipital pole to the temporal lobe. Moreover, most sites stimulated in the occipital cortex produced a visual percept, whereas few sites stimulated in the temporal cortex produced a visual percept. Also the visual percepts evoked from all areas tended to exhibit simple characteristic (e.g., flashes of light). Complex percepts (e.g., faces) were never evoked from the fusiform face area (also see Beauchamp et al., 2012), which runs contrary to what others have reported (Lee et al., 2000; Penfield, 1958; Puce et al., 1999). Based on the observations of Doty and colleagues (DeYoe et al., 2005; Doty et al., 1980; Doty and Rutledge, 1959), it is possible that the evocation of detection responses and complex percepts from the temporal lobe might have required additional training. Schmidt et al. (1996) observed that initial stimulation of V1 was not detected by a blind patient until she experienced eight sessions of electrical stimulation spanning 11 days to learn to detect a phosphene over the spontaneous background activity created by the blindness. Indeed, Murphey et al. (2009) have indicated that repeated stimulations may be required to strengthen connections from an electrically activated area so that currents may be detected by human subjects.

Even though monkeys can generalize stimulation delivered to any location within the V1 map, they can be trained to detect changes in the properties of electrical stimulation delivered to the same site or region within V1 (Bartlett et al., 2005; Doty, 1965; Doty et al., 1980). For example, they can detect a 5% change in the frequency of stimulation going from 50 to 52.5 Hz delivered to a site in V1 (Bartlett et al., 2005; Doty et al., 1980). Also monkeys can detect a 5–10% change in current delivered to V1. These sensitivities correspond to a monkey's ability to detect a 5–10% difference in visual contrast over background illumination or by way of discriminating between two targets differing in illumination (Ni and Maunsell, 2010; Schiller et al., 2011; Tehovnik and Slocum, 2005, 2007b). Also two stimulations delayed by 20 ms or more and each delivered through separate electrodes in V1 are judged as occurring in sequence by a monkey (Bartlett et al., 2005; Doty et al., 1980). This temporal resolution corresponds to a monkey's ability to judge which of two visual targets is presented first (Tehovnik et al., 2002).

Furthermore, it has been demonstrated that monkeys can discriminate between the polarity of stimulation pulses delivered to