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ARTICLE

Saccade-Related Potentials During Eye-Hand Coordination: Effects of Hand Movements on Saccade Preparation

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This study investigated the effect of hand movements on behavioral and electrophysiological parameters of saccade preparation. While event-related potentials were recorded in 17 subjects, they performed saccades to a visual target either together with a hand movement in the same direction, a hand movement in the opposite direction, a hand movement to a third, independent direction, or without any accompanying hand movements. Saccade latencies increased with any kind of accompanying hand movement. Both saccade and manual latencies were largest when both movements aimed at opposite directions. In contrast, saccade-related potentials indicating preparatory activity were mainly affected by hand movements in the same direction. The data suggest that concomitant hand movements interfere with saccade preparation, particularly when the two movements involve motor preparations that access the same visual stimulus. This indicates that saccade preparation is continually informed about hand movement preparation.

Under natural conditions, hand movements are often performed under visual guidance. Such visual input is provided by saccades that bring the object of interest onto the fovea. This temporal coincidence of eye and hand movements has raised the question how the planning of the two types of movement mutually affect each other. Numerous studies have shown that saccade planning informs hand movements, and also, that hand movement planning informs eye movements (Bekkering & Sailer, 2002). The present study focuses on the effect of hand movement planning on saccades.

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Typically, existing studies mainly relied on behavioral measures such as movement latency and end position. For example, hand movement planning has been shown to affect saccade latencies (Lünenburger, Kutz & Hoffmann, 2000; Mather & Fisk, 1985; Neggers & Bekkering, 2001; Sailer, Eggert, Ditterich & Straube, 2002a), saccade amplitude (Sailer et al., 2002a), and eye movement trajectories (Tipper, Howard & Paul, 2001). In monkey, saccades that were accompanied by hand movements were faster (Snyder, Calton, Dickinson, & Lawrence, 2002). And finally, static eye position can serve as a target for hand movements in the absence of a visual target (Blouin, Amade, Vercher, Teasdale & Gauthier, 2002).

In addition to these purely behavioral measures, single-cell studies in monkey provided evidence for hand movements and even static hand position influencing saccade-related neuronal activity. This influence was observed in key structures for controlling eye movements such as the frontal eye fields (Thura, Hadj-Bouziane, Meunier & Boussaoud, 2011), the lateral intraparietal area (Oristaglio, Schneider, Balan, Gottlieb, 2006) and the superior colliculus (Stuphorn, Bauswein, Hoffmann, 2000; Werner, 1993). These findings indicate that hand movement signals are integrated into eye movement planning and/or execution.

The present study investigated the influence of hand movements on the oculomotor system by means of event-related potentials (ERPs). This method can shed new light on this question because of the excellent temporal resolution of ERPs. In particular, scalp potentials that occur time-locked to the onset of a saccade and precede saccadic eye movements were the focus of this study. As saccadic latencies include the whole interval from stimulus onset to movement onset, it is difficult to attribute latency variations to a particular cognitive process. Event-related potentials, in contrast, represent a continuous measure of the processing steps occurring in between stimulus and response, with different components corresponding to different processes. As a particular manifestation of ERPs, saccade-related potentials are locked to the onset of the saccade, that is, the single trials are aligned to the response instead of to the stimulus. Therefore, saccade-related potentials capture particularly those cognitive processes immediately preceding and following eye movement onset. Since saccade-related potentials allow focusing on the aspect of response preparation, they are expected to provide important additional information to the measure of saccade latencies. To our knowledge, this is the first study investigating the effect of hand movements on both behavioral and electrophysiological parameters of saccades.

Three saccade-locked potentials which precede a saccade and occur sequentially can be distinguished. First, the premotion negativity, or presaccadic negativity, builds up over the vertex at around 500–1000 ms before saccade onset (Becker, Hoehne, Iwase & Kornhuber, 1972; Klostermann, Kömpf, Heide & Verleger, 1994; Kurtzberg & Vaughan, 1980, 1982; Moster & Goldberg, 1990). The premotion negativity is then followed by a slowly increasing positive component, the premotion positivity (Becker et al., 1972; Kurtzberg & Vaughan, 1980, 1982; Moster & Goldberg, 1990; Richards, 2003). The premotion positivity, also termed the antecedent potential (Balaban & Weinstein, 1985; Parks & Corballis, 2008), occurs about 300–50 ms before saccade onset at parietal leads. About 40–10 ms preceding saccade onset, a sharp positive deflection can be observed over the parietal cortex, the presaccadic spike potential (Becker et al., 1972; Brooks-Eidelberg & Adler, 1992; Kurtzberg & Vaughan, 1980, 1982; Thickbroom & Mastaglia, 1986; Wein-

stein, Balaban, VerHoeve, 1991). It is the most pronounced and reliably occurring potential of the three known saccade-related potentials.

As to the functional meaning of these components, the premotion negativity has been conceptualized as the eye-movement-equivalent of the movement-related potentials that occur before voluntary hand or leg movements (Becker et al., 1972; Moster & Goldberg, 1990). More specifically, it has been suggested that the premotion negativity reflects preparatory activity of the FEF (Kurtzberg & Vaughan, 1982) or the supplementary eye field (Klostermann et al., 1994; Moster & Goldberg, 1990). This suggestion was not based on source localization, but on the finding that the premotion negativity was most evident with self-initiated saccades, fitting well to the SMA's role in controlling self-initiated movements. An alternative account of the premotion negativity holds that it rather codes for expectancy of target onset and target evaluation than motor preparation. The component that more clearly reflects oculomotor preparation is the premotion positivity (Jagla, Jergelová, Riecanský, 2007). The premotion positivity has been found to occur before voluntary saccades even in the absence of a visual stimulus (Moster & Goldberg, 1990). Therefore, it may correspond to the actual motor command for an eye movement (Becker et al., 1972).

Finally, the presaccadic spike potential (SP) has also been associated with saccadic planning. Its origin is, however, debated. The SP has been suggested to be generated by contraction of extraocular muscles (Becker et al., 1972; Thickbroom & Mastaglia, 1986) and/or the activity of ocular motor neurons (Moster & Goldberg, 1990; Riemslag, Van der Heijde, Van Dongen, Ottenhoff, 1988). However, there is also evidence for a parietal origin of the SP (Csibra, Johnson, Tucker, 1997; Kurtzberg & Vaughan, 1982). In accordance with a cortical origin, the SP has been reported to be larger for voluntary than reactive eye movements (Balaban & Weinstein, 1985). Moreover, shifting the stimulus between visual fields during an impending saccade and therefore shifting the visual representation of the stimulus also affected the SP (Parks & Corballis, 2008). These findings demonstrate the influence of cognitive factors on the SP. Hence, the SP has been proposed to represent both the execution and the "attentional/motivational value" of a saccade (Ignocheck, Weinstein & Balaban, 1986).

The present study investigated how concurrent hand movements affect these saccade-related potentials. It was assumed that this influence would depend on the amount of shared or competing information required for movement planning. To this aim, visually guided saccades were executed without concurrent hand movement, together with a hand movement in the same direction, a hand movement in the opposite direction, or a hand movement in a third, independent direction. Based on previous findings (e.g., Frens & Erkelens 1991; Mather & Fisk 1985; Sailer et al. 2002a, Sailer, Eggert & Straube, 2002b; Sailer, Eggert, Ditterich, Hassenzahl & Straube, 2003), hand movement planning can be expected to inform saccade planning. We hypothesized that the programming of a saccade would always be influenced by a simultaneous hand movement, but that the degree of this influence would depend on the amount of shared information about target direction and the congruence of the required movements. When hand and eye go into the same direction, there is no conflicting information regarding the requirements for the two types of movements. In contrast, when hand and eye movements go into opposite directions, both movements share information about the required amplitude, but need

to be directed at spatially opposite goals. Therefore, the programming of eye and hand movements with otherwise similar parameters may interfere with each other. Indeed, dissociating the directions of simultaneous eye and hand movements has been found to change the kinematic properties of both effectors (Gorbet & Sergio, 2009). Thus, we hypothesized that the largest alteration of both saccade-related potentials and saccade latency should occur with a simultaneous hand movement in the opposite direction of the eye movement.

Saccades accompanied by hand movements in the same direction should show less interference. Therefore, we expected that saccade-related potentials and saccade latency in this condition would be slightly altered when compared with saccades executed alone. However, the degree of alteration should be less than with a hand movement in the opposite direction. The condition featuring a hand movement to a third, independent position served to determine whether any concomitant hand movement, independent of its direction and relation to the saccade goal, would affect saccade-related potentials.

Materials and Methods

Subjects

Twenty-one subjects were recruited from the University of Vienna community. They were right-handed according to the Edinburgh Handedness Inventory (Oldfield, 1971), had normal or corrected-to-normal vision and no history of neurological disorder. One experimental session had to be aborted midway due to amplifier failure. A further subject was later excluded from further analysis because the data contained too many artifacts. In addition, the data of 2 subjects were excluded because too few trials with distinctive EMG remained in the condition Hand-central.

The remaining 17 subjects (9 males) were aged between 21 and 36 years (mean = 27). Subjects gave their written informed consent before the start of the experiment. The study was approved by the local ethical committee of the University of Vienna and performed in accord with the Declaration of Helsinki.

Experimental Setup

Subjects were seated in a sound-attenuated and dimly lit chamber in front of a table with their head resting on a chin and head rest (see Figure 1). Stimuli were displayed on a Sony Trinitron Multicsan G520 CRT monitor with a resolution of 1024 × 768 pixels at a viewing distance of 45 cm. The frame rate was set to 85 Hz. Stimulus presentation and synchronization with the EEG recording was controlled by E-Prime 2.0 (Psychology Software Tools, Inc.; Sharpsburg, USA). In front of the monitor on the table, there was a 17.5 cm × 46.5 cm response box made from plywood that contained a keyboard. Three black buttons on the box, each 2.5 cm in diameter, corresponded to an extension of three keys in horizontal arrangement whose centers were 17 cm apart. Thus, pressing one of the three buttons meant pressing one of these keys. The response box built around the keyboard had the advantage to avoid distraction from irrelevant keys, and to provide buttons large enough to be easily reached with peripheral visual feedback only. The response box was placed below the monitor so that the buttons were located approximately

underneath the positions of the target and fixation cross that were presented on the screen.

The subject's right hand rested on a padded support on the response box, located on the midline in front of the middle button. For pressing any of the buttons on the response box, the hand had to be lifted and moved away from the starting position. For the subject's comfort, the forearm was supported by a folded towel.

Task and Stimuli

On each of altogether 400 trials, subjects were presented a black fixation cross of 0.7 cm diameter on a gray background in the center of the screen for a variable interval of 1.2–2.2 s. Following this interval, a green dot of 0.7 cm diameter appeared either to the left or the right of the fixation cross at a distance of 15.5 cm for a duration of 1.5 s. In all conditions, subjects were instructed to look at this target as soon as it appeared, keep their eyes there until it disappeared, and then return gaze to the fixation spot. Four conditions were administered which only differed with regard to the hand movement task. The instructions were given in written form and presented on the screen before each condition. In condition Eye-only, subjects were instructed not to make any hand movements and to leave their hand on the starting position. In condition Hand-central, subjects were asked to lift their hand and press the middle button on the response box at the same time as they made an eye movement toward the target. In condition Hand-aligned, subjects were told to lift their hand and press the right button on the response box when the green dot appeared on the right side, and to press the left button when the dot appeared on the left. Thus, the targets for eye and hand were on the same side relative to the fixation spot from the perspective of the subject. In condition Hand-opposed, subjects were

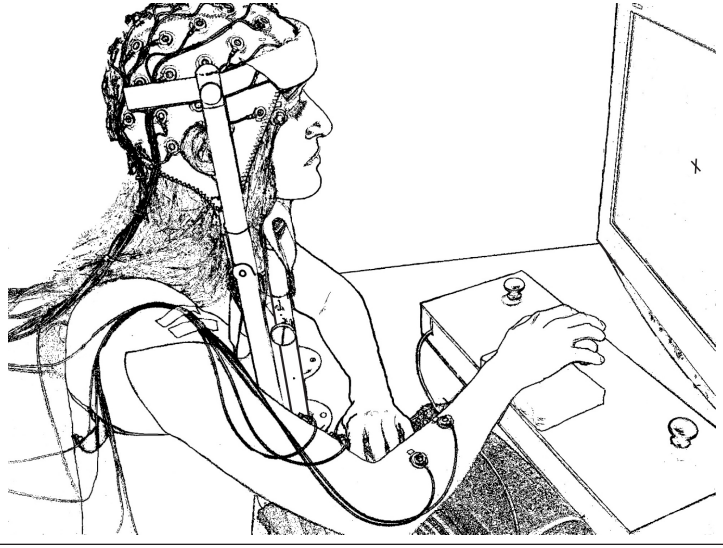

Figure 1 — Schematic view of the experimental setup and apparatus

told to press the left button when the dot appeared on the right side, and the right button when the dot appeared on the left side. The order in which to move eye and hand was not further specified to keep the movements as natural as possible. For the same reason, no instructions were given regarding speed or accuracy

In the three conditions that required hand movements, subjects were instructed to lift the hand only shortly before the button press and to return to the starting position afterward. This way, it was avoided that subjects take a starting position at an undefined position in the air. Furthermore, they were urged to keep their head still and not to look at their hand.

Each condition contained 50 trials with the dot on the right side and 50 with the dot on the left side in randomized order. The order of conditions was randomized across participants. Following each condition, there was a break in which the subjects were encouraged to leave the chin rest and relax for a self-determined period of time.

Before each condition, the subjects completed a number of practice trials to get familiar with the task: 10 in conditions Eye-only and Hand-central and 14 in conditions Hand-aligned and Hand-opposed. During the practice section, on-screen feedback regarding the correctness of the button press response was given after each trial. In addition, the experimenter stood next to the subjects during the practice session to verify that they complied with task instructions.

ERP and EMG Recording

EEG was recorded from 19 electrodes spread across the scalp. These electrodes represented a subsample of 61 electrodes embedded into an elastic cap with equidistant montage (easycap, Herrsching, Germany). They correspond approximately to the positions Fp1, Fp2, AFz, Fz, FCz, FC3, FC4, FT7, FT8, Cz, CP3, CP4, CPz, TP7,TP8, Pz, O1, O2, Oz of the extended 10–20 system. A balanced sterno-vertebral site, above the seventh vertebra and the right sternoclavicular joint, served as reference for the EEG channels (Stephenson and Gibbs, 1951). Vertical and horizontal electrooculogram (EOG) was recorded bipolarly by placing two electrodes 1 cm above and below the right eye, and two on the outer canthi. EMG was recorded bipolarly from 4 electrodes on the musculus biceps brachii and the musculus extensor digitorum following the recommendations of Zipp (1982). Only the signals of the finger extensor were further analyzed since they proved to be more reliable across subjects.

Before EEG recordings, skin scratching was performed with a sterile needle at each electrode site. All electrode impedances were kept below 5 kΩ as checked with an impedance meter. The electrodes were then filled with degassed electrode gel (Electro-Gel, Electrode-Cap International, Inc., Eaton/OH, USA). Signals were amplified using a DC-amplifier with an input impedance of 100 GΩ (Ing. Kurt Zickler GmbH, Pfaffstätten, Austria). The data were recorded at 3 kHz with a frequency range from DC to 500 Hz and sampled to 1 kHz for digital storage.

Data Processing

The horizontal EOG (HEOG) was calibrated by first determining fixation periods, defined as time intervals in which eye velocities stayed below 30 deg/s, whereby the

first rough estimate of eye velocity was computed using fixed gain factor (30 raw data steps/deg). For each of these fixations, the raw-position signal (uncalibrated DC-HEOG) was averaged across the fixation period, and each of these raw eye positions was assigned, by means of a cluster algorithm (subtractive clustering; Matlab-function "subclust"), to the three positions of target and fixation cross. A time-variant calibration function was defined on the basis of the remaining pairs of DC-HEOG fixation values and the corresponding target positions in the following way. Eye position of each fixation was computed by multiplication of the DC-HEOG signal with a constant gain, and by adding a time-variant offset which was expressed by a cubic spline function determined by one sampling value per 5 subsequent fixations. The parameters of this calibration function, i.e., the gain and the spline samples were computed by minimizing the mean squared error between target and eye position across all fixations. This method differs from the commonly used AC-EOG in clinical studies where high-pass filtering is used to eliminate drifts (e.g., Augustin, 2007; Heide, Koenig, Trillenberg, Kömpf, Zee, 1999). Due to high pass-filtering, only short-term changes of eye position can be assessed, whereas information about absolute eye position is lost. In contrast, our calibration method allows eliminating drifts of the DC potential and errors due to slow head movements while preserving absolute eye position information.

The calibrated eye position signal was filtered with a zero-phase Gaussian low-pass filter (cut-off frequency: 33 Hz, transmission gain at 85 Hz: 0.1). The final estimate of eye velocity was calculated by two-point differentiation of the calibrated eye position. The onset of a saccade was automatically determined as the point in time when eye velocity exceeded 50 deg/s The end of a saccade was defined by the time when the absolute eye velocity dropped below 5% of peak velocity. Saccade latency was defined as the interval between target onset and saccade onset. To be detected as valid primary saccade, saccade amplitude had to be larger than 5 deg, saccade duration in the range of 20–200 ms, a saccade onset within the latency interval between 80 and 100 ms, and saccade velocity below 700 deg/s Saccade amplitude was measured as the difference in eye position from the saccade's beginning to its end. Trials with a saccade in a direction opposite to the target, with a press of the wrong button, or with no saccade at all were eliminated. Moreover, only saccades with a starting position between 0 and +-2 deg and an end position between +-8 and +-25 deg were kept for further analysis. Only the primary saccade following target onset was further analyzed. This way, an average of 14% of all trials was eliminated across subjects (individual range from 3 to 24%).

As the EMG data were found to be contaminated by electrocardiogram (ECG) signal, a common problem in EMG measurement (e.g., Marque et al. 2005; Redfern, Hughes, Chaffin, 1993, Drake & Callaghan 2006), the following procedure was applied to obtain a clear EMG signal. First a number of representative 'R-peaks' (peaks of the ECG QRS-complex) were selected in the ECG signal. A template of the heartbeat response in the EMG signal was established for each subject by averaging the sections of the EMG signal across the selected R-peaks. The EMG-sections were cut out within 40 ms intervals around each R-peak and they were each corrected to zero-mean before averaging by fitting and subtracting a second-order polynomial. The weighted response templates, aligned to the R-peaks, were then subtracted from the original EMG signal, whereby the weights were computed as

the covariance of template and EMG signal divided by the variance of the template (Bauer & Lauber 1979).

According to the processing steps recommended in Blumenthal et al. (2005), the resulting EMG signal was then bandpass-filtered with a 4th order Butterworth IIR-filter from 10–499 Hz before the filtered signal was rectified and smoothed by a running average with a window width of 45 ms. The hand movement related EMG onset was then defined by means of a EMG response model established by averaging across trials. This response model was then fitted to the single trial via a cross-correlation based alignment. The EMG onset was defined by the time when the fitted EMG model first increased above the baseline by more 33.3% of the peak-baseline distance. Thereby, the baseline was computed as the average model activity across the first two hundred samples. EMG latency was defined as the interval between target onset and EMG onset.

The EEG data were filtered with a 30 Hz lowpass-filter (6 dB/oct roll-off). Trials with voltage amplitudes greater than ± 75 µV were manually deleted after visual inspection, as were trials with atypical artifacts. The data were epoched to saccade-onset and baseline-corrected by subtracting the averaged activity in the interval of 600–500 ms before saccade onset from the entire recording. For each subject and condition, averaged ERPs of the saccade-locked trials were then computed.

To make sure that the saccades-locked ERPs observed in this study reflect processes related to saccade preparation and execution only, a possible superposition of these saccade-related potentials with brain potentials related to the preparation of hand movements was corrected for by means of a frequency-based decomposition. To eliminate all activity related to hand movements from the saccade-locked ERP (*ps*), we assumed that saccade-locked EEG data were composed of a superposition of a saccade-related component (cs) and a hand movement related component (ch)

$$\hat{ps}_i(t) = cs(t) + ch(t - Lat_i), \qquad \text{(Eq. 1)}$$

where Lat_i denotes the time difference between saccade onset and EMG onset in Trial i. The two components *cs(t)* and *ch(t)* were estimated in the Fourier domain by the linear regression model

$$\hat{PS}_i(f) = CS(f) + CH(f) \cdot \exp(-j \cdot 2 \cdot \pi \cdot f \cdot Lat_i). \qquad \text{(Eq. 2)}$$

For each frequency, *CS(f)* and *CH(f)* were estimated separately to minimize the sum of the squared residuals

$$\sum_{i=1}^{NTrials} \left| PS_i(f) - \hat{PS}_i(f) \right|^2 .$$

Since a unique solution for this minimization problem exists only for $f > 0$, it is not possible with this approach to find an unambiguous decomposition of the DC-component and of very low frequency components. Therefore, for each spectral component it was tested whether the sum of squared residual was significantly reduced adding the phase factor $\exp(-j \cdot 2 \cdot \pi \cdot f \cdot Lat_i)$ into the linear model (Eq. 2) compared with the simpler model

$$\hat{PS}_i(f) = CS(f). \qquad \text{(Eq. 3)}$$

The test was performed by the standard F-test on the semipartial correlation for the phase factor. If this semi partial correlation was not significant ($p > .05$), the

model of Eq. 3 was used instead of Eq. 2, and the respective spectral component was estimated by

$$CS(f) = \frac{1}{NTrials} \cdot \sum_{i=1}^{NTrials} PS_i(f) \; .$$

Inverse Fourier transformation of *CS(f)* was then used to compute the saccade related component *cs(t)*. The saccade-related component *cs(t)* was considered the best estimate of the saccade related ERP after eliminating potential hand-related components. Baseline correction was applied after decomposition by subtracting *cs(t*=-600 ms*)* from *cs(t)*. Grand means were computed by averaging these decomposed saccade related ERPs across subjects. We assume that the decomposed saccade-related potentials (*cs*(*t*)) represent activity related to saccade preparation, not to hand movement preparation.

A validation of the decomposition method is provided in the Appendix.

Data Analysis

As an additional behavioral measure, the mean difference between saccade and EMG latencies was calculated. Thus, negative values would indicate that saccade onset preceded EMG onset. Mean saccade latencies, mean saccade amplitude, mean EMG latencies and the latency differences were computed for each subject by averaging across trials. Each of these dependent variables was compared across conditions with separate linear mixed-model analyses of variance for repeated measures using the factor condition which had four levels in the case of saccade measures (Eye-only, Hand-central, Hand-aligned, Hand-opposed), and three in the case of EMG latency and the latency difference measure (levels: Hand-central, Hand-aligned, Hand-opposed).

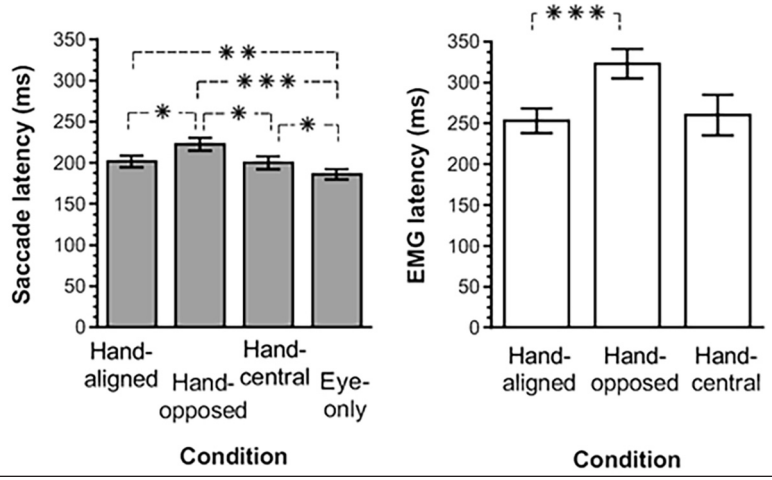

Figure 2 — Mean saccade (left) and EMG latency (right) with standard error of the mean for the different conditions. Asterisks indicate significant post hoc paired comparisons with F(3,16) for saccade-related data, and F(2,16) for Hand-movement related data. ***$p < .001$; **$p < .01$; * $p < .05$.

The premotion negativity is typically largest over the vertex and the posterior parietal cortex (Becker et al., 1972; Klostermann, Kömpf, Heide, & Verleger, 1994; Kurtzberg & Vaughan, 1982; Moster & Goldberg, 1990). Based on previous reports and the Grand Mean data (Figure 2), the premotion negativity was calculated as the mean amplitude in the interval of -500 to -100 ms before saccade onset at the medial vertex electrodes Cz, Fz, and Pz. The mean amplitude of the premotion negativity was then submitted to a mixed-model analysis with the factors condition (levels: Eye-only, Hand-central, Hand-aligned, Hand-opposed) and electrode (levels: Fz, Cz, Pz).

The premotion positivity, also called the antecedent potential or the presaccadic positivity, is typically greatest over parietal regions (Csibra et al., 1997; Kurtzberg & Vaughan, 1980, 1982; Moster & Goldberg, 1990; Richards, 2003). However, maxima have also been observed at occipital sites (Kurtzberg & Vaughan, 1982; Moster & Goldberg, 1990) and the vertex (Becker et al., 1972). Due to this widespread topography, the premotion positivity was calculated at electrodes Cz, Pz, and Oz as the mean amplitude in the interval of -200 to -50 before saccade onset. The mean amplitude of the premotion positivity was then submitted to a mixed-model analysis with the factors condition (levels: Eye-only, Hand-central, Hand-aligned, Hand-opposed) and electrode (levels: Cz, Pz, Oz).

To characterize the main features of the ERP we defined three different potentials, that were all computed in the decomposed saccade-locked ERP (*cs(t)*) at electrode Pz. The peak amplitude of the spike potential was defined by the maximum of the ERP in the interval [-50 100] ms around the saccade onset (0 ms). The peak amplitude of the preceding onset spike potential (Onset SP), and of the subsequent negativity (N1) were defined by the minima in the intervals [-50 0] ms or [0 100] ms, respectively (see Figure 3).

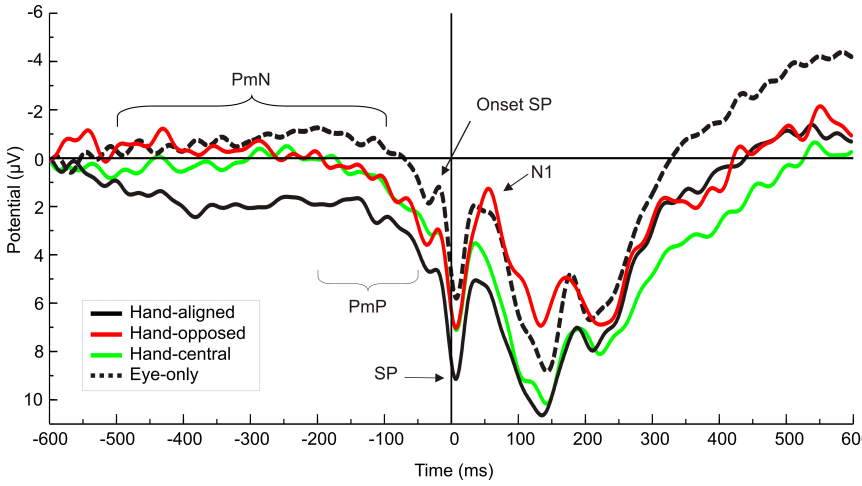

Figure 3 — Grand Mean waveform of saccade-locked averages at electrode Pz (decomposed waveform). Time 0 indicates saccade onset. The interval of -600 to -500 served as baseline. PmN= premotion negativity, PmP= premotion positivity, Onset SP= Onset spike potential, SP = spike potential.

These potential amplitude values were each submitted to separate mixed-model analyses with the repeated factor condition (levels: Eye-only, Hand-central, Hand-aligned, Hand-opposed).

In all mixed-model analyses, relationships between observations in different conditions were modeled as an unstructured covariance matrix. Post hoc pairwise comparisons were Bonferroni-adjusted.

In addition, intertrial Pearson correlations were computed between saccade and EMG latencies for each subject and each of the three Eye-hand conditions. Median and 95% confidence interval of Pearson correlations across subjects and conditions were computed by submitting the median and the 95%-confidence intervals of the Fisher-transformed correlations to the inverse Fisher transformation. The Fisher-transformation and its inverse are defined by z = atanh(x), and x = tanh(z), respectively. The difference of the median correlation from zero was tested by submitting the Fisher-transformed correlations to a *t* test.

Results

Saccade and EMG Latency

Across the four conditions, 99.8% of all the saccades generated had latencies below 500 ms, 93.8% had latencies below 300 ms, and 51.0% had latencies below 200 ms.

A main effect of *condition*, $F(3,16) = 14.41$, $p < .0001$, indicated that saccade latency was influenced by an accompanying hand movement. With a mean of 186ms (*SD* = 26ms), saccade latency was significantly smaller in condition Eye-only than in either condition Hand-central (Mean = 200 ms, *SD* = 33ms; $p < .05$; Figure 2), Hand-aligned (Mean = 201 ms, *SD* = 29; $p < .01$) or Hand-opposed (Mean = 222 ms, *SD* = 32 ms; $p < .0001$). Whereas saccade latency was not different for Hand-central and Hand-aligned, saccade latencies in both these conditions were smaller than in condition Hand-opposed (both *p*'s < .05; Figure 2).

Similarly, EMG-latencies differed across conditions (main effect, $F(2, 16)=17.50$, $p = .0001$). They were higher for Hand-opposed (Mean = 323ms, *SD* = 74ms) than for Hand-aligned (Mean = 253 ms, *SD* = 62; $p < .0001$). Again, the latencies were not different for Hand-central and Hand-aligned. Thus, in accordance with saccade latencies, EMG latencies were the same for movements in the same direction as the saccade and in a third, independent direction (Figure 2). Also paralleling saccade latencies, EMG latencies were highest for the most complex task, namely condition Hand-opposed.

The mean difference between saccade and EMG latencies (-71 ± 60 ms, *N* = 17) did not differ across conditions, $F(2,32)=2.37$; $p = .109$. This indicates that both effectors were similarly affected by the different task requirements. In addition, the standard deviation of the latency difference across trials (101 ms) was even larger than its average, which corroborates the efficiency of our decomposition procedure. Pearson's correlation coefficient between saccade and EMG latency differed in 17 of 51 cases (17 subject × 3 conditions) significantly from zero. 95% of Pearson's correlation, evaluated for each subject and condition fell within the range of [-0.25, 0.57]. The median ($r = .20$) differed significantly from zero, $T(50)=6.07$; $p < .001$.

Saccade Amplitude

Absolute saccade amplitude did not differ between the 4 conditions, F(3,16)=1.02; $p = .41$. On average, saccadic amplitude was 18.23 deg ($SD = 0.62$). Mean saccade amplitude was 18.46 deg (SD=.70) in Eye-only, 18.31 deg (SD=.88) in Hand-central, 18.13 deg (SD= 1.04) in Hand-aligned, and 18.00 deg ($SD = 1.02$) in Hand-opposed.

Grand Mean ERPs

Since it cannot be excluded that activity related to saccade preparation was superposed by activity related to hand movement preparation, a decomposition analysis was performed as described in the Materials and Methods section. Figure 3 shows the grand mean of the saccade-locked potentials, $cs(t)$, as provided by this analysis at electrode Pz from 600 ms before to 600 ms after saccade onset separately for each condition. The potential 600 ms before saccade onset served as baseline. Between 500 and 150 ms before saccade onset, the premotion negativity is visible, particularly in conditions Eye-only and Hand-central, until the premotion positivity (antecedent positivity) starts around -150 ms before saccade onset. Embedded into the premotion positivity, a sharp negative-going potential occurs at around 20 ms before saccade onset. In the following, this negativity will be called "onset spike potential". Coinciding with saccade onset at time 0, the spike potential (SP) can be seen. This SP is then followed by a larger negative-going component peaking at about 50 ms following saccade onset, presumably corresponding to the N1 reported by Marton, Szirtes, and Donauer (1982). This N1 was followed by a positive component at around 180 ms. This additional biphasic positive/negative complex was not present in all of the subjects (one subject did not show it at all, and 3 others did not show it in one condition), but it is visible in the grand means (Figure 3). Already during the premotion negativity (about 500 ms before saccade onset), the average potential differs between conditions.

The decomposed saccade-locked ERPs, $cs(t)$, computed separately for each subject, are also the basis for all following analyses.

ERP Amplitudes

A main effect of *condition* indicated that the amplitude of the premotion negativity differed depending on the accompanying hand movement ($F(3, 16) = 13.74$, $p < .0001$). The premotion negativity was only present in conditions Hand-opposed (Mean = -0.01 μV, SD =1.76 μV) and Eye-only (Mean = -0.39 μV, SD = .81 μV). In contrast, it was not present in conditions Hand-aligned (Mean = 1.83 μV, SD = 1.66 μV) and Hand-central (Mean = 0.23 μV, SD = 2.44 μV), where the amplitudes were positive (see Figure 4). Paired comparisons confirmed that the premotion negativity was more negative in conditions Hand-opposed than Hand-aligned ($p < .05$), as well as in Eye-only than in Hand-aligned ($p < .0001$) (Figure 4). The premotion negativity did not differ between the three electrodes Fz, Cz, or Pz.

Similarly, the amplitude of the premotion positivity varied depending on the accompanying hand movement, as indicated by a main effect of *condition* ($F(3,16) = 16.02$, $p < .0001$). As for the premotion negativity, that condition that "popped out" was Hand-aligned (Figure 4). The amplitudes for Hand-opposed (Mean = 0.90 μV, SD = 2.45 μV) and Hand-central (Mean = 1.17 μV, SD = 3.07 μV) resembled

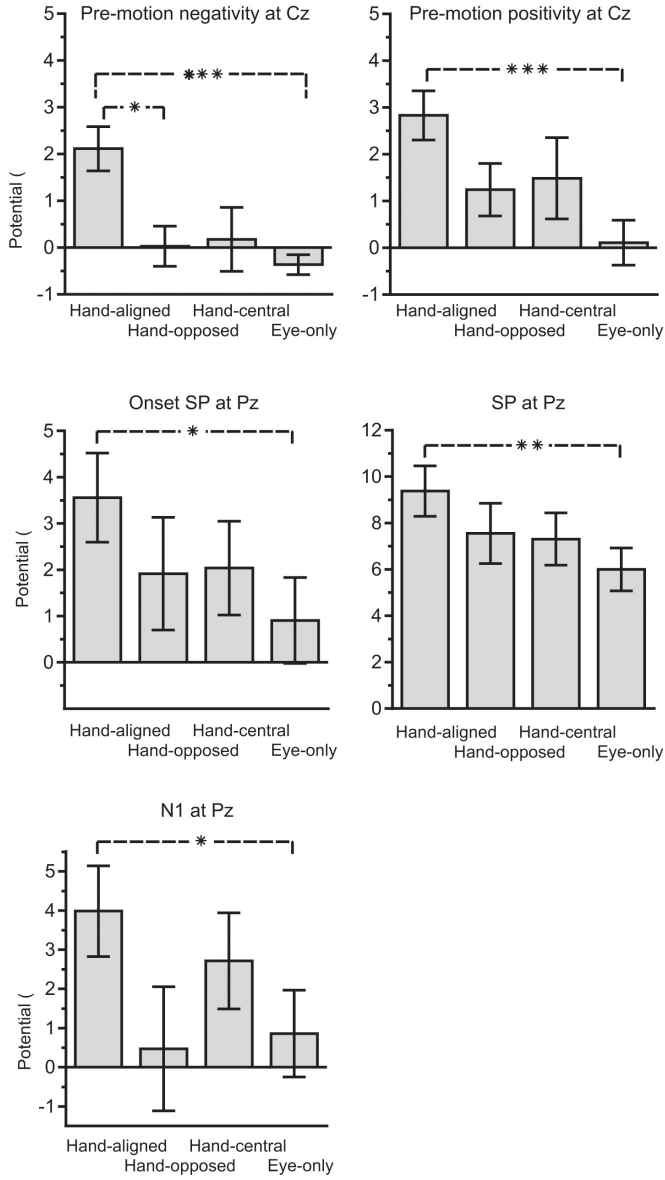

Figure 4 — Mean potential amplitudes (N = 17) and standard error of the mean for the four experimental conditions. Asterisks indicate significant post hoc paired comparisons with F(3,16). $^{**}p < .01$; $^{*}p < .05$

each other, and were not significantly different from those for Hand-aligned (Mean = 2.37 μV, *SD* = 2.13 μV) and Eye-only (Mean = -0.14 μV, *SD* = 1.87 μV). The largest premotion positivity was observed in condition Hand-aligned, where the amplitude was significantly larger than in condition Eye-only ($p < .0001$). The amplitude of the premotion positivity also differed across electrodes, as indicated by an interaction between *electrode* and *condition*, $F(2,16) = 4.29$, $p < .01$, with a smaller amplitude at Oz than at Cz, particularly in condition Hand-aligned.

The Onset SP, $F(3,16)=4.42$, $p < .05$, and the SP itself, $F(3,16)=5.95$, $p < .01$, also differed significantly across conditions (Figure 4). Both these potentials were larger in condition Hand-aligned than Eye-only ($p < .05$ for the Onset SP and $p < .01$ for the SP).

The same was true for the N1, $F(3,16) = 6.66$, $p < .01$. Similar to all other saccade-related potentials, the N1 was larger in condition Hand-aligned than Eye-only ($p < .05$).

Discussion

The present study investigated the influence of concomitant hand movements on saccade programming by combining electrophysiological and latency measures of saccades. Saccade latencies increased with any kind of accompanying hand movement as compared with the no-hand-movement condition. Both saccade and manual latencies were largest during incongruent hand movements, i.e., when eye and hand went into opposite directions. Saccade-related ERPs related to preparatory activity were also affected by the type of concomitant hand movements. However, unlike latencies, the largest differences from the Eye-alone condition were not observed with incongruent but with congruent hand movements.

Saccade Latency

Saccade latency was smallest when eye movements were executed without concomitant hand movements compared with all other three conditions with concomitant hand movement. Thus, the programming of any hand movement delayed the saccade onset. This suggests that the differences in latencies across conditions are mainly due to a dual-task effect. For example, saccadic latencies were longer for an accompanying hand movement toward the central target than for an eye movement without accompanying hand movement even though the hand movement to the central target was rather easy, i.e., it did not involve deciding between two targets.

At the same time, saccade latency was larger for an accompanying hand movement toward the opposite direction compared with the same direction, thus replicating the findings of Gorbet and Sergio (2009). These authors suggested that dissociating the movement directions for eye and hand disrupts a neural default network that normally couples both types of movement. In daily life, the goals for eye and hand movements are usually identical, although they may not be targeted at the same time (Hayhoe 2002; Land, Mennie, & Rusted, 1999). In contrast, the Hand-opposite-condition not only required the representation and programming of two separate movement vectors, but may additionally have required the suppression of a saccade toward the hand movement goal or the suppression of a hand movement toward the saccade goal. These additional requirements make the condition

"hand opposite" more complex and may explain the increase in both saccade and EMG latency under this condition.

Saccade-Locked ERPs

Saccade-related potentials varied differently across conditions than saccadic latencies. In contrast to saccadic latencies which were similar in conditions Hand-central and Hand-aligned, the presaccadic potentials in condition Hand-aligned differed from those in all other conditions. Thus, saccade-related potentials were not simply affected by any accompanying hand movement, only by those who were directly linked to the saccade goal.

For the premotion negativity, which has been related to target expectancy and target evaluation (e.g., Richards, 2003), this may indicate an interference of the target representations for eye and hand. When a hand movement in the same direction than the saccade is under preparation, the representation of saccade target may contain additional information about its relation to the hand target. Moreover, the data suggest that in addition to a target representation for the eye, there may be a separate target representation for the hand (Sailer et al., 2003), which influenced saccade preparation. This may explain why the premotion negativity disappeared in the condition Hand-aligned. Furthermore, during Hand-aligned the targets for both eye and hand are represented in the same hemisphere. Thus, regions, which are involved with the preparation of Eye-and hand movements are in closer vicinity in condition Hand-aligned than in the other conditions. It seems plausible that neuronal activation in adjacent brain regions may influence each other more than activation in brain regions that are farther away from each other. According to the functional cerebral distance model (Kinsbourne and Hicks 1987), the amount of interaction between two tasks is the larger, the closer the cortical regions that control the tasks are. Interaction is predicted to be greater for tasks that are processed within the same hemisphere rather than in two separate hemispheres. This may also explain why the interaction between eye and hand motor preparation was larger in condition Hand-aligned.

The need to process, during eye movement preparation, a hand target that is spatially incongruent with the saccade target, might be suspected to constitute a potential cause for interference with the premotion negativity. However, this factor was apparently irrelevant for the observed interference because the premotion negativity was similar in conditions with (Hand-opposed, Hand-centered) and without (Eye-alone) incongruent hand-target.

The premotion negativity captures an important aspect that is not included in saccadic latencies, namely processes that occur before stimulus-onset. In our experiment, the premotion negativity was measured starting from 500 ms before saccade onset. The differential effect of the two groups of conditions could be observed from around 500 ms before saccade onset (see Figure 3). However, only 0.2% of all saccades hat latencies larger than 500 ms. The premotion negativity therefore also captures preparatory processes that begin before the stimulus is presented. The premotion negativity has been suggested to be an indicator of target expectation (e.g., Richards, 2003), which is also supported by findings of it being enhanced with knowledge of distractor presence (Kelly et al., 2010). Since the different conditions were presented blockwise in the present experiment, the subjects in our experiment

could well have built up such an expectation. As the physical characteristics of the target were the same in all conditions, these expectations most probably referred to the different hand movement requirements. Thus, our data provide evidence that information about the upcoming hand movement may influence saccade preparation even before stimulus onset.

The premotion negativity is followed by the premotion positivity, which is more clearly indicating pure motor processes (e.g., Richards, 2003). In our experiment, the premotion positivity showed a similar effect as the premotion negativity: Hand movements in the same direction of the saccade influenced the premotion positivity more than hand movements toward a third or the opposite direction. The literature about the premotion positivity is scarce, but it has been related to eye movement preparation, more precisely to the actual motor command controlling the eye muscles (Becker et al., 1972). Thus, saccade preparation was mostly affected by hand movements that shared directional information. The effect persisted for the Onset-SP and the SP, therefore suggesting that the SP is affected by cortical processes.

These findings may be related to a study demonstrating visual activity in the FEF of monkey to be modulated by static hand position (Thura et al., 2011). Likewise, perturbations of hand movements have been shown to alter the internal models for saccade planning (Nanayakkara & Shadmehr 2003). Our data may indicate a similar integration of somatosensory signals into saccade preparation. This integrative process would be more pronounced in conditions Hand-aligned where more information is shared between eye and hand, and therefore, more coordinative effort of eye and hand is required.

Conclusion

Both the behavioral and the ERP data point to an influence of hand movements on eye movement programming. Saccade latencies showed a gradual increase with the degree of shared and conflicting information with the hand. In contrast, saccade-related potentials, which allow focusing on the aspect of saccade preparation differed most when the goals for eye and hand movements were most similar (Hand-aligned). This suggests that the preparatory activity of saccade related motor areas depends on the relative location between saccade target and hand target. Moreover, the findings show that the expectation of different requirements for accompanying hand movements can influence saccade preparation even before stimulus onset.

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Appendix

To validate the method of ERP decomposition, we simulated the superposition of a saccade related potential (*cs*(*t*)) with a supposed Hand-movement-related potential *ch(t-Lat$_i$)* for 64 Trials (1≤ i ≤64) (see section 1.5 Eq. 1). For this simulation we used *cs*(*t*) as we estimated it in the manuscript for the "aligned" condition (Figure 3, solid black line). This potential was then added on a delayed Hand-related component *ch*(*t-Lat$_i$*) that resulted from the very same decomposition procedure (not reported in the manuscript).

Both of these potentials are shown in Figure R1, where the delay *Lat$_i$* of the Hand-locked potential was set to the average of a sample of 64 Hand-eye latency values taken from the actual data of one subject (mean ± *SD* = 25 ± 40 ms).

The superposition shown in Fig. R1 was repeated for all 64 Hand-eye latency difference values. Each of these superpositions was additionally contaminated by a colored noise (variance: 1.5 μV^2; 95% of the variance below 22 Hz). These 64 simulated saccade-locked potentials are shown in Figure R2/A. These superimposed noisy data, together with the known 64 Hand-eye latency values were submitted to our decomposition algorithm described in the methods section. The results are shown in Figure R2/B. The result shows that the decomposed saccade-related ERP (Figure R2/B, green) approximates the true saccade-related component cs(t) (Fig. R2/B, black, Fig. R1, black) much better than the standard saccade-locked ERP (Fig. R2/B, red) computed by averaging all traces of Fig. R2/A.

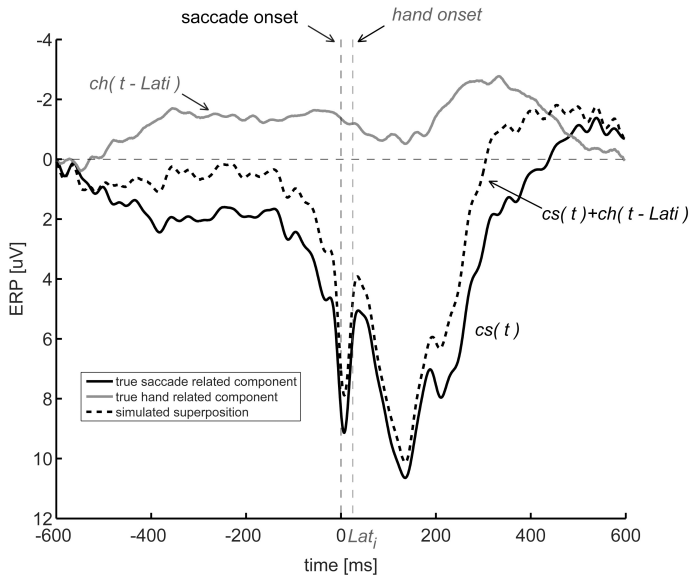

Figure R1 — Hypothetical saccade related component cs(t) (black), and delayed hand-related component ch(t-Lati) (blue) that was added to simulate the saccade-aligned EEG potential of a single trial (red). Here ch(t-Lati) is delayed by Lati = 25 ms.

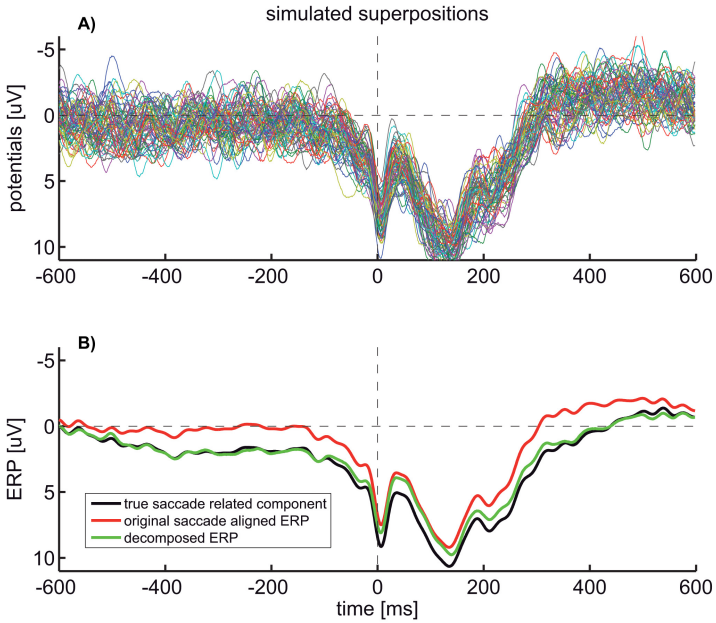

Figure R2 — A) 64 saccade-locked EMG potentials simulated by the same superposition shown in Fig. R1 (red) but with 64 different Hand-eye latencies take from a real data set. Each of these superpositions was additionally contaminated by colored noise (see text). B) Black: true saccade-related potential underlying the simulated superpositions (this trace is identical with that shown in Fig. R1, black). Red: standard saccade-locked ERP computed by averaging across all 64 simulations shown in A. Green: Decomposed saccade-aligned ERP estimated by our decomposition method.

This shows that our method is valid for cleaning ERPs with respect to additive potentials (here: the hypothesized Hand-locked potential) that are time-locked to a secondary event occurring at known latency relative to the event of interest (here: the saccade onset). The only precondition for applying this algorithm is that the interevent latency shows a sufficiently large variability across trials. Since the algorithm works with the actual latencies observed in each trial, it does not make any assumptions about the latency distribution. The standard deviation of the latency sample used for the simulation (40 ms) was even smaller than the average intertrial *SD* of the Hand-eye latency (100 ms). Thus, for most of the decompositions computed for the study, cleaning for hand-locked potentials was even more efficient than in the shown example.