



Research report

Oculomotor control after hemidecortication: A single hemisphere encodes corollary discharges for bilateral saccades



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ABSTRACT

Patients who have had a cerebral hemisphere surgically removed as adults can generate accurate leftward and rightward saccadic eye movements, a task classically thought to require two hemispheres each controlling contralateral saccades. Here, we asked whether one hemisphere can generate sequences of saccades, the success of which requires the use of corollary discharges. Using a double-step saccade paradigm, we tested two hemidecorticate subjects who, by definition, are contralesionally hemianopic. In experiment 1, two targets, T1 and T2, were flashed in their seeing hemifield and subjects had to look in the dark to T1, then T2. In experiment 2, only one target was flashed; before looking at it, the subject had first to saccade voluntarily elsewhere. Both subjects were able to complete the tasks, independent of first and second saccade direction and whether the saccades were voluntarily or visually triggered. Both subjects displayed a strategy, typical in hemianopia, of making multiple-step saccades and placing, at overall movement-end, the recalled locations of T1 and T2 on off-foveal locations in their seeing hemifield, in a retinal area typically spanning a 5–15° window, depending on the subject, trial type and target eccentricity. In summary, a single hemisphere monitored the amplitude and direction of the first multiple-step saccade sequence bilaterally, and combined this information with the recalled initial retinotopic location of T2 (no longer visible) to generate a correct target-directed second saccade sequence in the dark. Unexpectedly, our hemidecorticate subjects performed better on the double-step task than subjects with isolated unilateral parietal lesions, reported in the literature to have marked deficiencies in monitoring contralesional saccadic eye movements. Thus, plasticity-dependent mechanisms that lead to recovery of function after hemidecortication are different than those deployed after smaller lesions. This implies a reconsideration of the classical links between behavioural deficits and discrete cortical lesions.

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1. Introduction

Saccadic eye movements are used to scan a visual scene by displacing rapidly the fovea from one point of interest to another. Saccades are generated via a complex bilateral network involving many cortical and subcortical areas within one hemisphere and interactive links between the two hemispheres. Electrical stimulation of major areas controlling saccades in one hemisphere such as the cortical frontal eye fields (FEF) and midbrain's superior colliculus (SC) evokes contralaterally-directed saccades. Neurons in these areas have contralateral movement fields and their deactivation severely impairs contralateral saccades. These observations have led to the generally accepted proposition that each hemisphere controls saccades directed contralateral to itself (reviewed in Leigh & Zee, 1999; Pierrot-Deseilligny, Ploner, Muri, Gaymard, & Rivaud-Pechoux, 2002).

There is considerable evidence, however, against this strict left brain – right saccade, and vice versa, view of the saccadic system's organization. For example, microstimulation of the supplementary eye field (SEF) in one hemisphere can evoke either contralateral or ipsilateral saccades (Penfield & Jasper, 1954; Schlag & Schlag-Rey, 1987). Neurons in the FEF of each hemisphere project to both the contralateral and ipsilateral SC (Distel & Fries, 1982; Leichnetz, Spencer, Hardy, & Astruc, 1981). At the behavioural level, callosotomy patients can direct their saccades either to the left or right depending on the colour of a cue presented to the same single hemisphere (Hughes, Reuter-Lorenz, Fendrich, & Gazzaniga, 1992). Finally, and particularly relevant to the present study is that hemidecorticate subjects – who have had an entire cortical hemisphere surgically removed – are able to generate accurate bilateral saccades (humans: Herter & Guitton, 2004; monkeys: Tusa, Zee, & Herdman, 1986).

If one hemisphere contains circuits for bilateral saccade control, an important question is whether, in this hemisphere, the circuits that drive leftward and rightward saccades can communicate with each other and with the visual system. The classical model postulates that information about the vector of a saccade is communicated to various brain areas, including the opposite hemisphere, by a copy of the motor command called the “corollary discharge” (CD) or efference copy (von Holst & Mittelstaedt, 1950; Sperry, 1950). This mechanism is critical for vision because it contributes to our abilities to maintain: 1) a perceptually stable visual world by combining visual information from the retina with motor information about saccades to determine whether an image movement on the retina is due to movement of our own eyes or that of the environment (von Helmholtz, 1925); and 2) an updated internal representation of the position of our eyes in the orbit and where they are pointing in space during scanning eye movements consisting of multiple saccade steps (Guthrie, Porter, & Sparks, 1983). Point 2 is the subject of this paper.

A common tool used to study the encoding of multiple saccades is the double-step paradigm (Hallett & Lightstone, 1976) wherein a subject, in the dark, typically fixates

centrally while two targets (T1 and T2) are briefly flashed sequentially in the periphery. The subject must make two saccades (S1 and S2) in complete darkness to the remembered locations of the targets in the order in which they were presented. The visual information about T1 and T2 is available in retinal coordinates. Therefore, the subject must use CD information about S1 – called CD_{S1} – in order to make an accurate S2, according to the simple vector equation: $S2 = T2 - CD_{S1}$. It is known that normal humans and monkeys can perform the double-step task successfully (Baizer & Bender, 1989; Becker & Jurgens, 1979; Gellman & Carl, 1991; Gnadt & Andersen, 1988; Goldberg & Bruce, 1990; Hallett & Lightstone, 1976; Li & Andersen, 2001; Mays & Sparks, 1980; Medendorp, Goltz, & Vilis, 2006; Ray, Schall, & Murthy, 2004), by monitoring ongoing motor output and appropriately adjusting the motor plan for subsequent eye movements (Quaia, Joiner, Fitzgibbon, Optican, & Smith, 2010).

Patients with parietal lobe lesions present with a stereotyped deficit in the double-step task: they are unable to complete an ipsilesionally-directed saccade if it follows a contralesionally-directed saccade (Duhamel, Goldberg, Fitzgibbon, Sirigu, & Grafman, 1992; Heide, Blankenburg, Zimmermann, & Kompf, 1995). The latter authors have also shown a left-right asymmetry in hemispheric control. Other studies have found that transient inactivation of the human posterior parietal cortex in healthy control subjects can cause errors in saccades that follow a contralesionally-directed saccade (van Donkelaar & Muri, 2002; Morris, Chambers, & Mattingley, 2007). All these authors suggest that the CD of the contralesional saccade, S1, executed by the lesioned hemisphere, is not transmitted to the planning areas of S2 either within the lesioned hemisphere or in the other, intact hemisphere, thereby implicating the parietal lobe in the processing of CD. Imaging studies in healthy control subjects have also implicated the parietal lobes in the processing of CD information (Bellebaum, Hoffmann, & Daum, 2005). These studies do not reveal, however, whether the CD is generated by the parietal lobe itself or whether a lack of the intact parietal region prevents the contralateral transmission of the CD generated somewhere else in the hemisphere. They also do not show by which pathways and mechanisms a CD, generated by one hemisphere, can be made available to the other. This is a complicated topic considered further in the Discussion.

One sure way to avoid concern about the involvement of commissural pathways is to study hemidecorticate patients which we do here. No study to date has demonstrated convincingly whether a single hemisphere can control bilateral saccades when information about the bilateral CD for these saccades is required. Our investigation probes whether a single hemisphere is able to track contraversive and ipsiversive saccades. Previous studies in hemidecorticate subjects have showed that they are able to generate accurate bilateral saccades following intervening pursuit movements (Herter & Guitton, 2004). Here we determine if this ability extends to saccadic eye movement monitoring.

Previous results have been presented as an abstract in the Journal of Eye Movement Research ‘Book of Abstracts from the European Conference on Eye Movements (2013)’.

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