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Effects of pointing direction and direction predictability on event-related lateralizations of the EEG

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Abstract

In two experiments, we investigated hemispheric electroencephalography (EEG) differences in 9(12) healthy volunteers during pointing to lateral and central targets. The questions addressed were whether horizontal pointing direction and the predictability of pointing direction modulated hemispheric differences (event-related lateralizations of the EEG = ERLs). To vary pointing direction predictability, targets were displayed either randomly at one of nine different positions on a screen (random) or at the same horizontal position in five subsequent trials (sequenced) while vertical positions varied randomly. Event-related lateralizations (ERLs) varied with pointing direction. This was true across changes in target eccentricity and pointing distance. Foci of the ERLs were in premotor and posterior parietal cortex, which might reflect the critical involvement of these areas in the control of visually guided reaching. Direction predictability reduced the parietal and premotor ERL before pointing onset, probably reflecting a lesser effort in visuomotor transformation. Predictability also added an overlying N2pc component to the early ERL after target onset and increased direction effects during movement.

PsycINFO classification: 2530; 2320; 2330
Keywords: Electroencephalography; Event-related lateralizations; Pointing movements; Pointing direction

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1. Introduction

To reach towards a target, visual and somatosensory information have to be integrated and transformed into the appropriate motor output. Several areas of the brain are involved in the underlying neural processes in a network of fronto-parietal connections (Glickstein, 2000; Johnson, Ferraina, Bianchi, & Caminti, 1996; Kertzman, Schwarz, Zeffiro, & Hallett, 1997). At one 'end' of this network, posterior parietal cortex is concerned with planning and controlling goal directed reaching movements. It is involved in visuospatial attention and spatial orienting (Grafton, Mazziotta, Woods, & Phelps, 1992; Kastner & Ungerleider, 2000; Yamaguchi, Tsuchiya, & Kobayashi, 1994) and in transforming the location of the visual target into motor coordinates (Lacquaniti & Caminti, 1998). Internal representations of limb and target position are formed and updated in posterior parietal cortex (Clower et al., 1996). At the other 'end', premotor neurons receive visual input from parietal cortex and project to the primary motor cortex. Little is known about the temporal aspects of processing in this cortical network for reaching movements in humans.

Electroencephalography (EEG) is a means of investigating cortical processes with high temporal resolution. A number of EEG studies have provided insights into some critical aspects of visuomotor processing including target selection, directional encoding, and movement preparation. These studies investigated contra-ipsilateral hemispheric differences in cortical activity. Contra-ipsilateral EEG asymmetries were first used to analyze movement preparation (De Jong, Wierda, Mulder, & Mulder, 1988; Gratton, Coles, Sirevaag, Eriksen, & Donchin, 1988) and revealed the well-investigated component called 'lateralized readiness potential' (LRP) over the motor cortex, which reflects lateralized activation of hand motor areas prior to movement execution. The attentional selection of task relevant stimuli is reflected in another lateralized but non-motor component called the 'N2 posterior contralateral' or N2pc (Luck & Hillyard, 1994a,b) that reflects a negative component contralateral to a relevant stimulus position. Lateralized EEG components encoding directional information relevant for the motor response have been found in lateral premotor cortex (Verleger, Vollmer, Wauschkuhn, van der Lubbe, & Wascher, 2000) and posterior parietal cortex (Wauschkuhn, Wascher, & Verleger, 1997). Of the two areas, posterior parietal cortex seems to encode directional information about the response irrespective of the effector: In a four-choice response task, in which a cue either did or did not provide directional information about the required response, Wauschkuhn et al. (1997) found two lateralized temporo-parietal components during the preparation phase of the response after the stimulus had delivered directional information. Participants had to perform either saccades to the left or right or move the left or right finger according to the direction indicated by a central cue. A first component (early temporo-parietal lateralization, ETPL) was evident irrespective of the effector and indicated an increase in negativity contralateral to the direction indicated by the cue. The second component (late temporo-parietal lateralization, LTPL) was reversed in polarity and only evident with finger movements. The authors concluded that the ETPL represented encoding of directional information in posterior parietal cortex necessary for any movement, whereas the LTPL might reflect effector specific

reafferent anticipatory activation of areas in somatosensory cortex where the finger is represented.

It might be suggested that directional components in posterior parietal cortex might not only be elicited by eye or finger movements, but might also reflect the direction of visually triggered reaching movements. The present study explored the directional aspect of pointing movements, i.e., pointing to a target in the ipsilateral or contralateral hemifield with respect to the pointing arm. We applied an LRP-like subtraction method to electrode sites distributed over the whole scalp (illustrated in Fig. 1) to gain insights into the interaction of the different cortical areas involved in visuomotor coordination (Eimer, 1996; Wascher, & Wauschkuhn, 1996). To analyze EEG asymmetries (event-related lateralizations, ERLs), activity at electrode sites ipsilateral to the response or the stimulus is subtracted from that at the corresponding contralateral sites.

Data from two different experiments will be presented, in which participants pointed to a target that could appear at different positions on a screen. The horizontal position of the target determined, which of three types of pointing movements was required. These movements differed in pointing direction: contralateral (from a right starting position to a target on the left side of the screen or vice versa), ipsilateral (from a right starting position to a right-sided target or from a left starting position to a left-sided target), and central (from a left or right starting position

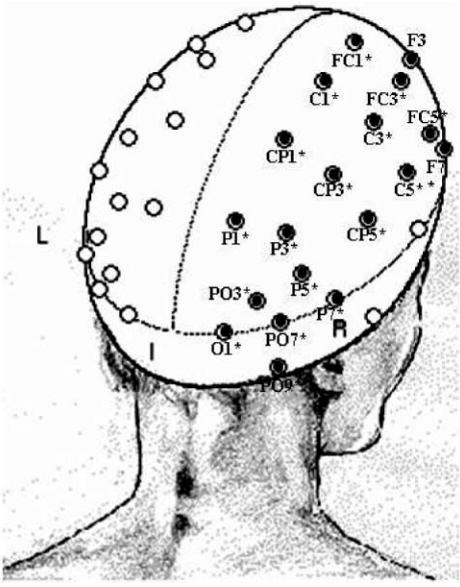

Fig. 1. Experiment 1: map of electrode sites, for which difference potentials were calculated. Names of sites are given only in the right hemisphere. The asterisk indicates the fact that contralateral and ipsilateral electrode sites were combined in the difference potential (i.e., $P1^* = P1/2$). F: frontal, FC: fronto-central, C: central, CP: centro-parietal, P: parietal, PO: parieto-occipital, and O: occipital areas.

to a target on the centerline of the screen). This allowed us to study effects of target position, and consequently movement direction, on hemispheric EEG asymmetries at different times during processing.

Additionally, we examined whether predictability of the horizontal target position, which corresponded to pointing direction, had an effect on visuomotor processing. Predictable target position might have opposite effects on attentional orienting and response preparation. Visuospatial attention in the hemifield in which the target predictably appears might be increased. This should result in increased activation in posterior parietal cortex, which is involved in visual attention. As an indicator of increased visuospatial attention, the N2pc might be larger. On the other hand, response preparation might be facilitated. Detecting spatial information and transforming it into response coordinates might be less relevant, since spatial codes do not need to be redefined. This might result in decreased activity in the fronto-parietal network for reaching. It might especially reduce the directional ETPL component proposed by Wauschkuhn et al. (1997). Thus, by varying target position predictability, additional information about the functional relevance of components could be derived from the ERLs.

The aim of the present study was to identify ERL components of visuomotor transformation from target onset to movement execution that are (a) reflected in contra-ipsilateral EEG asymmetries and (b) modulated by pointing direction and/or direction predictability and the cortical areas, which are involved in these directional processes.

2. Experiment 1

In Experiment 1, we investigated whether pointing to ipsilateral, central, or contralateral targets with respect to the active arm changed ERLs from target onset to movement execution and whether these effects were modulated by the predictability of pointing direction.

2.1. Methods

2.1.1. Participants

Event-related potentials (ERPs) were recorded from nine right-handed healthy participants (six females). Age ranged from 17 to 27 (average 20.7 years). Vision was normal or corrected to normal.

2.1.2. Apparatus

During the recording, participants were seated in a soundproof EEG cabin that shielded electromagnetic fields. Participants sat on a chair with their chin and forehead fixed in a headrest. Stimuli were presented on a 21 in. computer monitor that was located 47 cm in front of the participants. The center of the screen was aligned with participants' eye height. At the beginning of each trial, the hands were placed in the starting positions on a table in 27 cm distance to the participants and 17 cm

distance between the left and right hand positions. When in the starting positions, participants' forearms and upper arms were aligned in a 90° angle. Starting positions were haptically detectable small ridges, which the index fingers rested on. A shield prevented the participants from seeing their hands in the starting positions. The hand used for pointing became visible when it approached the screen during a pointing movement. Lights in the cabin were turned off during the recording.

2.1.3. Stimuli

Targets were filled white circles (1 cm or 1.2° of visual angle) on a black background. A trial started with a fixation cross presented in the center of the screen for 200 ms. After an ISI of 750 ms (±250 ms) the target was presented and stayed visible for 1500 ms. The target could appear in one of nine different positions on the screen, which were spaced on the nodes of a notional 3×3 grid with a vertical distance of 13.7° (11.5 cm) and a horizontal distance of 11.4° (9.5 cm). The central target was in the center of the screen. Hence, pointing to a target contralateral to the active arm required a movement across the body center and pointing to an ipsilateral target a more or less straightforward movement.

2.1.4. Procedure

In one part of the experiment, targets were presented randomly in one of the nine positions (random). In the other part, the horizontal position of the target was the same in five subsequent trials, whereas the vertical position varied randomly (sequenced). Therefore, in four out of five trials in the sequenced condition, the participants could predict the horizontal position of the target and thus the horizontal direction of the pointing movement. Nonetheless, the pure motor demands in both conditions were the same. The arm moved vertically and horizontally from the starting position to the target on the screen.

Participants were instructed to keep both hands in the starting positions before and after each pointing movement with the index fingers extended. Once the target appeared, participants were to point as quickly and accurately as possible with one hand and touch the target on the screen briefly with the index finger. Participants were instructed not to slow down before touching the screen, thereby avoiding visually guided corrections of the trajectories. The movement should be completed (i.e., the hand should be back in the starting position) when the target disappeared.

Participants performed four blocks. The random and sequenced conditions were performed with the left and right hand in separate blocks. The hands were changed in subsequent blocks in order to avoid tiring of the arms. The order of blocks was counterbalanced. The random condition blocks consisted of 450 trials (9 positions $\times$ 50 repetitions). In the sequenced condition, the blocks consisted of 900 trials (3 horizontal positions $\times$ 5 trials in a sequence $\times$ 60 repetitions). The trajectories of the pointing movements were recorded by means of an ultrasonic tracking device (ZEBRIS system). For this purpose, a marker was fixed to the tip of the index finger. ZEBRIS data were used to compute response times and response-locked potentials and to exclude invalid trials.

2.1.5. Recording

EEG was recorded with Ag/AgCl electrodes from 53 scalp positions distributed over the entire scalp. An electrode attached to the tip of the nose was used as reference. Vertical EOG (vEOG) was recorded bipolarly from above and below the right eye and horizontal EOG (hEOG) from the outer canthi of both eyes. EEG and EOG were amplified and filtered by seven PSYLAB amplifiers (EEG8) with a 5.31 s time constant and a 0.03–35 Hz bandpass. EEG and EOG were digitized at 100 Hz for a period of 3 s, starting 190 ms before the fixation cross. ZEBRIS data were sampled at 100 Hz. The PC that presented the stimuli triggered ZEBRIS and EEG recordings simultaneously.

2.1.6. Data processing and analysis

Trials with zero lines, out-of-scale values, slow drifts larger than 80 μV in the measurement, and fast shifts larger than 120 μV/500 ms were excluded from further analyses. The transmission of vEOG and hEOG into the EEG was estimated separately in areas of maximum EOG variance and was subtracted from the EEG data. The hEOG was removed from the EEG more effectively than the vEOG. Nonetheless, since we evaluated contra-ipsilateral differences in the EEG, and vertical eye movements were symmetrical in both directions, they did not appear in the ERLs.

Response time was defined as the moment when the finger was 20 mm away from the starting position. Only trials in which the movement started with a minimal response time of 100 ms after target onset and which met an accuracy criterion (15 mm maximal distance to the target when participants first touched the screen) were analyzed. Thus, on average, 3.9% of the trials were rejected due to response data analysis (random: 2.5%, sequenced: 4.9%). ANOVAs with factors target predictability (levels 'sequenced' and 'random'), and direction (levels 'ipsilateral', 'central', and 'contralateral') were computed for response times, duration of movement (time from start of movement until the target was hit), and accuracy (measured as the absolute horizontal deviation from the target). ANOVAs with factors direction and sequence were performed to compare early and late trials in the sequenced condition. For this purpose, we computed means of the first two trials in a sequence and the last two trials, respectively.

ERLs: To assess hemispheric EEG differences, two types of difference potentials were calculated for 21 electrode pairs (see Fig. 1). For response-coded lateralizations, activity at an electrode site ipsilateral to the moving arm was subtracted from the activity at the corresponding contralateral electrode: In the blocks, in which the participants pointed with their right arm, activity at the electrodes over the right hemisphere was subtracted from activity at the corresponding electrode sites over the left hemisphere. In left hand blocks, activity at left hemisphere electrodes was subtracted from activity at the corresponding right hemisphere electrodes. These two difference waves were averaged and the resulting difference potentials reflected response-coded lateralizations irrespective left or right arm movements. To render visible hemispheric asymmetries that depended on the horizontal target position, stimulus-coded lateralizations were computed. In this case, activity at electrode sites ipsilateral to the hemifield in which the target appeared was subtracted from

the activity in the contralateral hemisphere. ERLs were averaged across trials and participants (grand mean), time locked to the onset of the target (stimulus-locked) or time locked to the start of the pointing movement (response-locked).

ERLs were analyzed in seven areas: frontal (pooled across F3/4, FC1/2, and FC3/4), centro-temporal (C3/4, C5/6), central (exclusively electrodes C1/2 over motor cortex), centro-parietal (CP3/4, CP5/6) parietal (P1/2, P3/4, PO3/4), temporo-parietal (P5/6, P7/8, PO7/8), and occipital (O1/2, closest to primary visual areas). These electrode groups represented the levels of the factor scalp site. If an interaction between factor scalp site and any other factor was significant, further ANOVAs were performed for each electrode group separately. ANOVAs with factors scalp site and sequence were performed to compare early and late trials in the sequenced condition. For this purpose, we computed means of the first two trials in a sequence and the last two trials, respectively. In this analysis, ERLs were averaged across directions. In the EEG analysis, *F*-statistics of the ANOVAs were corrected by Greenhouse Geisser Epsilon.

2.2. Results

Behavioral data: The effect of pointing direction on response times almost reached significance ($F(2,16) = 3.62$, $p = 0.051$). Responses tended to be slowest when pointing to a central target (average across random and sequenced: ipsilateral: 415 ms, contralateral: 416 ms, central: 423 ms).

No main effect of predictability was found when the random was compared to the sequenced design ($F(1,8) = 0.24$, $p = 0.639$), but response times were significantly faster in the late trials than in the early trials in a sequence of repeated pointing direction (average across directions: early: 419 ms, late: 414 ms, $F(1,8) = 6.60$, $p = 0.033$). As a consequence of the difference in movement distances between ipsilateral and contralateral pointing movements, movement duration varied with pointing direction and was shortest for ipsilateral movements and longest for contralateral movements (average across random and sequenced: ipsilateral: 564 ms, central: 600 ms, contralateral: 650 ms, $F(2,16) = 122.05$, $p < 0.001$). Pointing accuracy was highest with ipsilateral targets and lowest with contralateral targets (averaged deviations across random and sequenced: ipsilateral: 5.7 mm, central: 6.3 mm, contralateral: 7.6 mm, $F(2,16) = 18.794$, $p < 0.001$).

EOG: The hEOG was measured at the time when it reached the plateau (300–500 ms after movement onset) in the stimulus-coded data (see Fig. 2). The effect of factor predictability on the hEOG almost reached significance ($F(1,8) = 5.04$, $p = 0.055$). It tended to be smaller in the sequenced compared to the random condition. Factor direction had a significant effect on the hEOG ($F(1,18) = 13.63$, $p = 0.006$). It was smaller when targets were presented ipsilateral to the response hand compared to contralateral targets. The hEOG was smaller in the late trials in a sequence compared to the early trials ($F(1,8) = 15.23$, $p = 0.005$).

ERL data: From the time of target onset to the execution of the pointing movement, we identified five ERL components. Two anterior ERLs were lateralized contralateral to the response side: As expected, an LRP (measured between 150

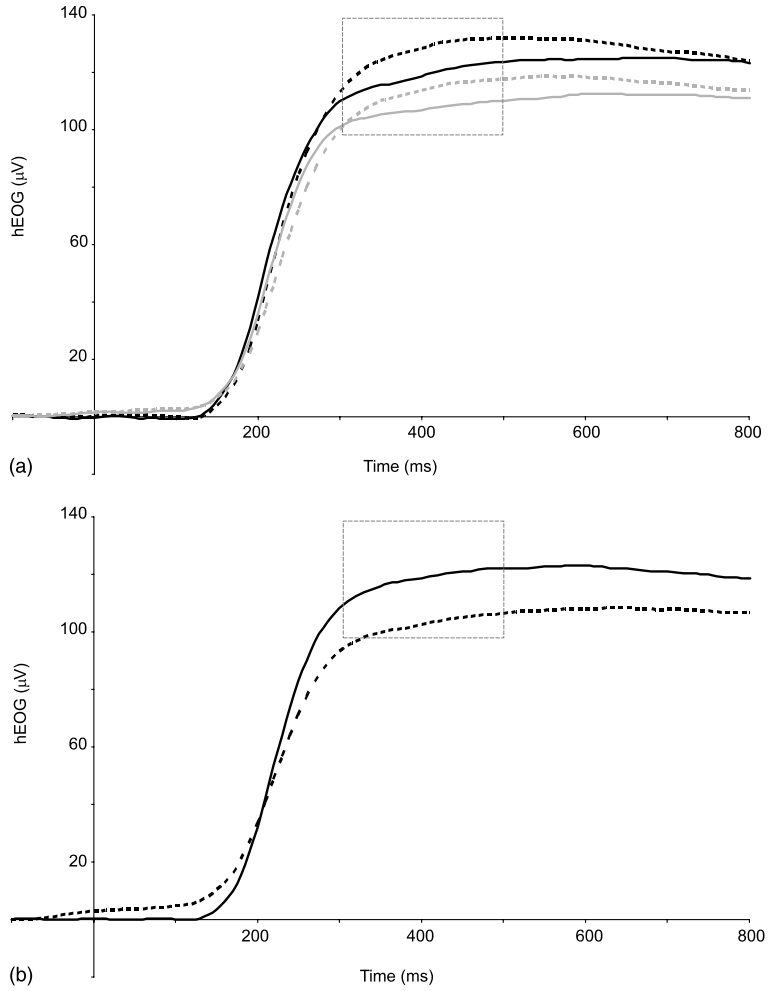

Fig. 2. Experiment 1: horizontal EOG. (a) Sequenced vs. random condition. Black lines: random; gray lines: sequenced condition. Solid lines: ipsilateral targets; dashed lines: contralateral targets. (b) Early vs. late trials in a sequence. Solid lines: early trials, dashed lines: late trials. The dashed rectangle indicates the interval in which the hEOG was analyzed. Zero on the time scale is target onset.

and 50 ms before movement onset in the response-locked data) was evident over the motor cortex (electrode pair C1/2, see Fig. 8) that did not vary significantly with direction ($F(2,16) = 3.88$, $p = 0.078$) nor with predictability ($F(1,8) = 0.07$, $p = 0.801$). Thus, the LRP will not be discussed further in this section. All other components varied either with movement direction or predictability. The second anterior component was located over frontal sites at an intermediate latency between target and response. In this component, negativity was increased contralateral to the response side (see Fig. 6). Three posterior ERL components were lateralized with re-

spect to the target: A lateralized N1 at about 180 ms after target onset reflected increased negativity contralateral to the target, a component at intermediate latency (between 280 and 430 ms) with reversed polarity (i.e., ipsilateral to the target), and a late component during the movement (movement ERL), again contralateral to the target. Fig. 3 shows the posterior ERLs relative to the response side (response-coded) and relative to the target (stimulus-coded). The fact that the posterior components depended on target/pointing direction is evident in the response-coded ERLs as a change in polarity with ipsilateral compared to contralateral targets. This fact becomes even more obvious in the stimulus-coded ERLs. The hEOG was analyzed in the stimulus-coded data. The further analysis of the components was performed using the response-coded difference potentials. For the comparison of early and late trials in the sequenced design, stimulus-coded ERLs were analyzed, averaged across ipsilateral and contralateral targets. The components were measured as mean amplitudes in time intervals around the maximal amplitudes derived from the grand means. Only if peaks were well-defined in the single subjects data, which was the case in the anterior intermediate component, peak latencies and amplitudes were analyzed.

Early posterior components: A lateralized N1 was maximal at temporo-parietal and parieto-occipital sites and spread up to anterior sites. This component was measured as the mean amplitude between 160 and 200 ms after target onset. When targets were lateralized, negativity was increased in the hemisphere contralateral to the target (see Fig. 3). Factor direction interacted with factor scalp site ($F(12,96) = 4.67$, $p = 0.024$). This interaction indicated that the lateralized N1 was evident at posterior sites, reflected in the significant effect of direction at centro-parietal ($F(2,16) = 5.59$, $p = 0.044$) and at occipital sites ($F(2,16) = 5.37$, $p = 0.049$). Scalp topographies of the lateralized N1 and the intermediate posterior component are illustrated in Fig. 4.

The component showed a second overlying peak around 240 ms after target onset in the sequenced condition, which probably reflected an N2pc component (see Fig. 3). It was measured as the mean amplitude between 220 and 260 ms after target onset. Since the posterior components changed polarity with target/pointing direction, effects of predictability on these ERLs are reflected in an interaction of factors direction and predictability. For the N2pc, a significant interaction of factors predictability, direction, and scalp site ($F(12,16) = 2.84$, $p = 0.042$) was found, indicating that the effect of predictability was evident at central and posterior sites: Significant interactions of factors predictability and direction were found at centro-temporal ($F(2, 16) = 4.79$, $p = 0.041$), centro-parietal ($F(2,16) = 5.36$, $p = 0.033$), parietal ($F(2, 16) = 9.00$, $p = 0.012$), temporo-parietal ($F(2,16) = 5.05$, $p = 0.032$), and occipital ($F(2,16) = 5.94$, $p = 0.031$) sites. In the sequenced condition, the N2pc was more prominent in late trials ($F(1,8) = 7.36$, $p = 0.027$). Posterior ERLs for early and late trials in the sequenced condition are illustrated in Fig. 5.

Anterior intermediate component: At frontal sites (F3/4, FC3/4, and FC1/2), negativity was increased in the hemisphere contralateral to the responding arm ($F(1, 8) = 41.82$, $p < 0.001$). Fig. 6 shows ERLs at these electrode pairs. In this component, well-defined peaks allowed reliable peak measurement. Peak latency, measured

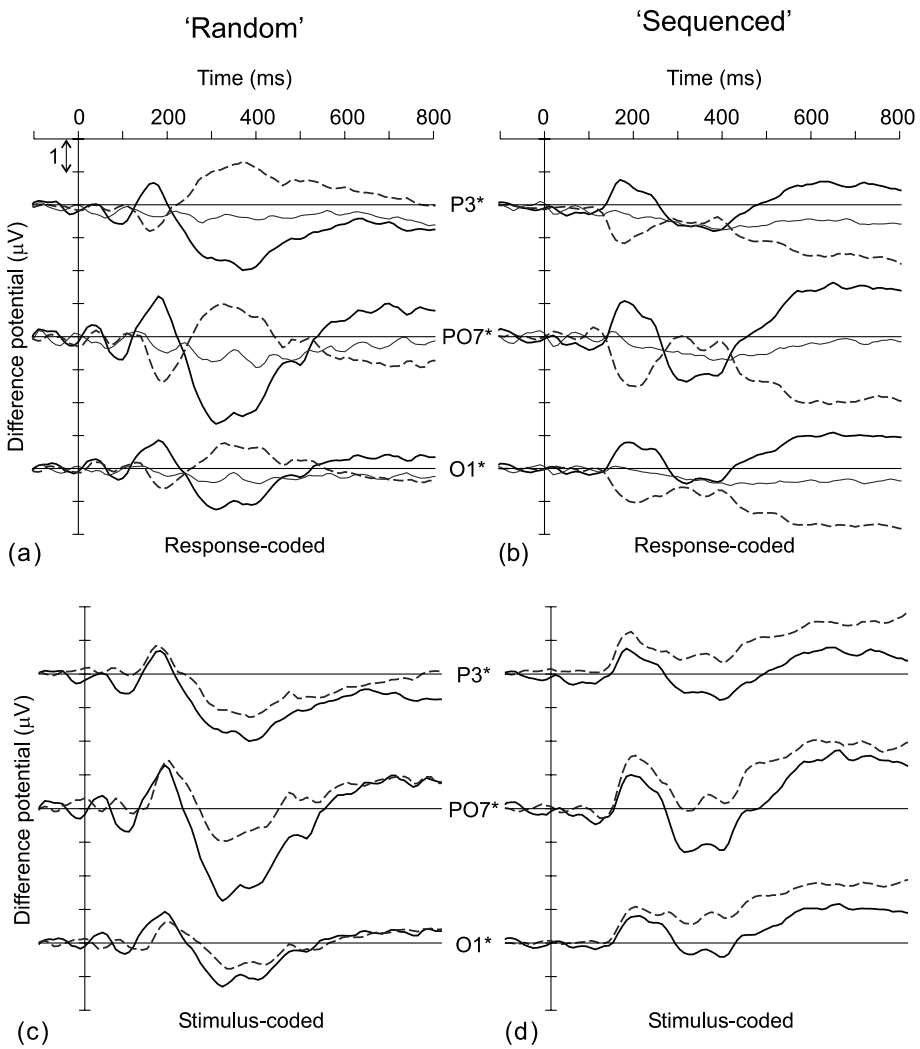

Fig. 3. Experiment 1: stimulus-locked difference potentials at exemplary parietal, temporo-parietal, and occipital sites. (a) and (b) response-coded: negativity contralateral to response side plotted upwards, (c) and (d) stimulus-coded: negativity contralateral to target upwards. Solid lines: targets ipsilateral to response side; dashed lines: contralateral targets; thin lines: central targets. Note that central targets cannot appear in the stimulus-coded plots. Zero on the time scale is target onset. Note the lateralized N1 component at ≈180 ms after target onset with higher negativity in the hemisphere contralateral to the target and the intermediate ERL at around 350 ms with higher negativity in the hemisphere ipsilateral to the target, when compared with central targets. Note also that in the sequenced condition, a second peak in the lateralized N1 emerges at about 240 ms.

between 280 and 430 ms after target onset, varied with direction ($F(2,16) = 10.86$, $p = 0.003$) and with predictability ($F(1,8) = 10.76$, $p = 0.011$). ERLs peaked earlier

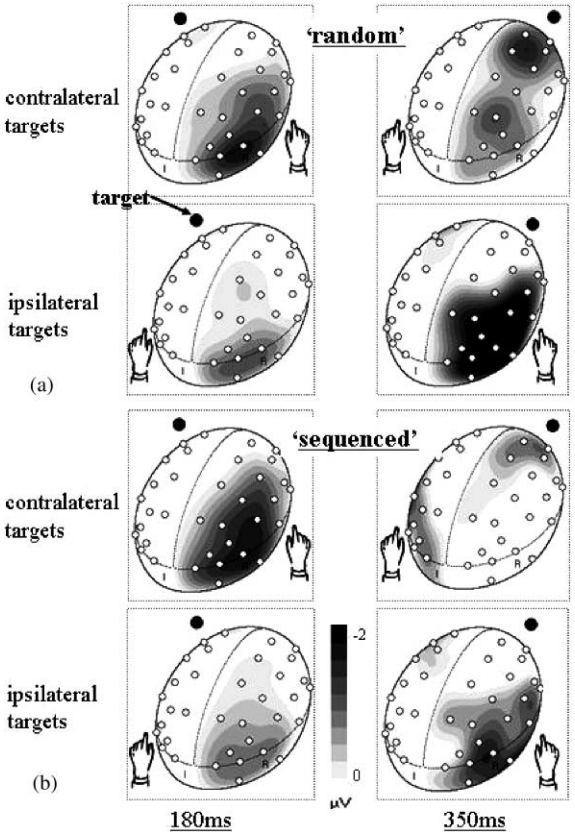

Fig. 4. Experiment 1: topography maps of stimulus-coded difference potentials at 180 and 350 ms. (a) Random, (b) sequenced. At 180 ms, the right hemisphere shows negative difference potentials contralateral to the target and at 350 ms, negative difference potentials ipsilateral to the target. In the random condition, parietal negativity at 350 ms is increased in the hemisphere ipsilateral to the target, whereas in the sequenced condition, this effect was decreased for ipsilateral targets and non-existent for contralateral targets. Note, that central targets cannot be regarded in this kind of averages. Frontal activity at 350 ms is higher in the hemisphere contralateral to the response side.

when stimuli were presented ipsilateral to the active arm and latest with contralateral targets (ipsilateral targets: 320 ms, central targets: 345 ms, contralateral targets: 370 ms) and earlier in random (335 ms) than in sequenced trials (354 ms), respectively. Peak amplitude varied with predictability ($F(1,8) = 6.94$, $p = 0.030$) and was higher in the random than in the sequenced condition. The effect of predictability on the peak latencies measured in the same time interval at the central electrodes over motor cortex (C1/2) reached significance ($F(1,8) = 8.96$, $p = 0.017$; random: 347 ms, sequenced: 371 ms). However, the effect of predictability on peak amplitudes at central sites was not significant ($F(1,8) = 3.52$, $p = 0.098$) suggesting that this effect of predictability on peak amplitudes is attributable to premotor areas. No significant

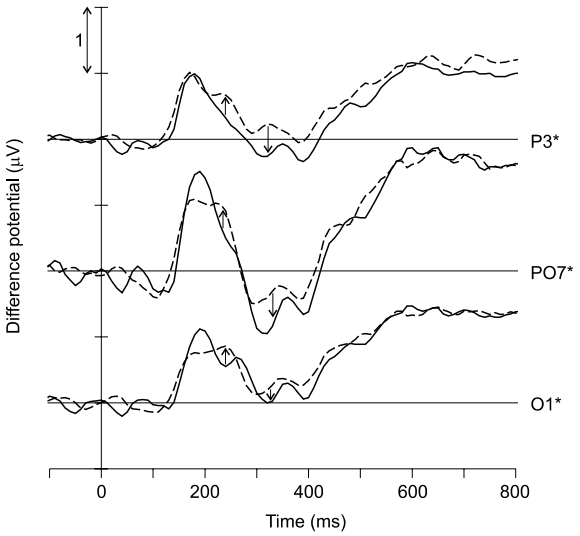

Fig. 5. Experiment 1: stimulus-locked difference potentials of early vs. late trials in the sequenced condition. Exemplary parietal, temporo-parietal, and occipital sites. Stimulus-coded: negativity contralateral to target plotted upwards. ERLs averaged across directions. Solid lines: early trials; dashed lines: late trials. Zero on the time scale is target onset. Note higher 2nd peak in early ERL and decreased intermediate ERL in late trials. (The decrease in the lateralized N1 at temporo-parietal sites is not significant.)

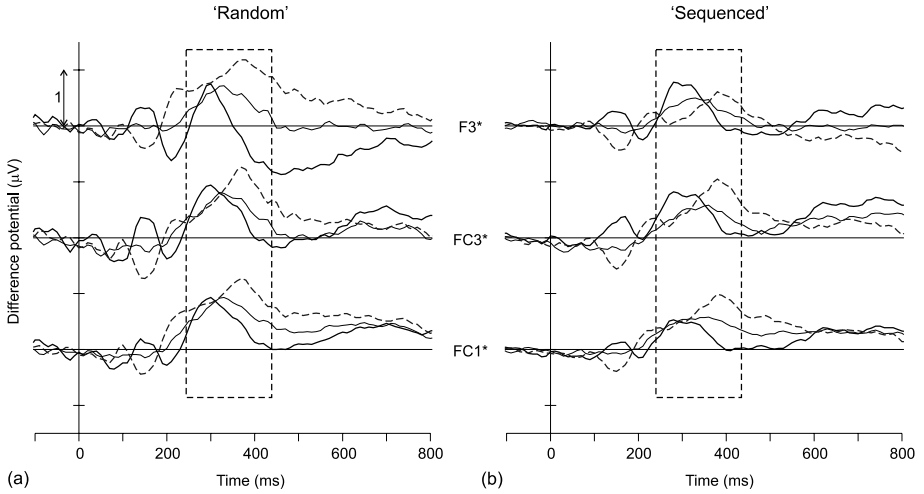

Fig. 6. Experiment 1: stimulus-locked difference potentials at frontal sites. Response-coded: negativity contralateral to response side plotted upwards. Solid lines: targets ipsilateral to response side; dashed lines: contralateral targets; thin lines: central targets. Zero on the time scale is target onset. The dashed rectangle indicates the interval in which the anterior intermediate ERL was analyzed. Note that peak amplitudes were higher in the random than in the sequenced condition.

differences in this component between early and late trials in a sequence were evident ($F(1,8) = 3.79$, $p = 0.087$).

Posterior intermediate component: This component had its maximum at temporo-parietal sites and spread up to central sites (Fig. 4 shows the scalp topography). It was measured as the mean amplitude between 280 and 430 ms after target onset. When targets were presented laterally, ERLs deviated from those with central targets towards the hemisphere ipsilateral to the target (see Fig. 3(a) and (b)). This dependence on pointing direction was reflected in a main effect of direction ($F(2,16) = 11.00$, $p = 0.006$). However, we also found a significant interaction of direction with factor scalp site ($F(12,96) = 3.21$, $p = 0.036$) indicating that the ERL was evident at posterior sites: Significant main effects of direction were evident at parietal and temporo-parietal sites ($F(2,16) = 9.74$, $p = 0.010$ and $F(2,16) = 22.44$, $p = 0.001$, respectively). Predictability reduced the ERL. This effect of predictability was reflected in the interaction with factor direction ($F(2,16) = 8.5$, $p = 0.018$), which indicated that in the sequenced condition, the direction effect was absent ($F(2,16) = 0.81$, $p = 0.426$), but was evident in the random condition ($F(2,16) = 12.02$, $p = 0.006$). We also found an interaction of factors predictability, direction, and scalp site ($F(12,96) = 3.35$, $p = 0.025$). This showed that the interaction of predictability and direction was evident at central and posterior sites. It reached significance at centro-parietal ($F(2,16) = 8.42$, $p = 0.017$), parietal ($F(2,16) = 12.02$, $p = 0.007$), temporo-parietal ($F(2,16) = 7.32$, $p = 0.023$), and occipital ($F(2,16) = 6.04$, $p = 0.031$) electrode sites. Fig. 7 illustrates differences in ERLs between the random and sequenced condition at site P7/8. Early trials in the sequenced condition showed increased intermediate component amplitudes when compared to late trials ($F(1,8) = 8.7$, $p = 0.018$).

Movement ERL: During the pointing movement, negativity was increased contralateral to the target ($F(2,16) = 5.99$, $p = 0.035$). This ERL reached maximal amplitudes at posterior sites, but the interaction of factors direction and scalp site did not reach significance ($F(12,96) = 3.71$, $p = 0.059$). Fig. 8 shows posterior ERLs relative to the response side time-locked to the start of the movement. The movement ERL was measured as the average amplitude between 200 and 300 ms after movement onset. In this component, predictability interacted with factor direction ($F(2,16) = 8.71$, $p = 0.015$), such that the direction effect was absent in the random condition ($F(2,16) = 0.11$, $p = 0.792$), but evident with sequenced target presentation ($F(2,16) = 14.12$, $p = 0.005$). No differences between early and late trials in the sequenced condition were evident ($F(1,8) = 0.01$, $p = 0.918$).

2.3. Discussion

Four ERL components during the visuomotor transformation process in posterior parietal and premotor cortex reflected directional encoding of the target and the pointing movement. Three of the components that had maximal amplitudes at posterior scalp sites were lateralized with respect to the side of target presentation. An anterior component was evident contralateral to the responding arm, but varied in latency with pointing direction. Predictability of target and pointing direction

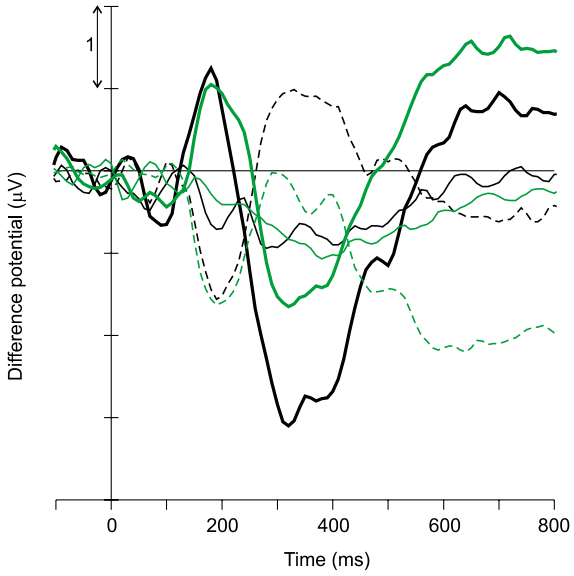

Fig. 7. Experiment 1: stimulus-locked difference potentials at electrode pair P7/8. Random and sequenced trials are compared. Response-coded: negativity contralateral to response side plotted upwards. Black lines: random trials, green lines: sequenced trials, bold lines: target ipsilateral to response side; thin lines: central targets; dashed lines: target contralateral to response side. Note the second peak in the early ERL in sequenced trials and the reduced intermediate ERL in sequenced trials.

modified these components. Visuospatial representation of the target in parietal visual areas seemed to be enhanced by predictable direction, whereas directional ERLs in posterior parietal and premotor cortex were reduced. These findings differed from the LRP over the motor cortex that was not affected by pointing direction or predictability.

A lateralized N1 component around 160–200 ms after the onset of the target reflected increased negativity in the hemisphere contralateral to the target. It reached highest amplitudes at electrode sites over visual areas (temporo-parietal and parieto-occipital). With higher predictability of target position (both sequenced vs. random and late vs. early trials) a second peak at about 240 ms in the component became more prominent. This second peak was probably evoked by an overlying N2pc component, which increased with predictable direction. The endogenous N2pc was proposed to indicate attentional selection of task relevant stimuli (Eimer, 1996; Luck, 1995; Luck & Hillyard, 1994a). It has been shown that the earlier exogenous N1 of the ERP increases in amplitude when attention had been directed to the stimulus position (Eimer, 1999; Mangun & Hillyard, 1991). However, we did not find a significant effect of predictability on the lateralization of the N1 in the present study, which might have indicated enhanced visual attention. In contrast, the N2pc most probably was elicited by enhanced visuospatial representation of the target when its direction was predictable.

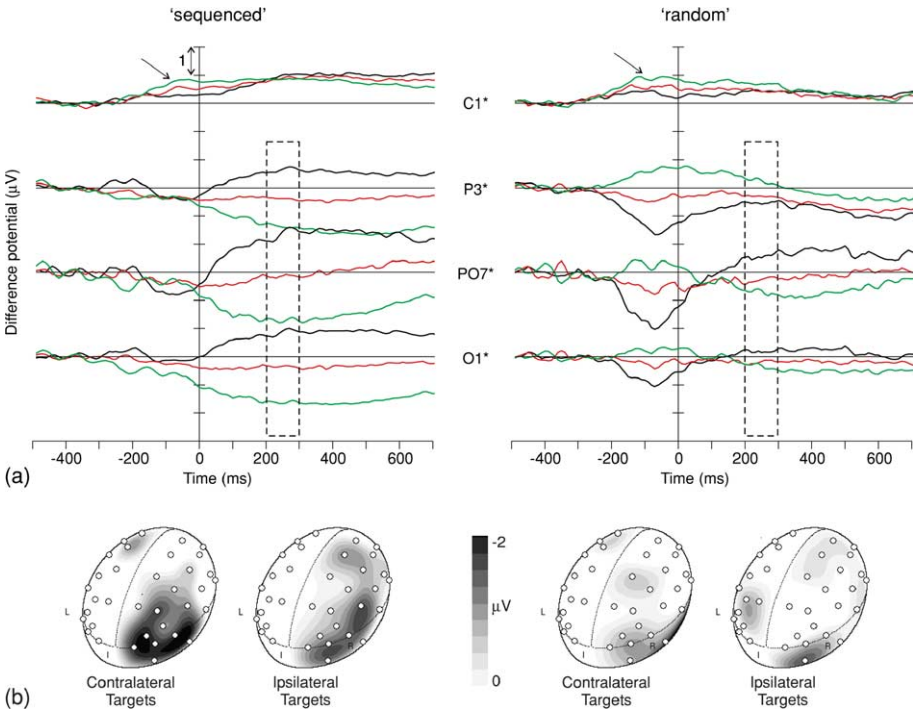

Fig. 8. Experiment 1: response-locked difference potentials. (a) LRP and exemplary parietal, temporo-parietal, and occipital electrode sites. Response-coded: negativity contralateral to response side plotted upwards. Black lines: target ipsilateral to response side; green lines: contralateral targets; red lines: central targets. Zero on the time scale is movement onset. The dashed rectangle depicts the time interval in which the movement ERL was analyzed. Note coincidence of LRP (arrows) and intermediate ERL component. The effect of horizontal target position on the movement ERL is reduced in random compared to sequenced trials. (b) Topography maps at 250 ms after movement onset. Stimulus-coded: the right hemisphere shows negativity that is higher contralateral to the target. Note that parietal negativity was increased in the hemisphere contralateral to the target. In the random condition, the movement ERL was reduced in amplitude and expansion. Negativity over motor sites was higher in the hemisphere contralateral to the responding arm.

Intermediate ERL components were evident at fronto-central and temporo-parietal sites. The posterior ERL consisted of a deviance of negativity towards the hemisphere ipsilateral to a lateral target, when compared to central targets. It had maximal amplitudes at temporo-parietal and parieto-occipital electrode sites and extended in time from about 250 ms after the target to the start of movement. This component decreased with target and therefore movement direction predictability. Over premotor sites on the other hand, negativity was higher in the hemisphere contralateral to the responding arm. Predictability reduced the amplitude of this component. This effect was not evident at the electrodes over primary motor cortex, which suggests that the effect of predictability on the ERL amplitudes is attributable to premotor areas.

A functional relation of the premotor and parietal intermediate ERL components is likely due to anatomical fronto-parietal connections mediating the exchange of information in the execution of visually guided movements (Deiber et al., 1991; Glickstein, 2000). Evidence for a movement relevant function of the intermediate ERLs comes from the fact that they were evident at a time before movement when there was already increased activity over contralateral motor cortex—the LRP. We suggest that the intermediate ERL components reflect the transformation of target position into the direction of the motor response in the fronto-parietal network for reaching.

The parietal ERL most likely was evoked by the processing of visuospatial stimulus properties relevant for the response in parietal cortex. This interpretation is supported by its maximal amplitude preceding movement onset as well as by its dependency on pointing/target direction and direction predictability. Supporting evidence also comes from electrophysiological studies in monkeys. Arm movements towards a visual target modulate the activity of reach-related neurons in the superior parietal lobule of monkeys (Fattori, Gamberini, Kutz & Galletti, 2001; Galletti, Fattori, Kutz & Battaglini, 1997). This reach-related discharge was not only found during the execution of the arm movements, but also during the preparation of the reaches.

It might be suggested that the anterior component reflects the encoding of spatial information in arm-centered coordinates in premotor cortex. Imaging studies in humans (Galati et al., 2000) and electrophysiological studies in monkeys (Fogassi et al., 1992; Graziano, Yap, & Gross, 1994) have shown that in premotor areas, stimulus position is coded in egocentric coordinate systems.

The fact that direction predictability reduced the amplitudes of the intermediate ERLs might be due to the reduced relevance of encoding directional information when movement direction can be predefined. This interpretation is consistent with the reduced posterior component in late trials in a sequence compared to early trials. Evidence for this interpretation also comes from a study by Deiber et al. (1997). They found decreasing regional cerebral blood flow in posterior parietal cortex during learning of stimulus-response mapping tasks, in which participants had to move a joystick in the direction indicated by a stimulus. They concluded that in the tasks used, a conversion of visual information into the spatial/motor domain was required and that this mapping may be reflected by the changes of activity in the posterior parietal cortex. Furthermore, as the coordinate transformation process became routine (i.e., more automatic), the importance of posterior parietal cortex decreased.

While the visuomotor transformation processes in the preparatory phase lost importance with predictable direction, guidance of the ongoing movement seemed to gain relevance. This is indicated by the increased movement ERL in the sequenced when compared to the random design, although the required movements were the same in both conditions. It has been shown that posterior parietal cortex is involved in the control of ongoing visually guided movements in humans (Desmurget et al., 1999). The movement ERL probably indicated the increased involvement of posterior parietal cortex in the visuospatial guidance of movement when the direction was predictable.

An objection to the interpretation of the ERLs, especially the posterior intermediate ERL, might be that they are caused by eye movements rather than reflecting the processing of directional information. Indeed, similar to the posterior intermediate ERL, the hEOG tends to be smaller in the predictable condition and, like the ERL, is smaller in the late trials of a sequence compared to the early trials. However, there are several reasons for which it seems implausible that the ERLs are caused by eye movements. First, the onset of the intermediate ERL seems too late for the ERL to reflect the generation of eye movements. At the time of the intermediate ERL, the eyes are directed on the target, where they stay for the rest of the trial. Hence, there is no more variation in the EOG at the time of the intermediate ERL. Furthermore, the relations between the conditions in the hEOG and in the ERLs are inconsistent. Direction has the inverse effect on the EOG than it has on the intermediate ERL: The hEOG is larger for contralateral targets than for ipsilateral targets, whereas the intermediate ERL is larger for ipsilateral targets (see Fig. 3 in the stimulus-coded plots (c) and (d)). Additionally, predictability has an inverse effect on the hEOG than it has on the movement ERL: The movement ERL is increased by predictability, whereas the hEOG is smaller in the predictable condition. Therefore, it seems feasible to suggest that the ERLs are not caused by eye movements but reflect the directional encoding of target position and pointing movement.

3. Experiment 2

In Experiment 2, we confirmed the principle pattern of direction dependent ERLs with reduced target laterality. In Experiment 1, targets were presented at peripheral locations. With parafoveal targets, stimulus detection and processing might be modified, since parafoveal stimuli are closer to the focus of attention. If the pattern of lateralizations found in Experiment 1 critically depended on attentional processes, rather than on defining directional codes, it should substantially change in Experiment 2.

Furthermore, we minimized the directional differences in the pointing movements by moving the starting positions closer to the centerline and closer to the screen. This should reduce the directional component during the ongoing pointing movement.

In addition, the above changes not only reduced movement dimensions, which was more favorable for the EEG recordings, but also reduced eye movements to the target. Therefore, Experiment 2 verified that eye movements did not interfere with ERL components in Experiment 1.

3.1. Methods

Unless stated explicitly, setup and methods were the same as in Experiment 1.

3.1.1. Participants

Twelve healthy right-handed participants (eight females) aged 17 to 27 (average 22.42 years) took part in this experiment. Vision was normal or corrected to normal.

3.1.2. Apparatus

The starting positions were moved closer to each other and to the screen (distance between the starting positions 7 cm and to the screen 7.2 cm). As in Experiment 1, the pointing hand became visible once the movement was in progress and the hand approached the screen. In the second part of Experiment 2, which will not be reported here, the visual field was reduced both horizontally and vertically by a prism device, which left–right inverted participants' vision. To allow direct comparison between the two parts of Experiment 2, in the first part of the experiment, the visual field was also restricted to a similar degree. It yielded full vision of the screen, but prevented vision of the space to the left and right and above the screen.

3.1.3. Stimuli

The lateral target positions were moved closer to the initial fixation point in the center of the screen (2.4° to the left or right from the center). Additionally, to prevent vertical eye movements, there was no variation in vertical target position. The three target locations were presented in random order.

3.1.4. Procedure

Participants performed this part of the experiment with their left and right hands in separate blocks. One block consisted of 450 trials (3 positions × 150 repetitions).

3.1.5. Data processing and analysis

The accuracy criterion was loosened in this experiment due to the increased difficulty in the part with inverted vision. Trials were analyzed, if the participant first touched the screen either at the target location or within 20 mm below the target, independent of horizontal deviance. Thereby, 1.8% of the trials were excluded from further analysis. For EEG analysis, ANOVAs were performed with factors direction and scalp site, as described in Experiment 1. We performed no statistical comparison between Experiments 1 and 2, since the experiments differed in too many aspects.

3.2. Results

Behavioral data: Response times were fastest with ipsilateral targets and slowest with contralateral targets (ipsilateral: 409 ms, central: 410 ms, and contralateral: 418 ms, $F(2,22) = 4.15$, $p = 0.030$). Deviation from the target (i.e., horizontal distance) was smallest with contralateral targets and largest with ipsilateral targets (ipsilateral: 6.4 mm, central: 5.2 mm, contralateral: 4.7 mm, $F(2,22) = 11.20$, $p < 0.001$). Movement duration varied with direction and was 498 ms for ipsilateral targets, 505 ms for central, and 514 ms for contralateral targets ($F(2,22) = 9.33$, $p = 0.001$).

EOG: The hEOG is displayed in Fig. 9. The hEOG, measured between 300 and 500 ms after target onset in the stimulus-coded data, was significantly larger for contralateral targets than for ipsilateral targets ($F(1,11) = 5.85$, $p = 0.034$). Eye movements were manifestly reduced in Experiment 2.

ERL data: Fig. 10 shows ERLs in Experiment 2. Though target laterality and the directional requirements of the movements were substantially reduced, movement-

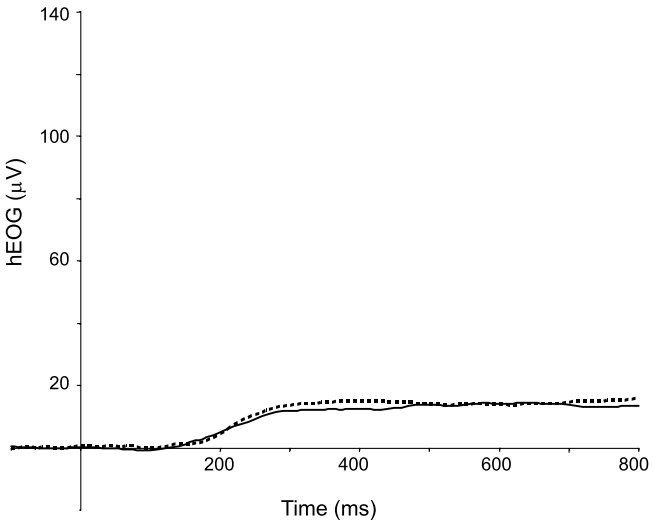

Fig. 9. Experiment 2: hEOG. Solid lines: ipsilateral targets; dashed lines: contralateral targets.

preceding activity showed a similar pattern of lateralizations as in Experiment 1. The early and intermediate ERL components were evident with comparable latencies. With reduction of the lateral expanse of arm movements, no directional component was evident during the pointing movement.

Lateralized N1: With the smaller lateral distance of the stimuli, the lateralized N1 component was more pronounced with sharper and higher amplitudes than in Experiment 1.

Intermediate components: The posterior intermediate ERL was reduced in amplitude and in its temporal as well as topographical extension. It was measured as the mean amplitude between 280 and 370 ms after target onset. The main effect of direction did not reach significance, but interacted with factor scalp site ($F(12, 132) = 11.65$, $p < 0.001$). At frontal sites, we found a significant effect of direction ($F(2, 22) = 4.84$, $p = 0.042$), which reflected the effect of direction on the amplitudes of the anterior intermediate ERL (see below). The fact that the polarity of the posterior intermediate ERL depended on pointing direction (see Fig. 10(a), electrode sites P3*, PO7*, O1*) was evident in the significant effect of factor direction at central ($F(2, 22) = 4.54$, $p = 0.047$), temporo-parietal ($F(2, 22) = 5.23$, $p = 0.038$), and occipital ($F(2, 22) = 4.79$, $p = 0.047$) sites.

At frontal sites, the intermediate component showed an effect of pointing direction on peak amplitudes only ($F(2, 22) = 6.05$, $p = 0.008$). Amplitudes were largest with ipsilateral and smallest with contralateral targets. This contrasts Experiment 1, where factor direction had a significant effect on peak latency ($F(2, 16) = 10.86$, $p = 0.003$). However, peaks of this component in Experiment 2 were not as well-defined as in Experiment 1. Therefore, measurement of the peak latencies here may not be as reliable.

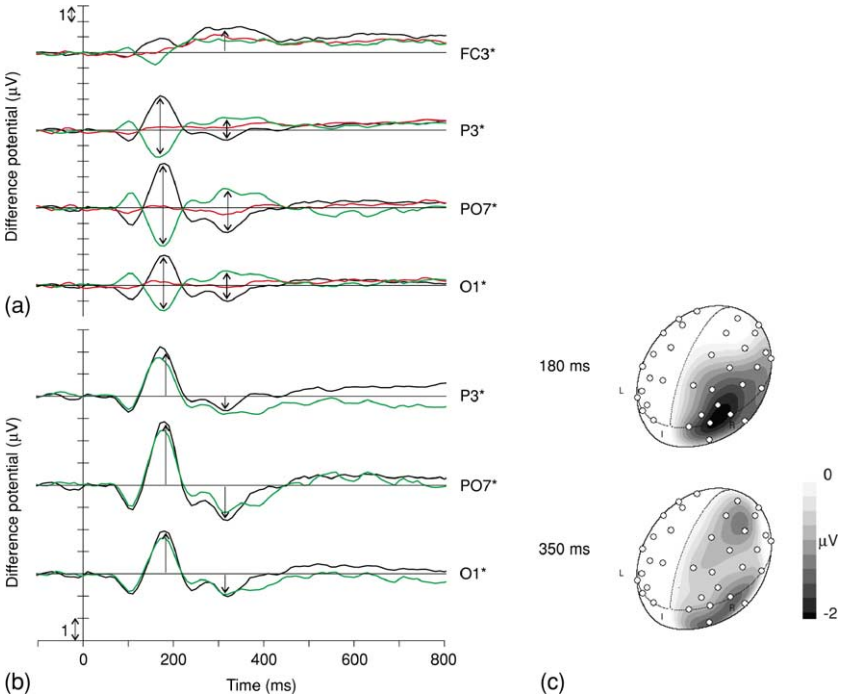

Fig. 10. Experiment 2: stimulus-locked difference potentials. (a) Response-coded: negativity contralateral to response side plotted upwards; (b) stimulus-coded: negativity contralateral to target upwards. Black lines: target ipsilateral to response side, green lines: contralateral targets, red lines: central targets. Zero on the time scale is target onset. Note effect of target position on amplitudes of anterior intermediate ERL (FC3*). (c) Topography maps 180 and 350 ms; exemplary for targets contralateral to the response side. At 180 ms, the right hemisphere shows negative difference potentials contralateral to the target and at 350 ms, negative difference potentials ipsilateral to the target.

In Experiment 2, there was no effect of target position on lateralization after movement onset ($F(2, 22) = 0.76$, $p = 0.48$).

3.3. Discussion

Even with parafoveal targets near the initial visual and attentional focus, similar effects of direction on pre-movement ERLs were evident. This result suggests that the pattern of ERLs in visually triggered pointing does not depend on eye movements to peripheral targets, but rather reflects directional processing of the target and the response. In Experiment 2, the hEOG was about eight times smaller than in Experiment 1 (15 vs. 120 μV), whereas the distance of the lateral targets from the center was only about 5.7 times smaller (13.7° vs. 2.4° of visual angle). Nonetheless, the pre-movement ERLs are comparably large in Experiment 2 as they are in Experiment 1. Additionally, the temporal relation between the hEOG and the ERLs in Experiments 2 and 1 are inconsistent: The emergence of the posterior intermediate ERL

in Experiment 1 precedes the plateau of the hEOG, whereas in Experiment 2 it does not. Furthermore, the finding that the hEOG is increased for contralateral targets is not reflected in the ERLs (see Fig. 10 in the stimulus-coded data (b)), which again shows that the relation between the EOG and ERLs are inconsistent. These findings corroborate the notion that the ERLs in the present experiments are not caused by eye movements.

The lateralized N1 tended to be more sharply pronounced with higher amplitudes. This might be due to a facilitation of target detection near the initial focus of attention.

The posterior intermediate ERL component was reduced in extension, compared to Experiment 1. This component most probably reflects the processing of response relevant visuospatial information in posterior parietal cortex. The observed reduction of the ERL might be explained by the fact that target space was more restricted in Experiment 2 with regard to the small eccentricity as well as the missing vertical variation in target positions. Therefore, parietal areas involved in this computation were also more restricted. In addition, the directional requirements of the response were also minimal, which might have contributed to this reduction.

The movement ERL in Experiment 1 was proposed to reflect the involvement of posterior parietal cortex in the directional guidance of movement. The absence of this directional component during movement in Experiment 2, when directional aspects of the movements were minimal, supports this interpretation.

4. General discussion and conclusions

ERLs provide valuable information about the cortical processes during visually triggered pointing movements with especially high resolution in the time domain. These processes include target localization, visuomotor transformation, and directional guidance of the movement. In Experiment 1, we investigated the effect of pointing direction and direction predictability on ERLs. Both factors influenced hemispheric asymmetries. Experiment 2 confirmed directional effects despite considerable reduction of target and pointing laterality.

ERLs captured lateralized visuomotor processing within the fronto-parietal network for reaching: An N1 component over parietal visual areas indicated target localization and an overlapping N2pc was evoked by increased attentional orienting to the target when the direction was predictable. A posterior component preceding movement onset depended on visuomotor integration processes in posterior parietal cortex. Simultaneously, a component at anterior sites reflected context dependent encoding of response direction in premotor cortex.

Furthermore, lateralizations during the pointing movement to peripheral targets reflected visuospatial guidance of the movement in posterior parietal cortex.

Whereas lateralization of activity in parietal and parieto-occipital cortex changed with pointing direction, activity in premotor cortex was consistently higher in the hemisphere contralateral to the response side. Peak latency and amplitude of the premotor component varied with target/pointing direction and predictability. This

component most likely reflected the encoding of spatial information in arm-centered coordinates in premotor cortex. Evidence for this interpretation comes from monkey studies. Neurons in the ventral premotor cortex of primates code the location of a target in space after it had disappeared (Graziano, Hu, & Gross, 1997) and activity in dorsal premotor cortex ultimately encodes the direction of intended reaching movements (Crammond & Kalaska, 1994).

The posterior intermediate component most probably reflected the lateralized sensorimotor integration process in posterior parietal cortex. Posterior parietal cortex is known to be involved in visuomotor coordination and the selection of directed movements (Grafton et al., 1992; Kertzman et al., 1997; Lacquaniti & Caminti, 1998). By neurons with multisensory receptive fields in parietal cortex, sensory locations of stimuli are converted into motor coordinates required for directed movements (Andersen, Snyder, Bradley, & Xing, 1997; Graziano, Cooke, & Taylor, 2000).

The movement ERL over posterior areas during pointing to predictable peripheral targets suggests that posterior parietal cortex is not only involved in directional encoding in the movement preparatory phase, but also in the control of the target directed movement itself.

Predictability of target and pointing direction modified ERLs: On the one hand, visuospatial attention was more strongly focused on the hemifield in which the target would predictably appear. This was reflected in an increase of the N2pc, overlapping the early ERL when target direction was predictable. On the other hand, processing of spatial information was facilitated when target and pointing direction were predictable. The amplitudes of the intermediate components in parietal and premotor cortex decreased with predictable direction. This might the consequence of the reduced relevance of visuospatial information and visuomotor transformation, since spatial codes may have been predefined.

In summary, two directional ERL components preceding movement onset reflected lateralized visuomotor processing in premotor and parietal cortex. The premotor component was evident contralateral to the arm used for pointing and varied in latency and amplitude with pointing direction. It reflected the encoding of spatial information in arm-centered coordinates. The parietal component represented an increase of negativity ipsilateral to the target and indicated the processing of response relevant visuospatial information in posterior parietal cortex. Both components decreased when pointing direction was predictable. This result suggests that the computation of the spatial codes for action is of reduced relevance when they can be predefined.

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