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Research Report

# Cortical activity preceding vertical saccades: A MEG study

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ABSTRACT

Previous studies have shown that upward saccade latencies are faster than downward saccade latencies in certain tasks. This asymmetry does not appear to represent a general main effect of the visual, or the vertical oculomotor system. In this study we examined the cortical activity underlying this latency asymmetry. We used MEG to assess cortical activity related to horizontal and vertical saccade preparation, and eye movement recordings to assess saccade latencies in a modified delay task. The reconstructed cortical activity was examined with respect to the onset of the target stimulus and the onset of the saccade. Upward saccades were faster than downward saccades, in agreement with previous studies. Although to a large extent, horizontal and vertical targets activated similar areas, there were also some differences. The earlier difference was found 100–150 ms after target onset over the right supramarginal gyrus when subjects attended to location-cues. Down cues activated this area faster than up cues. Moreover, cue-related activity was stronger over the left frontal cortex for up than down cues. In contrast, saccade-related activity over the same area was stronger when preceding downward than upward saccades. The results suggest that stimuli in the upper and lower visual field may have different impacts on accessing networks related to visual attention and motor preparation resulting in different behavioral asymmetries.



## 1. Introduction

Previous studies have shown that vertical saccades demonstrate a latency asymmetry (Goldring and Fischer, 1997; Heywood and Churcher, 1980; Honda and Findlay, 1992; Pitzalis and Di Russo, 2001; Schlykowa et al., 1996). Most observers appear to be faster upwards than downwards. However, this asymmetry is greatly reduced and tends to disappear in certain oculomotor tasks, indicating that there is no general advantage of the vertical motor system organization and ocular muscle control favoring upward saccades (Bell et al., 2000; Zhou and King, 2002). On the other hand, experiments with manual reaction time did not demonstrate a general advantage for detecting targets in the upper visual field, and in many cases superior visual performance was reported for targets in the lower visual field (Carrasco et al., 2004; Carrasco et al., 2001; He et al., 1996; Levine and McAnany, 2005; Payne, 1967; Rubin et al., 1996; Talgar and Carrasco, 2002; Tartaglione et al., 1979). Thus, this asymmetry does not appear to apply generally to the visual system.

In a previous study on vertical saccade latency using TMS (Tzelepi et al., 2005), we found a different effect of TMS on

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upward and downward saccade latency in a delay task. We suggested an interaction between the locations of the target, up or down, with the processes of shifting attention and preparing a saccade towards the upper or the lower visual field. Here, we examine this issue further and we study the cortical activity related to the preparation of vertical saccades, starting from the attentional shift to the target and ending to the initiation of the saccade. We used magnetoencephalography (MEG) which can provide the temporal and spatial resolution to follow the underlying changes of activity in this task in a millisecond scale in localized cortical areas. We employed a delay task with peripheral spatial cueing, in an attempt to temporally dissociate, as much as possible, cortical activity related to attention shifts from that related to saccade preparation. Both horizontal and vertical targets were used to provide a basis for comparison with the horizontal saccadic system under the same conditions, as well as to provide a basis for comparison with existing studies on saccade preparation, as almost all studies on saccade preparation are concerned with horizontal saccades.

## 2. Results

### 2.1. *Behavioral data*

The mean latencies (±std) for saccades in the different directions were as follows: (Up) 247 ± 22 ms, (Down) 289 ± 41 ms, (Left) 276 ± 45 ms, (Right) 265 ± 44 ms. Upward saccades were faster than downward saccades (mean latency difference 42 ms). In fact, upward saccade latencies tended to be shorter than latencies in all other directions. There were no differences between Left and Right saccade latencies. The repeated measures ANOVA with factor Direction (Up, Down, Left, Right) confirmed that Direction had a significant effect on saccade latency ($F = 12.659$, $p < 0.001$). Posthoc analysis showed that upward saccade latencies were significantly shorter than downward saccade latencies. No other significant differences were found.

### 2.2. *MEG data*

In the following, we present the main results for each condition starting with the findings for horizontal targets and then comparing with the corresponding ones for vertical targets.

#### 2.2.1. *Brain activation during the spatial attention shift to the location cue (SPA)*

In the SPA condition, subjects had to detect the target (triangle) without making an eye movement. Fig. 1a shows in different colors, clusters of brain areas which share the same activation pattern for the different cue directions in the whole duration of the trial (0–1000 ms). The representative time course (prototype) for each cluster is illustrated in the same color. The first and second prototype clusters (in brown and red color, respectively) correspond to significant activations. The remaining clusters (in green, cyan and blue color) were below significance threshold and they were not further evaluated.

2.2.1.1. *Horizontal cues*. The first cluster of significant activations (Fig. 1a) was mainly related to sustained activity in frontal cortex starting around 400 ms after the stimulus onset and lasting until the end of the trial. The main cluster of activations enclosed middle frontal, inferior frontal, and posterior superior frontal areas.

The second cluster indicated significant activations over the posterior cortex between 0 and 400 ms. Because of the multiple components in this early time interval and in order to obtain a more detailed picture of the underlying topography, we performed separately the prototype analysis restricting the time interval between 0 and 400 ms (Fig. 1b). The results for left and right cues were similar. The earlier significant activity was found in the occipital poles (peak around 150 ms), shortly followed by a weaker but significant activation in parietal cortex (peak around 170 ms). At around 200 ms, there was a pronounced peak over the posterior temporal cortex. A second peak of activity was found in the occipital areas later, around 300 ms.

2.2.1.2. *Vertical cues*. For down cues, the frontal sustained activity was weaker than the corresponding activity for the rest of cue directions. Fig. 1a shows that for down cues the first and second clusters of significant activations were located over the posterior cortex. In contrast, for up cues, as well as for horizontal cues, the most significant cluster (in brown) corresponded mainly to frontal activations. This result was confirmed statistically with ANOVA. We examined mean activity for up and down cues in different frontal areas between 400 and 1000 ms. There was a significant interaction Target direction × Hemisphere (ANOVA with factors Target Direction, Frontal Areas, Hemisphere, $F = 7.489$, $p = 0.029$) which show that down cues activated significantly less the left frontal cortex compared to cues up especially over the left posterior superior frontal area and left middle frontal area. Weaker activity over the left frontal cortex could be related to the slower latencies of downward saccades. Horizontal cues also gave higher activity than down cues over the left frontal cortex. In agreement, horizontal saccades were also faster than downward saccades. However, they were not as fast as upward saccades. We performed similar ANOVAs to compare frontal activity between i) down and left cues, and ii) down and right cues. We did not find any significant effect for the comparison of activity between down and left cues. For the activity between down and right cues there was a significant interaction (Target direction × Hemisphere $F = 10.416$, $p = 0.015$), similar to the one we found for the comparison between down and up cues. Indeed, there is also greater mean latency difference between downward and right saccades than downward and left saccades. However, this activity difference between down and right cues should be interpreted with caution as there may exist lateralization issues. Some of the frontal subareas demonstrated lateralized topography, at least in certain subjects, which could have enhanced the participation of the left frontal cortex for right cues (although it is noted that we did not find overall higher activity on right frontal cortex for left cues). Further research is required in this direction to clarify if and what degree lateralization issues are involved for horizontal cues. Overall, the results are consistent with the notion that significant differences in saccade latency