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Early event-related potentials indicate context-specific target processing for eye and hand motor systems☆

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Abstract

Concurrent eye and hand movements toward a common visual target require different motor programs based on identical visual input. We used event-related brain potentials (ERP) to determine if and when the processing of the visual target differs for the two motor systems.

The N2, an index for target evaluation, was more negative for the target of a hand than of an eye movement in two experiments. A possible interpretation for this finding is different visual target processing. Targets for hand movements require a different weighting of visual information, for example concerning features such as surface structure which are important for hand but not for eye movements.

In experiment 2, the early C1-component, which had an average maximum at 67 ms following target onset, was significantly more negative when subjects pointed at the stimuli. Traditionally, the C1 has been regarded as a sensory component, but recent studies have linked it to higher order processing, such as attention and expectations. Thus, the present data indicate that target processing for eye or hand movements is already context-specific during early visual information processing. We suggest that differences in a target's relevance for upcoming movements modify target processing as well as sensory expectations.

Keywords

Eye-hand-coordination; EEG; Sensory expectation; Attention; N2-component; C1-component

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1. Introduction

Saccades and hand reaches toward targets are programmed based on the same source of visual input. Traditionally, a tight coupling during eye–hand-coordination was assumed. This implied shared processing of visual information for hand and eye motor systems before programming different movements (e.g. Bekkering et al., 1995; van Donkelaar, 1998). In contrast to that, behavioral studies provided evidence for separate processing already at the stage of target selection (Sailer et al., 2002a; Sailer et al., 2002b), during the orienting of attention (Gherri and Forster, 2012), and when new visual information about the target is integrated in visual short-term memory (Issen and Knill, 2012). In one study, haptic texture, a characteristic important for hand movements, but not for eye movements, influenced the kinematics of pointing movements only (Sailer et al., 2003). These results suggest that processing of targets for eye and hand movements depends on these features' relevance to the respective motor system. Recently, Rauss et al. (2011) suggested a predictive coding framework, in which early visual processing is modulated by predictions about forthcoming visual stimuli. Thus, top-down effects in the form of expectations about target features required for hand movements, including relative hand-target positions (Beurze et al., 2006; Crawford et al., 2011; Vesia and Crawford, 2012), may influence processing of incoming sensory data.

We hypothesized that target relevance for eye or eye–hand movements would have an impact on target representation and evaluation. The next question then is whether the earliest stages of visual processing are modulated based on predictions about sensory input required for planning different movements. We aimed to use the excellent temporal resolution of event-related potentials (ERP) extracted from EEG to investigate effects of target relevance for distinct motor systems on indices of target representation, as well as the earliest visual components. Namely, in the first experiment, we compared the N2-component, reflecting target evaluation (Potts and Tucker, 2001; Holguín et al., 2009), during planning of eye–hand movements compared to eye movements only. In the second experiment, stimuli were adapted to replicate the effect on the N2-component and to examine the influence of effectors to be used on the earliest visual component C1, which peaks during the first 50–90 ms and has been localized in the primary visual cortex V1 (Clark et al., 1994; DiRusso et al., 2003; Proverbio et al., 2010).

2. Materials and methods

2.1. Subjects

Twenty-four subjects (10 women) participated in experiment 1. Three of these subjects were later excluded from further analysis due to a high abundance of artifacts. The age of the remaining 21 subjects ranged between 22 and 36 years, with an average of 26.5 years and a standard deviation of ± 3.7 years.

Twenty-four subjects (15 women) participated in experiment 2. Two subjects were later excluded from further analysis because of problems with the instructions; two more were excluded due to technical problems. The age of the remaining 20 subjects ranged between 21 and 27 years, with an average of 23.9 years and a standard deviation of ± 1.9 years.

All subjects were students or former students from the University of Vienna. They were all right-handed (as assessed with the Edinburgh Handedness Inventory (Oldfield, 1971)) and gave written informed consent before the experiment. All subjects were naïve with regard to the hypotheses of the experiment. None had a previous history of neurological or psychiatric disorders. They all had normal or corrected-to-normal vision. Three of the subjects participated in both experiments.

The study was conducted in accordance with the Declaration of Helsinki (1981) and local guidelines of the University of Vienna. According to the Austrian Universities Act 2002 (UG2002) prevailing at the time the study was carried out, no ethical approval was required for the present study. Written informed consent was given by all participants acknowledging that they could withdraw at any time during the experiment without further consequences. All data were analyzed anonymously.

2.2. Apparatus

During the experiment, subjects were seated in front of a table in a sound-attenuated chamber during the experiment. The stimuli were presented on a 21 in. CRT monitor (Sony, Triniton, Multiscan G520 with a refreshing rate of 85 Hz) at a distance of approximately 42 cm from the subjects' eyes. The subjects' chin and forehead were stabilized by an adaptable rest. Their right elbow was placed on a padded support on the table and the resting position of the right hand was marked with tapes on the table. The resting position of the hand was not in view. The stimuli were presented using E-Prime 2.0 (Psychology Software Tools, Inc., Sharpsburg, PA, USA).

2.3. Stimuli and procedure

2.3.1. Experiment 1—The subjects were instructed to fixate a fixation cross in the middle of a white screen. Ten black circles were presented on the left and right of the fixation cross (Fig. 1). The diameter of the circles on the screen was 0.8 cm (1.1 degrees visual angle). The whole array measured 31 cm from left to right. The circles remained present during an interval ranging from 1200 to 1800 ms. At the end of this interval, one of the black circles turned either orange or green for 1800 ms. When it turned green, subjects were supposed to saccade toward it, focus their eyes on the circle until it turned black again, and then return their gaze to the fixation cross. When the circle turned orange, subjects were asked to point at it with their right index finger while directly touching the screen, and return to the starting position. The starting position of the hand was marked with a tape on the desk in front of them. The colored circles appeared in randomized order with equal frequency at all twenty possible positions. During the pointing condition, subjects were allowed to move their gaze freely. The reason for this was twofold. Firstly, we wanted to investigate pointing movements that are as natural as possible in this constrained environment. Secondly, we did not want to add an explicit second task in the hand movement condition, and alter stimulus processing by additional demands such as the suppression of eye movements.

In addition, the subjects were instructed not to follow their hand with their eyes when returning to the resting position, but to look at the fixation cross instead. All participants were also instructed to perform the movements naturally without any emphasis on speed and/or accuracy. Before the experiment, the participants performed 20 practice trials during which the experimenter verified that they performed the task correctly.

Six hundred forty trials were presented in randomized order including 320 trials of the pointing and 320 trials of the saccade condition. The trials were organized in four equal blocks with breaks in between. The subjects determined the duration of rest periods during the breaks. The entire experiment lasted for about 40 min including breaks.

Prior to the experiment, the subjects performed two calibration trials consisting of guided vertical and horizontal eye movements for the subsequent eye movement correction procedure.

2.3.2. Experiment 2—Experiment 2 used a smaller number of stimuli distinguished via shape and orientation instead of color. It consisted of 576 trials. Each condition (saccade and

pointing movement) contained 288 trials. The timing was the same as in experiment 1. During the interstimulus interval, three circles were presented on each side of the fixation cross (Fig. 2). In each experimental trial, two of the circles on opposite sides of the fixation cross morphed into either a horizontal and a vertical rectangle or a triangle pointing upwards and a triangle pointing downwards (the latter called “inverse” triangle). All targets and distractors appeared symmetrically around the fixation cross. The circles had a diameter of 3 cm (4.1 degrees visual angle), the triangles were 3 cm high (4.1 degree) and 2.5 cm wide (3.4 degree), the rectangles were 3 cm (4.1 degree) high and 1 cm wide (1.4 degree). The whole array measured 33 cm from left to right. The change from circle to target could occur at any of the six circle positions in randomized order.

Each of the four stimulus types was used as a target for pointing movements, as a target for saccades and as a distractor in order to exclude effects on the ERPs due to object recognition of different stimulus identities. For this purpose, the experiment was subdivided into two main blocks with an additional break in each case. Trials and trial blocks appeared in randomized order. The stimulus serving as target in the pointing condition in the first block served as target in the saccade condition in the second block. For example, if a rectangle was the target for a pointing movement in the first block, it would be a target for a saccade in the second block. Both blocks started with an instruction and 20 practice trials. The targets also appeared in a randomized order with equal frequency at all six possible conditions.

All subjects were numbered according to the order of appearance. For subjects with an uneven number, the target was an upright triangle in the pointing condition and a horizontal rectangle in the saccade condition during one of the blocks. The other stimuli served as distractors. For example, two trials could consist of first pointing at an upright triangle, and then fixating on a horizontal rectangle. In both trials, inverse triangles and vertical rectangles could be ignored. During the other block, the stimuli for pointing or saccades were exchanged. So, in the example, the subject would now fixate on upright triangles, and point at horizontal rectangles, and still ignore inverse triangles and vertical rectangles. For subjects with an even number, the target was an inverse triangle in the pointing condition and vertical rectangle in the saccade condition. Correspondingly, the stimuli for pointing and saccades were exchanged in the other block. Apart from the different stimuli, the participants were instructed as in experiment 1.

2.4. Data acquisition

In experiment 1, the EEG was recorded at seven central scalp electrodes mounted in an elastic cap with equidistant montage (EasyCap, Herrsching, Germany, Montage No. 10). Three of these positions corresponded to Fz, Cz, and Pz in the 10/20 system (Jasper, 1958). One electrode was located between P7 and PO7, one between P8 and PO8, and two corresponded to O1 and O2. EEG was recorded against a balanced sterno-vertebral site, above the seventh vertebra and the right sterno-clavicular joint (Stephenson and Gibbs, 1951). For recording eye movements and blinks, four electrodes were placed to the left and right of both eyes and above and below the left eye, in line with the subject's pupil. The ground electrode was placed on the forehead. Arm movement EMG was registered by means of four electrodes on the right arm. Two electrodes of a bipolar lead were placed on a position overlying the musculus biceps brachii, and two overlying the musculus extensor digitorum. Placement of electrodes followed the recommendations of Zipp (Zipp, 1982). The electrodes were of the same type as the ones in the elastic cap. To decrease the impedance of the skin under the electrodes, the skin was softly scratched with a sterile needle. The impedances of all electrodes were kept below 3 k Ω , as checked with an impedance meter. The electrodes were filled with degassed electrode gel (Electro-Gel, ElectroCap International Inc., Eaton/OH, USA). All signals were sampled at 1000 Hz using a DC-amplifier (Ing. Kurt Zickler GmbH, Pfaffstätten, Austria).

Experiment 2 was performed with an elastic cap for 27 electrodes arranged according to the 10/20 system (EasyCap, Herrsching, Germany, custom-made design). EEG was recorded from the positions Fz, Cz, Pz, P07 and P08. The procedure was the same as in experiment 1.

2.5. Data preprocessing

Based on the calibration trials recorded prior to the experiment, weighting coefficients were calculated for vertical and horizontal eye movement artifacts. For each subject and channel, the ratio of the covariance between each EEG and the electrooculograph (EOG) channel, and the variance of the EOG channels was calculated (Bauer and Lauber, 1979). Next, the weighted EOG signals were subtracted from the EEG channels. Blink coefficients were calculated using a template matching procedure and subtracted off-line from each EEG-channel and trial (Lamm et al., 2005).

The main data analysis was performed using the Matlab toolbox EEGLAB 6.03b (Delorme and Makeig, 2004). Separate epochs of 900 ms, 200 ms prior to and 700 ms following target onset, were extracted off-line for saccade and pointing trials separately for the left or right visual field (the last 200 ms were not considered for artifact inspection). The 200 ms before target onset were used as baseline. The data from the scalp electrodes were low-pass-filtered with 30 Hz (roll-off 6 dB/octave). An automatic artifact removal procedure eliminated trials containing voltages that exceeded $\pm 50 \mu\text{V}$ or drifts of more than $40 \mu\text{V}$. In addition, all trials were visually inspected. Based on the unfiltered EOG and EMG channels, the occurrence of saccades and arm movements was visually inspected. Trials in the pointing condition with no obvious arm and hand movements from either of the two EMG channels were rejected, as well as trials in the saccade condition where an arm or hand movement was falsely initiated. The same applied to trials where no saccade took place. Generally, an average of 22% of all trials was excluded per subject in experiment 1, and 28% in experiment 2.

2.6. ERP analysis

2.6.1. Experiment 1—In experiment 1 the N2 was analyzed at electrodes Fz, Cz, and Pz; with focus on Cz (Kopp et al., 1996; Nieuwenhuis et al., 2004; Bartholow et al., 2005; Czigler and Balázs, 2005). It was determined based on the second negative peak in the grand average waveforms which was detected on average at 270 ms following target onset. Mean N2 amplitude was calculated as the mean voltage in the interval from -30 ms to $+30$ ms around this peak (Wang and Suemitsu, 2007), in an interval from 240 to 300 ms.

The mean N2 amplitude was analyzed with a $3 \times 2 \times 2$ repeated-measures ANOVA with the within-subject factors *electrode site* (Fz, Cz, Pz), *stimulus position* in the right or left visual hemifield (right/left), and *motor system* (pointing/saccade). Moreover, planned contrasts were conducted for each motor system at each electrode.

2.6.2. Experiment 2—The N2-component was calculated according to the same procedure as in experiment 1. The maximum of the N2 was detected at 287 ms following target onset in the grand average across all participants and conditions. The N2-component was analyzed in an interval from 257 to 317 ms following target onset at Fz, Cz, and Pz.

In accordance with previous studies (Luck, 2005) the C1 was determined as the first peak at the posterior midline electrode side (Pz) in the grand average waveforms across all participants and all conditions. This peak was maximal at 67 ms following target onset. Mean C1 amplitude was calculated as the mean voltage in the interval from -30 ms to $+30$ ms around this peak (Wang and Suemitsu, 2007), resulting in an interval from 37 to 97 ms. Peak maxima for P1 and N1 components were 115 ms and 150 ms at electrode Pz. Mean P1

amplitudes were calculated in the interval of 85–115 ms; mean N1 amplitudes in the interval of 120–180 ms according to the procedure described above.

Two separate $3 \times 2 \times 2 \times 2$ repeated-measures ANOVAs were calculated for the mean N2- and the C1-amplitude using the factors *electrode site* (Fz, Cz, Pz for N2; PO7, Pz, PO8 for C1), *stimulus position* in visual hemifield (right/left), *motor system* (pointing/saccade) and *target type* (rectangle/triangle). Planned contrasts were used to compare the difference between the motor systems (pointing/saccade) when rectangles or triangles were presented as stimuli for each electrode. Mean P1 and N1 components were explored with the same $3 \times 2 \times 2 \times 2$ repeated-measures ANOVA at electrodes PO7, Pz, and PO8.

2.7. EOG analysis

In addition to correction of the EEG for eye movements, we tested for a remaining confounding effect from horizontal eye movements.

In experiment 1, the horizontal electrooculogram (HEOG) was analyzed with a 2×2 repeated-measures ANOVA with the factors *motor system* and *stimulus position* for the same time window as the N2-component (240–300 ms).

Correspondingly, in experiment 2, the mean amplitude of the HEOG was calculated in the same interval as the N2 (257–317 ms). The mean HEOG amplitude was then submitted to a $2 \times 2 \times 2$ repeated-measures ANOVA with the factors *motor system*, *stimulus position*, and *target type*, as was used to analyze the N2. We also computed Pearson's correlation between the HEOG mean amplitude and the mean amplitude of the C1- and N2-components within the analyzed timeframe of the two components. Moreover, the ANOVA for the C1-component was repeated using HEOG amplitudes in the same timeframe for all conditions entered as covariates to determine whether the impact of horizontal eye movements would change the results.

3. Results

3.1. Experiment 1

3.1.1. N2-component—The N2-component had a maximum at 270 ms at electrode Cz in the grand average waveforms from all participants (Fig. 3, panel B). The N2-amplitude at Cz was more negative during the pointing than during the saccade condition, yielding a significant interaction of *electrode site* and *motor system* ($F(2,40) = 8.70, p = 0.001$). Planned contrasts revealed significant differences between motor systems at electrode Cz ($p = 0.024$). The effect was, however, not significant at Fz ($p = 0.850$) and showed only a trend in the same direction at Pz ($p = 0.075$).

As expected, there was no effect of the stimulus being presented in the right or the left visual hemifield.

Fig. 3, panel B and C demonstrate the effect of motor systems at Cz and a trend in the same direction at Pz (p -value = 0.075). The trend observed at Pz (but not at Fz) indicates that the posterior subcomponent (N2p) was affected by use of different motor systems, but not the anterior subcomponent (N2a) (Patel and Azzam, 2005).

3.1.2. EOG—Fig. 3, panel D shows the uncorrected horizontal EOG. Apparently, there is no difference between the pointing and saccade condition which could have confounded the observed difference in the N2-component (240–300 ms). Correspondingly, the ANOVA for the horizontal EOG showed no significant main effects or interactions for the factor *motor system* (all p -values > .175).

3.2. Experiment 2

3.2.1. N2-component—The N2-amplitude had an average maximum at 287 ms post-stimulus at the Cz-electrode (Fig. 4, panel A). The ANOVA yielded an interaction for *target type* (triangle/rectangle) and *motor system* (pointing/saccade), ($F(1,19) = 4.61, p = .045$). Planned contrasts revealed that the mean N2-amplitude at Cz was more negative for pointing compared to making saccades when rectangles were presented ($F(1,19) = 5.23, p = .034$), but not when triangles were presented ($p > .143$). No significant interaction effects were observed for Fz and Pz. However, visual inspection of the waveforms indicates that the difference in motor systems affects the posterior N2-component, based on a trend in the same direction at electrode Pz ($F(1,19) = 3.91, p = .063$) but not at Fz ($F(1,19) = 0.94, p = .344$).

3.2.2. Earliest ERP-components—The early C1-component showed a maximum at 67 ms in the grand average (Fig. 4, panel B). Analysis of the C1 amplitude yielded an interaction between *electrode*, *target type*, and *motor system* ($F(2,38) = 17.10, p < .001$). Planned contrasts at Pz revealed that the amplitude of the C1 was more negative during pointing compared to saccades when rectangles were used as targets ($p = .006$). In contrast, the C1 was more negative during saccades compared to pointing when triangles were used as targets ($p = .023$). Rectangles serving as targets yielded similar results for the C1 amplitude for PO7 ($p = .023$) and PO8 ($p = .050$). No effects were found for triangles as targets (all p -values $> .734$). The ANOVAs of the components P1 ($F(2,38) = 7.59, p = .002$) and N1 ($F(2,38) = 4.31, p = 0.021$) both revealed a significant 3-way interaction between *electrode*, *target type* (triangle/rectangle) and *motor system* (pointing/saccade). Planned contrasts showed that both P1 ($p = .026$) and N1 components ($p = .003$) were more positive when pointing compared to saccades toward triangles. No other significant planned contrasts were observed for *motor system* during the earliest components (all p -values $> .110$).

3.2.3. EOG—The ANOVAs of HEOG amplitudes yielded no significant results. This indicates that the observed effects of different motor systems in the ERP-components are not caused by contamination from the EOG (Fig. 4, panel C). Correlations between the HEOG mean amplitude and mean C1 and N2 amplitude were not significant. The correlation between HEOG and C1 amplitude was $r = -0.161$ and $r = 0.054$ between HEOG and N2 amplitude in the saccade condition ($N = 20$). In the pointing condition, the correlation between HEOG and C1 amplitude was $r = 0.050$ and $r = -0.115$ between HEOG and N2 amplitude ($N = 20$). Similarly, the ANOVA with HEOG as covariate did not indicate confounding effects of the EOG.

4. Discussion

Both experiments provided evidence for a modulation of the investigated ERP-components depending on whether the target initiated only a saccade or an eye–hand movement. These differences in target processing are reflected by a more pronounced negativity in the time interval of the N2-component (Potts and Tucker, 2001; Holguín et al., 2009). The visual N2 has been associated with the identification and distinction of targets defined by features such as spatial location, spatial frequency, color, orientation and size (Hoffman, 1990; Potts and Tucker, 2001). Possibly, the modulation of the N2 amplitude is caused by changes in target processing which may derive from differences in the relevance of certain target characteristics for eye and hand movements. A detailed analysis of the target for a hand movement, including features such as surface structure which are less relevant for saccades, could lead to an enlarged N2-component.

In experiment 2, the effect of using different motor system on the N2-component was no longer significant when triangles served as targets. Fig. 4, panel A shows that the mean amplitudes for saccades were shifted toward more negative values, unspecific to all investigated ERP components. This shift results in saccades showing more negative potentials for all components in this time-frame. This divergence between the results for the two target types could be explained based on more inconsistent eye movements when triangles were presented (Fig. 4, panel C). More precisely, horizontal eye movements started about the same point in time compared to rectangles when triangles were presented, but took about 100 ms longer to move into one distinct direction. In accordance with this observation, several subjects consistently reported that they experienced the task as more difficult when triangles were presented. Potentially, the increased difficulty in detecting the correct target may have affected saccades more strongly and therefore led to more negative potentials for saccades across all components until the end of the N2 timeframe. For that reason, we focus the discussion of differences between the eye and hand motor systems on results obtained when rectangles were presented as targets.

Our findings of a larger N2 for manual responses than for saccades are in contrast to those of Eimer et al. (2006) who reported a larger negativity for saccades than manual responses. There are two possible explanations for this inconsistency. Firstly, their participants did not perform goal-directed pointing movements, but only lifted their index finger from the table. Therefore, target characteristics were not relevant for the manual response. In contrast, their target was only relevant for the saccade, which may explain the larger N2 accompanying saccades. Secondly, as their subjects maintained central fixation during the manual response, a possible confound of hand movement preparation and saccade inhibition could have occurred. For this reason, the present study investigated the difference between only making saccades versus pointing movements without any constraints to eye movements during the pointing condition. This avoided a dual task requirement in only one condition, and allowed natural movements.

Interestingly, a very early component was found to be modulated when the target required eye–hand movements versus only a saccade. The C1, which reflects early target processing was modulated as early as 37 to 97 ms after stimulus onset in experiment 2 when a reduced number of stimuli was distinguished via shape and orientation instead of color. This suggests a direct modulation of sensory processing as opposed to a re-entrant (back-projecting) activation, as re-entrant activation would be expected to take more time (Lamme, 2000). Thus, ours would be one of the few studies that provided evidence for top-down influences on the C1-component in humans (Fu et al., 2012; Kelly et al., 2008; Rauss et al., 2011).

In our experiment, the C1-component was significantly more negative for hand movements toward rectangles in the search array in experiment 2. Related to these findings, an fMRI study reported a modulation of activation in the human visual cortex for hand movements compared to saccades. In this study, the BOLD response in the lateral occipital cortex was found to be significantly stronger during pointing than during saccades (Astafiev et al., 2004). These observations were interpreted as a modulation of activation in visual cortex through limb movements.

As an alternative explanation, the modulation of the C1 in our study could be due to different expectations or deployment of attention associated with the upcoming movement. However, if the observed effect were driven exclusively by attentional differences, an effect on components P1 and N1 would have been expected (e.g. Vogel and Luck, 2000). In fact, the minimum time to process visual feedback and use this information for movement control is assumed to be 100 ms at the very least (Paulignan et al., 1991; Pélisson et al., 1986;

Carlton, 1981). Therefore, the modulation of the C1 is likely due to anticipation instead of online processing of the visual target. The primary visual area (V1) from which the C1 is assumed to originate can be influenced by expectations or imagery (Kosslyn et al., 2001). Expectations in this context may refer to sensory expectations about relevant information for a specific effector. For example, for a hand movement (as opposed to only a saccade) input about the target's surface texture would be expected. Additional sensory information is required to compute the spatial relationship between the hand and target locations. This weighting of sensory information concerning the relative importance of target features could be a basic principle for forming more efficient target representations. Along these lines, it has been suggested that low-level visual processing is modulated by predictions about upcoming sensory input (Rauss et al., 2009). The more negative C1 for the targets of upcoming hand movements may therefore be the result of such predictions. This interpretation would be in line with the predictive coding framework suggested by Rauss et al. (2011). The authors argue that influences of attention on components as early as the C1 could derive from efficient neural coding which is more related to internal goals and predictions than the stimulus per se. In the context of the present study, these internal goals would refer to the need to activate another motor system which requires different visual information (such as surface texture or size for hand movements, but not eye movements).

Future studies should aim to differentiate between these latent variables, for example with the inclusion of control conditions demanding attentional shifts without movements, and more complex grasping movements toward various targets.

5. Conclusion

The present study demonstrates that relevance of targets for programming eye–hand or eye movements not only influences target processing (N2-component), but also modulates the earliest stages of visual processing of a target (C1-component). Importantly, the data provide evidence for early context-specific processing of targets for eye–hand and hand movements, in contrast to a tight coupling of visual target processing during eye–hand-coordination (e.g. Bekkering et al., 1995; van Donkelaar, 1998). Our findings thus show that early visual information processing is dynamically modified based on immediate behavioral requirements.

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Fig. 1. Examples of stimulus events in experiment 1 on the left side. The search array consisted of 20 circles. The target appeared in orange in the pointing condition and in green in the saccade condition. The stimulus lasted for 1800 ms (a and c) and was followed by a variable interstimulus interval of 1200–1800 ms (b). On the right side, the applied electrode montage is displayed. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Fig. 2.

Examples of stimulus events in experiment 2 on the left side. The search arrays consisted of 6 geometric figures. The targets appeared (depending on the instruction) as triangles or rectangles. Black circles are distractors. All singletons were placed on a horizontal line left or right to a fixation cross. The stimulus lasted for 1800 ms (a and c) and was followed by a variable interstimulus interval of 1200–1800 ms (b). On the right side, the applied electrode montage is displayed.

Fig. 3. Grand average waveforms in the saccade (dotted line) and the pointing (straight line) condition of experiment 1 ($N = 21$). Panel A: electrode Fz, panel B: electrode Cz, panel C: electrode Pz, panel D: grand average HEOG waveforms.

Fig. 4. Grand average waveforms in the saccade (dotted line) and the pointing (straight line) condition of experiment 2 ($N = 20$). Left: rectangles presented as targets; Right: triangles presented as targets. Panel A: electrode Cz, panel B: electrode Pz, panel C: grand average HEOG waveforms.