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Biological Psychology 68 (2005) 15–39

BIOLOGICAL PSYCHOLOGY

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Effects of rearranged vision on event-related lateralizations of the EEG during pointing

Isabelle Berndt[a], Volker H. Franz[a], Heinrich H. Bülthoff[a],
Karl G. Gotz[a], Edmund Wascher[b,*]

[a] *Max Planck Institute for Biological Cybernetics, Tübingen, Germany*
[b] *Max Planck Institute for Human Cognitive and Brain Sciences, Amalienstrasse 33, D-80799 Munich, Germany*

Received 14 February 2003; accepted 10 March 2004

Abstract

We used event-related lateralizations of the EEG (ERLs) and reversed vision to study visuomotor processing with conflicting proprioceptive and visual information during pointing. Reversed vision decreased arm-related lateralization, probably reflecting the simultaneous activity of left and right arm specific neurons: neurons in the hemisphere contralateral to the observed action were probably activated by visual feedback, neurons in the hemisphere contralateral to the response side by the somatomotor feedback. Lateralization related to the target in parietal cortex increased, indicating that visual to motor transformation in parietal cortex required additional time and resources with reversed vision. A short period of adaptation to an additional lateral displacement of the visual field increased arm-contralateral activity in parietal cortex during the movement. This is in agreement with the Clower et al. study (1996), which showed that adaptation to a lateral displacement of the visual field is reflected in increased parietal involvement during pointing.

Keywords: EEG; Event-related lateralizations; Reversed vision; Pointing

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1. Introduction

When we direct our hand towards a visual target, our brain uses proprioceptive information about the position of our arm and visual information about the target of the reach. Visual

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* Corresponding author. Tel.: +49-89-38602-332; fax: +49-89-38602-199.
E-mail address: wascher@psy.mpg.de (E. Wascher).

doi:10.1016/j.biopsycho.2004.03.016

feedback about the current position of the hand as well as about the location of the target can also be used to compute the appropriate movement. The interaction between proprioceptive and visual information can be studied by introducing a discrepancy between visual and proprioceptive feedback. This is usually done by rearranging vision, since proprioceptive information is difficult to manipulate. Insights into the significance of visual feedback in motor control have been gained from psychophysical experiments that used modified visual feedback and typically behavioral measures (Welch et al., 1979; Yoshimura, 1996). These studies typically use prisms that distort the visual field, resulting in a conflict between visual and proprioceptive information.

According to the framework proposed by Milner and Goodale, vision for action is the function of the dorsal stream (Goodale and Milner, 1992; Milner and Goodale, 1995). Thus, correlates of the effect of modified vision on motor tasks are likely to be found in parietal cortex. In fact, imaging studies have identified parietal areas that are specifically involved in the recalibration of the visual to motor transformation process induced by distortions of the visual field (Clower et al., 1996; Inoue et al., 1997). Imaging techniques like functional magnetic resonance imaging (fMRI) or positron emission tomography (PET), which measure changes in the regional metabolism of the brain, have the advantage of identifying the sources of activation with high accuracy but provide very low temporal resolution. Therefore, they can assess only one aspect of plasticity, namely which areas undergo changes due to the exposure to rearranged vision. These studies cannot assess the modifications in the sensorimotor transformation process in the situation of conflicting inputs.

Such transformation processes can be studied by measuring brain activity online by means of EEG recordings. By recording event-related EEG potentials, the cortical activity at different stages in the visual to motor transformation process can be monitored with high temporal resolution. Several studies have assessed changes in the EEG during the preparation and execution of movements. The EEG has been shown to contain a lateralized component indicative of movement preparation. De Jong et al. (1988) and Gratton et al. (1988) first used the method of subtracting the activity at the electrode over the motor cortex ipsilateral to a hand movement from that at the contralateral electrode. This revealed the lateralized readiness potential (LRP) over contralateral hand motor areas prior to movement onset. The LRP like subtraction method has since been used to investigate event-related lateralizations of EEG activity (ERLs) not only relative to the side of the response but also in relation to the laterality of a visual stimulus (e.g. Luck and Hillyard, 1994; Wascher and Wauschkuhn, 1996; Verleger et al., 2000).

Besides the LRP, other lateralized components play a role in reaching movements as well. In a previous study, we identified parietal and premotor ERLs in a pointing task (Berndt et al., 2002). Two of these ERLs were evident at around 350 ms after target onset, following target detection and preceding the start of the movement. Over frontal motor areas the ERL reflected increased activity contralateral to the active arm. Contrastingly, parietal activity around the same latency was lateralized with respect to the target position, which coincided with pointing direction. A further target-oriented ERL over parietal areas was evident during the execution of the pointing movement. These ERLs were context dependent. When the pointing direction was predictable and visuomotor codes could be predefined, the ERLs decreased in amplitude. This responsiveness to direction predictability showed that these

ERLs were sensitive to changes in the visual to motor transformation process in parietal and premotor areas. They might also reflect the recalibration of visuomotor codes when vision is distorted.

In the present study, we used ERLs to investigate visuomotor processing with conflicting visual and proprioceptive feedback. Participants pointed to a target that was presented at one of three possible positions on a monitor. In a first experiment, we studied the effect of left–right reversed vision on the ERLs. In a further experiment, we added a lateral displacement to the visual field and investigated the effect of a short period of adaptation to the visuomotor distortion on the ERLs.

2. Experiment 1

A left–right reversal of the visual field represents an interesting case of visuomotor distortion. Several studies have previously assessed changes induced by several weeks exposure to reversed vision. For example, fMRI in humans revealed brain activity in frontal and parietal areas that was unique to new hand representations that emerged after 5 weeks exposure to reversing spectacles (Sekiyama et al., 2000). Studies that used visual evoked potentials or single cell recordings in the visual cortex of the monkey have also provided evidence for a functional reorganization at an early stage in visual processing as a consequence of adaptation to reversed vision (Sugita, 1994, 1996). Consequences of the visuomotor conflict induced by exposure to reversed vision have also been shown behaviorally (Yoshimura, 1996; Ninomiya et al., 1998).

Another interesting study investigating visuomotor plasticity was conducted by Linden et al. (Linden et al., 1999). In this study, participants wore inverting prisms and mirror spectacles for a period of 6–10 days and were scanned with fMRI several times during the experiment. Subjects showed adaptation of visuomotor skills to a certain degree, but no return of upright vision. No effect on visual areas was found with fMRI. However, in the Linden study, inverted vision was used. We believe that dealing with inverted vision requires rather different mechanisms than reversed vision does.

When performing arm movements with reversed vision, the visual feedback from the action is equivalent to that of the same movement performed with the opposite arm. This perceptual phenomenon was recently used in a study on phantom pain in patients with arm amputations (Ramachandran and Rogers-Ramachandran, 1996). The patients looked at an image of the healthy arm in a mirror while moving it or experiencing the arm being touched by the experimenter. The observation of the mirror image seemed to have an impact on the perceptual representation of the phantom, causing kinesthetic or tactile sensations in the phantom.

This phenomenon may be due to an effect of reversed vision on a number of areas in which neurons are multimodal, i.e., neurons with combined visual and motor properties that respond to the sight of the arm as well as to the somatomotor information from the arm.

In the monkey parietal and premotor cortex, a number of neurons are responsive not only to the felt position of the monkey's arm, but also to the seen position of a matching fake arm (Graziano, 1999; Graziano et al., 2000). It has been shown in monkeys that neurons in the parietal area PF that respond when the monkey observes others perform object-related arm movements respond selectively to actions with the contralateral arm (Fogassi et al., 1998). These neurons also discharge similarly when the monkey performs the observed action and have therefore been named PF mirror neurons according to the mirror neurons originally discovered in the monkey premotor cortex (Gallese et al., 1996; Rizzolatti et al., 1996).

Several studies have indicated that neurons in parietal and premotor cortex with combined visual and motor properties are the basis for the visual to motor transformation process that is required for visually triggered movements (Battaglia-Mayer et al., 2001; Colby and Goldberg, 1999; Andersen et al., 1997). The premotor and the parietal cortex have also been shown to be strongly involved when humans observe object-directed actions of others (Iacoboni et al., 1999; Buccino et al., 2001). There is growing evidence that a mirror system, similar to that in the monkey, exists also in humans (Fadiga et al., 1995; Hari et al., 1998; Cochin et al., 1999; Strafella and Paus, 2000).

When vision is left–right reversed, participants observe a movement with their left arm while performing the same movement with their right arm (see Fig. 1). This might result in co-activation of multimodal and mirror-neuron-like premotor and parietal neurons in both hemispheres.

It seems likely that ERL components will reflect the conflicting visual and proprioceptive information under reversed vision, as many neurons in the relevant areas in visuomotor coordination are responsive to input from one side of the body only: many of the multimodal neurons that respond to the felt and seen position of a monkeys arm are only sensitive to the

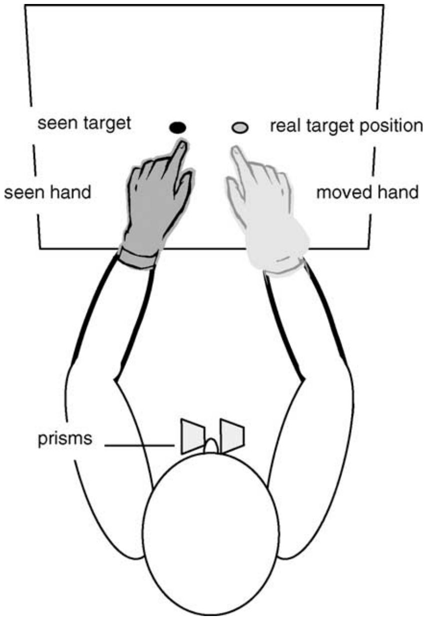

Fig. 1. Effect of a left–right reversal of vision when wearing reversing prism spectacles. During pointing, the target position, pointing direction, and the hand that is observed are reversed. When pointing with the right hand to a right sided target (light grey), the participant observes a left hand pointing movement to a target on the left side of the screen (dark grey).

contralateral arm (Graziano et al., 2000). In monkeys, neurons in the parietal area PF that respond to the observation of object-related arm movements respond selectively to actions with the contralateral arm (Fogassi et al., 1998).

When performing arm movements with left–right reversed vision, the visually perceived movement of the passive arm might influence its perceptual representation via neurons that are selective for visual feedback from this arm. Given the opposite origins of visual and felt feedback from the arm, reversed vision might activate neurons with visual and motor properties in both hemispheres. As a consequence, the inter-hemispheric lateralization of activity might be reduced. ERLs are a means of assessing these possible changes in the hemispheric asymmetries with high temporal resolution.

The influence of reversed visual feedback from the moving arm on neurons with combined motor and visual properties might not only be evident during the movement. Since multimodal neurons are important for the generation of spatial codes for reaching, their activity in planning the movement might also be modified. This effect might be reflected in a change in inter-hemispheric distribution of activity in parietal and/or premotor areas during the preparation phase of the movement.

In the first experiment of the present study, we compared ERLs during visually triggered pointing movements with normal and left–right reversed visual feedback. We measured ERLs relative to the response side, i.e., the arm used for pointing before and during the movement.

2.1. Methods

The EEG was recorded from 12 (four male) right-handed undergraduate students (average age: 22 years). Participants' vision was normal or corrected to normal.

2.1.1. 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. The starting positions were haptically detectable small ridges on a table at 7.2 cm distance to the screen and with 7 cm distance between the left hand and right hand position. When in the starting positions, participants' forearms and upper arms were aligned in a 90° angle. Lights in the cabin were turned off during the recording, the only source of lighting being the monitor.

The visual field could be left–right reversed by means of a prism device, which consisted of two Dove prisms that were adjustably mounted in a head rest. [1] For each participant the prisms were aligned according to individual eye distance and the prism axes focused the view on the monitor plane. The prisms reduced the visual field both horizontally and vertically. Therefore, we used a shield to restrict the visual field to a similar degree during the normal vision section of the experiment, in which no prisms were used. This was done

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[1] Adjustable mirror imaging binocular (AMIB). Design by Karl Götz.

to allow comparison between the two parts of the experiment. The shield was attached to the head rest and prevented downward vision and the participants from seeing their hands in the starting positions. The shield and the prism device allowed vision around the target space on the screen but prevented vision of the monitor frame. The hand used for pointing came into sight when it approached the screen about midway during a pointing movement.

2.1.2. Stimuli

The targets were filled white circles (1 cm or 1.2° of visual angle) on a black background. A trial started with a fixation cross that was 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 either in the center of the screen or 2 cm (2.4°) to the left or right from the center. The target positions were defined according to their position relative to the response side (irrespective of where the participants saw the target during reversed vision): ipsilateral targets (on the same side as the arm used for pointing), central targets (in the center of the screen), and contralateral targets (opposite the response side). The three target positions were presented in random order.

2.1.3. Procedure

The experiment consisted of four blocks: participants pointed with normal and reversed vision both with their left and right arms in separate blocks. One block consisted of 450 trials (3 positions × 150 repetitions). The order of blocks was counterbalanced and the arm used for pointing was changed in subsequent blocks to avoid tiring of the arms.

Participants were instructed to keep both hands in the starting positions before and after each pointing movement. Once the target appeared, participants were to point as quickly and accurately as possible 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 had to be completed, i.e., the hand had to be back in the starting position when the target disappeared.

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 of the EEG and to exclude invalid trials.

2.1.4. Recording

The EEG was recorded with Ag/AgCl electrodes from 53 scalp positions: FP1/2, Fz, F3/4, F7/8, FCz, FC1/2, FC3/4, FC5/6, FT9/10, T7/8, Cz, C1/2, C3/4, C5/6, TP9/10, CPz, CP1/2, CP3/4, CP5/6, Pz, P1/2, P3/4, P5/6, P7/8, POz, PO1/2, PO3/4, PO7/8, Oz, O1/2. An electrode on 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 three seconds, starting 190 ms before the fixation cross. The PC that presented the stimuli triggered the ZEBRIS and EEG recordings simultaneously.

2.1.5. Data processing and analysis

The response time was defined as the moment when the index finger had moved 20 mm away from the starting position. Valid trials were these in which the minimum response time was 100 ms after target onset and in which the participants first touched the screen either at the target location or less than 20 mm below the target, independent of horizontal deviance. 1.8% of the trials with normal vision and 6.3% of the trials with reversed vision did not meet these criteria and were rejected. ANOVAs with factors visual feedback condition (levels ‘normal’ and ‘reversed’) and target position (levels ‘ipsilateral’, ‘central’, and ‘contralateral’) were computed for response times, movement time (time from start of movement until the finger touched the screen), and accuracy (measured as the absolute horizontal deviation from the target).

Trials in which the EEG contained 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.

ERLs: to assess event-related hemispheric EEG asymmetries, difference potentials were calculated for 21 electrode pairs—activity at an electrode site ipsilateral to the moving arm was subtracted from the activity at the corresponding contralateral electrode. If participants pointed with their right arm, activity at 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. The resulting response-coded difference potentials reflected lateralizations of activity relative to the arm that was used for pointing, irrespective of left or right arm movements. Negative difference potentials reflected relatively higher negativity contralateral to the response side. Positive difference potentials were obtained, if the EEG was more negative ipsilateral to the response side. Difference potentials were averaged time locked to the onset of the target (stimulus-locked) and time locked to the start of the pointing movement (response-locked).

In a preceding study (Berndt et al., 2002), we identified ERL components that reflected the spatial codes underlying visually triggered pointing. Parietal activity was lateralized with respect to the target position: following target detection and preceding the start of the movement, parietal negativity was increased ipsilateral to a lateral target. This ‘posterior intermediate ERL’ reflected preparatory activity and was evident at around 350 ms after target onset. During the movement, however, posterior negativity was increased contralateral to the target (‘movement ERL’). Frontal activity was lateralized with respect to the arm used for pointing: an ERL over premotor areas was evident at around 350 ms after target onset. This ‘anterior intermediate ERL’ that coincided with the posterior intermediate component reflected increased preparatory negativity contralateral to the response side.

These ERLs (posterior intermediate, anterior intermediate, and movement ERL) were analyzed in the present experiments. Their context-dependence in the preceding experiment (i.e. sensitivity to pointing direction predictability) suggests that these ERLs are a suitable means to assess the effect of the visuomotor distortion on the processing of the spatial codes for pointing. Additionally, we analyzed the LRP to assess effects of the visuomotor distortion on motor preparation.

The ERLs were measured in the response-coded data. Mean amplitudes of the components were measured in time intervals around the maximal amplitudes derived from the overall means. ERLs were analyzed in seven areas of interest. Of the 21 recorded electrode pairs, 15 pairs were combined in groups: frontal (pooled across F3/4, FC1/2, and FC3/4), centro-temporal (C3/4 and C5/6), central (exclusively electrodes C1/2over motor cortex), centro-parietal (CP3/4 and CP5/6) parietal (P1/2, P3/4, and PO3/4), temporo-parietal (P5/6, P7/8, and PO7/8), and occipital (O1/2, closest to primary visual areas). To analyze the ERLs, ANOVAs were computed with factors visual feedback condition (levels ‘normal’ and ‘reversed’), target position (levels ‘ipsilateral’, ‘central’, and ‘contralateral’), and site (7 levels = electrode groups listed above). If an interaction between factor site and any other factor was significant, further ANOVAs were performed for each electrode group separately.

All ANOVAs were repeated measures ANOVAs. F-statistics of the ANOVAs were corrected by Greenhouse Geisser Epsilon (Greenhouse and Geisser, 1959) where necessary.

2.2. Results

When pointing with left–right reversed vision, a target on the left side of the screen was visually perceived as a right-sided target and vice versa. Here, the target position will be referred to as the visually perceived target position unless otherwise stated.

2.2.1. Response data

Response data reflected the increased difficulty of pointing with reversed vision. Response times were slower with reversed vision (506 ms) compared to normal vision (412 ms; $F(1, 11) = 24.17$, $P < 0.001$). Response times also depended on the visually perceived target position and were fastest when pointing to ipsilateral targets and slowest with contralateral targets (averaged across conditions: ipsilateral: 454 ms, central: 457 ms, contralateral: 466 ms). However, the effect of target position was only marginally significant after G.-G. correction ($F(2, 22) = 3.76$, $P > 0.050$).

Pointing accuracy, measured as the absolute horizontal distance to the physical position of the target, was poorer with reversed vision (20.7 mm) compared to normal vision (5.4 mm, $F(1, 11) = 48.51$, $P < 0.001$). Furthermore, accuracy varied with the physical position of the target. Errors were largest when pointing to an ipsilateral target and smallest with contralateral targets (averaged across visual feedback conditions: ipsilateral: 14.7 mm, central: 13.1 mm, contralateral: 11.3 mm, $F(2, 22) = 14.71$, $P < 0.001$). An interaction of factors position and visual feedback condition ($F(2, 22) = 5.01$, $P < 0.05$) indicated that the difference in pointing errors between the target positions was greater with reversed compared to normal vision.

The movement time (from start to the time when participants touched the screen) was longer with reversed vision than with normal vision (normal: 506 ms, reversed: 601 ms, $F(1, 11) = 13.03$, $P < 0.01$). Movement time also varied with the physical target position reflecting the difference in pointing distance. It was longest when pointing to a contralateral target and shortest with ipsilateral targets (averaged across visual feedback conditions: ipsilateral: 546 ms, central: 552 ms, contralateral: 562 ms, $F(2, 22) = 5.52$, $P < 0.05$).

No other effects reached significance ($P > 0.5$).

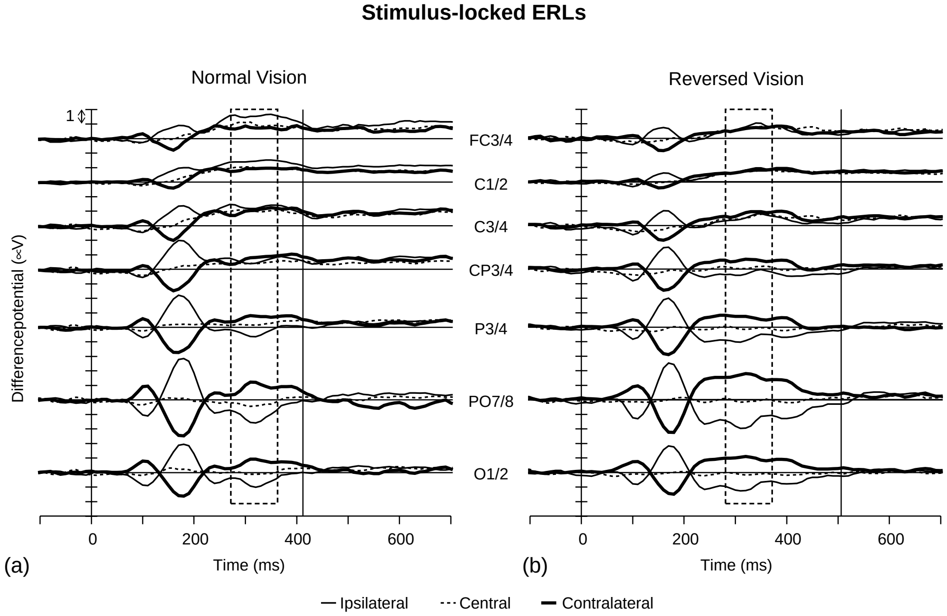

Fig. 2. ERLs in Experiment 1; stimulus-locked ERLs. (a) Normal vision, (b) reversed vision. Electrode sites are exemplary for the frontal to occipital electrode groups. The interval in which the intermediate ERL was analyzed is marked by a dashed rectangle. Lateralizations are plotted relative to the response side, i.e., the arm used for pointing (upwards: increased negativity contralateral to response side, downwards: increased negativity ipsilateral to response side). Thin lines: target perceived on response side (ipsilateral targets), broken lines: central targets, bold lines: targets perceived opposite to the response side (contralateral targets). Zero on the time scale is the onset of the target on the screen. The average response time is indicated by vertical lines. The anterior intermediate ERL contralateral to the response side is reduced with reversed vision, whereas the posterior intermediate ERL is increased with reversed vision. Note that the posterior ERL changes polarity with target position since it resembles increased negativity ipsilateral to the target.

2.2.2. ERL data

In both experiments described here, lateralized components are visible in the P1 and N1 range (between 75 and 240 ms after target onset) in the stimulus-locked data. We found no significant effects of the discussed factors on these components. Therefore, they will not be discussed further.

ERL components were either lateralized with respect to the arm used for pointing or with respect to the target. Therefore, we grouped the ERLs into arm-oriented (anterior intermediate ERL, movement ERL, and LRP) and target-oriented (posterior intermediate ERL). With the exception of the LRP, which was not affected by the distortion, arm-oriented ERLs decreased with reversed vision, whereas the target-oriented ERL increased.

2.2.2.1. Arm-oriented ERLs. Fig. 2 illustrates the stimulus-locked and Fig. 3 the response-locked ERLs relative to the arm used for pointing. Anterior intermediate ERL: over frontal

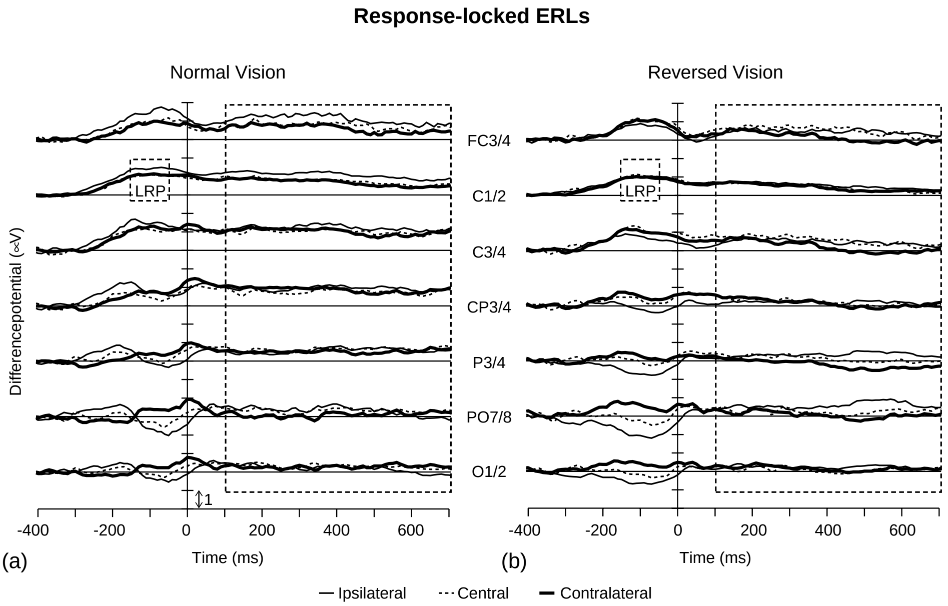
Response-locked ERLs

Fig. 3. ERLs in Experiment 1; response-locked ERLs. (a) Normal vision, (b) reversed vision: zero on the time scale is onset of the movement. The LRP and movement ERL are marked by dashed rectangles. The LRP does not change significantly between normal and reversed vision. During the movement, arm-related lateralization (negativity contralateral to the arm used for pointing) decreased with reversed vision.

($F(1, 11) = 16.41$, $P < 0.01$) and central sites ($F(1, 11) = 19.13$, $P < 0.001$), starting at around 240 ms after target onset negativity was increased contralateral to the arm used for pointing (see Fig. 2, rows FC3/4 and C1/2 in rectangle). This ERL was measured between 280 and 370 ms after target onset. It was reduced with reversed vision compared to normal vision ($F(1, 11) = 7.66$, $P < 0.05$ at frontal and $F(1, 11) = 5.33$, $P < 0.05$ at central sites; see also the topography maps in Fig. 4). Over centro-temporal and centro-parietal sites activity was still more arm-oriented with normal vision than with reversed vision (see Fig. 2, exemplary electrodes C3/4 and CP3/4; centro-temporal: $F(1, 11) = 5.36$, $P < 0.05$, centro-parietal: $F(1, 11) = 6.17$, $P < 0.05$). However, the overall mean did not differ significantly from zero at these sites (centro-temporal: $F(1, 11) = 4.32$, $P > 0.05$, centro-parietal: $F(1, 11) = 0.87$, $P > 0.05$). The effect of reversed vision at frontal to centro-parietal sites was evident in the condition by site interaction in the ANOVA ($F(6, 66) = 3.1$, $P < 0.05$). Factor site also resulted in a significant main effect($F(6, 66) = 15.48$, $P < 0.001$).

Movement ERL: During the movement, negativity was increased contralateral to the active arm (see Fig. 3 in rectangle; ($F(1, 11) = 5.87$, $P < 0.05$). Mean amplitudes varied with factor site ($F(6, 66) = 2.97$, $P < 0.05$). The ERL reached significance over central ($F(1, 11) = 5.19$, $P < 0.05$), centro-temporal ($F(1, 11) = 7.02$, $P < 0.05$), centro-parietal ($F(1, 11) = 7.11$, $P < 0.05$), and temporo-parietal sites ($F(1, 11) = 7.99$, $P < 0.05$). This ERL, measured from 100 to 700 ms after the start of the movement in the response-locked

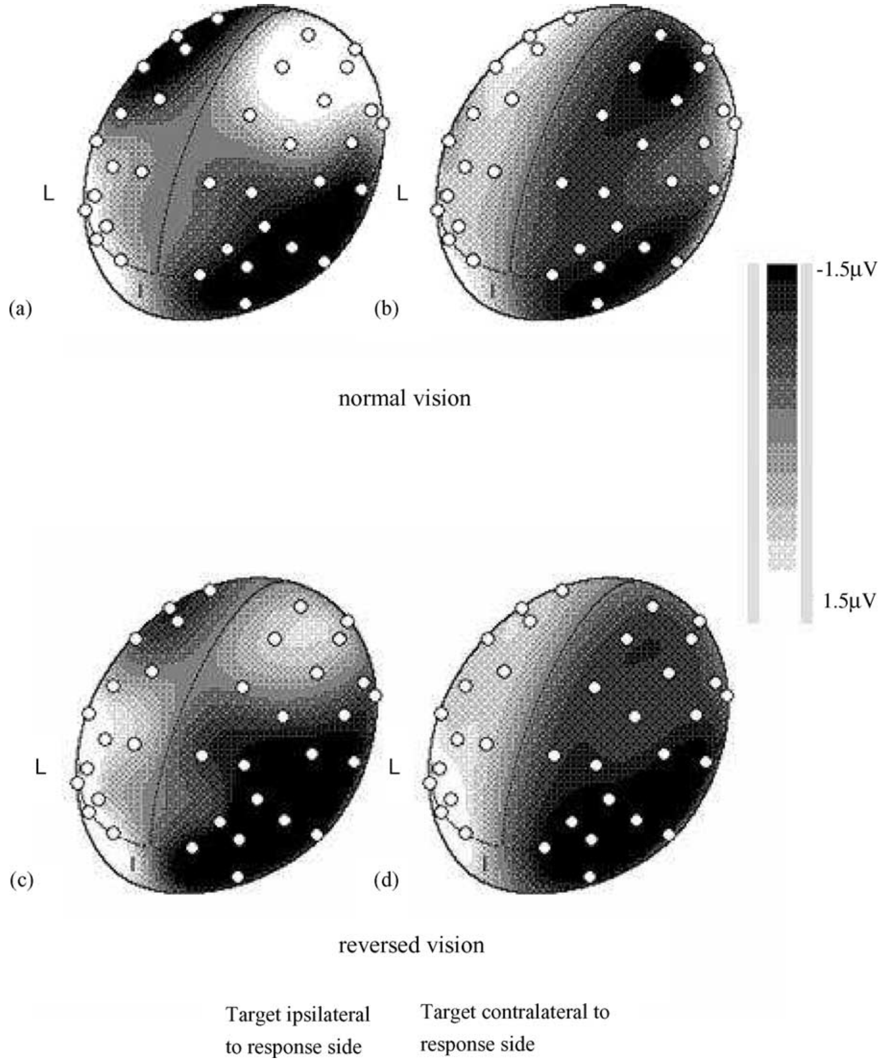

Fig. 4. Voltage maps of the intermediate ERLs at 300 ms after target onset in Experiment 1. The right hemisphere shows the hemisphere ipsilateral to the target. (a and c) Target ipsilalateral to the response side and (b and d) target contralateral to the response side. The images of the left hemisphere are the mirror images of the right hemisphere. (To obtain a correct calculation of scalp topographies of EEG difference waves, the hemispheres are assumed to be mirror-symmetric, i.e. negativity above the contralateral hemisphere has to be equated with positivity above the ipsilateral hemisphere. Therefore, also the voltage maps appear to be mirror-symmetric in the plot.) Note that the anterior and posterior intermediate ERLs can be seen on opposite hemispheres when the target was perceived on the response side (ipsilateral targets) and and on the same hemisphere with targets opposite the response side (contralateral targets), since the anterior ERL is response-oriented. Note the increase in posterior and decrease in anterior lateralization with reversed vision.

data, decreased when participants pointed with reversed visual feedback ($F(1, 11) = 7.15$, $P < 0.05$).

The LRP (see Fig. 3) was measured at central sites, closest to hand motor areas, between 150 and 50 ms before the start of the movement in the response-locked data. Neither condition ($F(1, 11) = 2.34$, $P > 0.05$) nor position ($F(2, 22) = 0.76$, $P < 0.05$) had an effect on the LRP.

2.2.2.2. Target-oriented ERL. Posterior intermediate ERL: At posterior sites, starting around 240 ms after target onset and lasting to the onset of the movement, activity was lateralized with respect to the target (see Fig. 2, rows PO7/8 and O1/2 in rectangle). Like the anterior intermediate component, this posterior ERL was measured between 280 and 370 ms after target onset. It reflected increased negativity ipsilateral to the visually perceived target position (see also the topography maps in Fig. 4). The fact that only the posterior ERL depended on the target position was evident in the interaction of factors position and site ($F(12, 132) = 14.12$, $P < 0.001$). Factor position resulted in a significant effect at temporo-parietal ($F(2, 22) = 8.50$, $P < 0.05$) and occipital ($F(2, 22) = 6.75$, $P < 0.05$) sites. The ERL was increased with reversed vision compared to normal vision. This was reflected in the ANOVA as a condition by position interaction ($F(2, 22) = 4.68$, $P < 0.05$). Temporally, the posterior intermediate ERL was limited by the onset of the movement. It lasted longer with reversed compared to normal vision, reflecting the delayed response times when vision was reversed.

Other effects did not reach significance ($P > 0.05$).

2.3. Discussion

With reversed vision, responses were less accurate and slower than with normal vision. Thus, the visual to motor transformation process seemed to be less efficient when vision was reversed. The delayed responses with reversed vision seem to reflect most directly the additional computational effort required in the generation of the spatial codes for pointing under these conditions.

With reversed vision, the EEG showed a decrease in arm-related lateralization, whereas lateralization related to the target increased.

ERLs contralateral to the active arm during the movement were reduced. This reduction might be attributable to the inconsistency of visual and somatomotor feedback, which might have resulted in simultaneous activity of left arm and right arm specific multimodal neurons in the contralateral hemisphere respectively. According to this interpretation, the neurons that code the representation of the active arm were activated by the somatomotor feedback, whereas the neurons that code the representation of the opposite arm were stimulated by the visual observation of the moving arm.

The decrease in lateralization over premotor and motor areas in the anterior intermediate ERL suggests that sensorimotor processing in the preparation phase of the movements was modified by the perceptual inconsistency during the execution of the pointing movements. The representation of both arms seemed to be activated when planning the movement. Motor preparation as such was not affected, since the LRP did not change significantly between normal and reversed vision.

These results suggest that the reversal of vision changed the hemispheric distribution of activity of neurons with combined visual and motor properties that code the representation of the arms.

In contrast, movement-preceding ERLs in the parietal cortex ipsilateral to the visually perceived target were increased with reversed vision. The parietal cortex is critically involved in the generation of spatial codes for reaching and in transforming the location of the visual target into motor coordinates (Kertzman et al., 1997; Lacquaniti and Caminiti, 1998). The present findings indicate that visual to motor transformation in parietal cortex required additional time and resources when vision was reversed. It has been suggested that the superior parietal lobule (SPL) in primates is the source of spatial information used by premotor cortex for visually triggered reaching movements (Caminiti et al., 1996; Marconi et al., 2001; Johnson et al., 1996). The delayed parietal generation of spatial codes for pointing with reversed vision probably accounted for the delayed reaction times in the present experiment.

3. Experiment 2

A lateral displacement of the visual field is another way to distort visuomotor transformation processes in the brain. Imaging studies have shown that the parietal cortex is selectively active in the recalibration of visual to motor mapping with visual distortions like a lateral displacement or rotation of the visual field (Clower et al., 1996; Inoue et al., 1997). Clower et al. identified a parietal area contralateral to the response side that was involved in the adaptation to a lateral displacement, whereas the hemisphere ipsilateral to the response side was involved in adaptation to a rotation of visual feedback in the Inoue et al. study. However, in both cases the adaptation specific activity was lateralized with respect to the active arm. Thus, ERLs in parietal cortex might also be sensitive to a change in the inter-hemispheric distribution of activity when adapting to a lateral displacement.

In the following experiment, we used a lateral displacement of the visual field to distort visuomotor behavior. In one condition, participants pointed with reversed vision and the pointing direction was repeated within a series of five trials. This was compared to the other condition in which a lateral displacement was added to the reversed visual field. Participants were able to adapt to the displacement within a series of five trials, after which the direction of the displacement was changed. We hypothesized that the additional displacement would enhance adaptation specific activation in posterior parietal cortex reflected in an increase of parietal ERLs relative to the arm use for pointing.

3.1. Methods

The EEG was recorded from 10 (five male) right-handed undergraduate students (average age: 23 years) with normal or corrected to normal vision.

3.1.1. Apparatus

In both parts of Experiment 2, participants' vision was left–right reversed by the prisms, as described in Experiment 1. A lateral displacement to the left or right could be added to the reversed visual field by computer triggered rotation of the prisms.

The experiment consisted of four blocks: participants pointed with their left and right arms, both in the displacement and in the no-displacement condition. The arms were changed in subsequent blocks and the order of blocks was counterbalanced.

3.1.2. Stimuli and procedure

In the no-displacement condition, the three target positions were the same as in Experiment 1: in the center of the screen and 2 cm (2.4°) to the left or right. The targets were presented at the same position in a series of five trials. The order of the target position in successive series was chosen randomly.

In the displacement condition, the target was always displayed in the center of the screen. However, by rotation of the prisms, the target was displaced so that the target positions perceptually equaled those in the no-displacement condition. The orientation of the prisms stayed unchanged in a series of five trials and the prism orientation in successive series was chosen randomly. The prisms were rotated in between successive series. The sound during prism rotation caused by the step motor that drove the prisms was masked by a tone after each series.

In terms of the required movements, the two conditions differed: Without displacement, pointing to central and lateral targets was required, while in the displacement condition pointing only to the central position was the correct response. In terms of target detection in visual space, the two conditions equaled each other. However, in the displacement condition, pointing to a contralateral or ipsilateral target was only visually perceived as a laterally directed reach. Effectively, all correct reaches were straightforward movements. The position of the target was of no relevance for the direction of the pointing movement.

3.1.3. Data processing and analysis

The criteria for valid trials were the same as in Experiment 1. 5.9% of the trials (6.0% in the no-displacement condition and 5.8% in the displacement condition) were rejected since they did not meet these criteria.

To assess adaptation effects, means were computed for the first two trials (early adaptation) and the last two trials (late adaptation) in a series.

Response data: ANOVAs with factors condition (levels ‘no-displacement’ and ‘displacement’), visually perceived target position (levels ‘ipsilateral’, ‘central’, and ‘contralateral’), and adaptation (levels ‘early’ and ‘late’) were computed for response times, movement time, and accuracy (absolute horizontal deviation from the physical target).

ERL data: ANOVAs were performed with factors condition (levels ‘no-displacement’ and ‘displacement’), visually perceived target position (levels ‘ipsilateral’, ‘central’, and ‘contralateral’), adaptation (levels ‘early’ and ‘late’), and site (levels ‘frontal’, ‘centro-temporal’, ‘central’, ‘centro-parietal’, ‘parietal’, ‘temporo-parietal’, and ‘occipital’).

All ANOVAs were repeated measures ANOVAs. *F*-statistics of the ANOVAs were corrected by Greenhouse Geisser Epsilon where necessary.

3.2. Results

Target positions will be referred to as the visually perceived positions unless otherwise stated.

3.2.1. Response data

Response data showed no effect of the lateral displacement. However, adaptation improved performance.

The response times did not change significantly in the two conditions ($F(1, 9) = 0.93$, $P > 0.05$). Adaptation reduced response times ($F(1, 9) = 34.92$, $P < 0.001$). Response times were 464 ms in the early and 407 ms in the late adaptation phase. Response times varied with the visually perceived target position ($F(2, 18) = 5.73$, $P < 0.05$). On average, responses were fastest when pointing to a central target (central targets: 427 ms, ipsilateral targets: 436 ms, contralateral targets: 442 ms). However, there was also a significant adaptation by target position interaction ($F(2, 18) = 5.17$, $P < 0.05$). This was due to the fact that during early adaptation, responses were fastest to central (452 ms) and slowest to ipsilateral targets (471 ms; contralateral targets: 469 ms), whereas during late adaptation, response times were equally fast to central and ipsilateral targets (402 ms) but slowest to contralateral targets (416 ms; effect of direction in early trials: $F(2, 18) = 5.94$, $P < 0.05$ and in late trials: $F(2, 18) = 4.98$, $P < 0.05$).

Pointing accuracy (absolute horizontal distance to the physical target) did not change significantly with lateral displacement ($F(1, 9) = 0.00$, $P > 0.05$) nor with target position ($F(2, 18) = 0.06$, $P > 0.05$), but errors decreased with adaptation ($F(1, 9) = 9.96$, $P < 0.05$) from 23.2 mm during early to 21.3 mm during late adaptation. Movement time was significantly reduced by adaptation ($F(1, 9) = 24.24$, $P < 0.001$) from 649 ms during early to 616 ms during late adaptation. Movement time did not vary significantly with target position ($F(2, 18) = 0.30$, $P < 0.05$) nor with lateral displacement ($F(1, 9) = 0.47$, $P > 0.05$).

No other effects reached significance ($P > 0.05$).

3.2.2. ERL data

3.2.2.1. Arm-oriented ERLs. Anterior intermediate ERL: Figs. 5–8 illustrate the ERLs in Experiment 2 in the first two trials of a sequence (early adaptation) and the last two trials (late adaptation). Arm-contralateral activity in the anterior intermediate ERL was evident at frontal ($F(1, 9) = 48.73$, $P < 0.001$), central ($F(1, 9) = 31.44$, $P < 0.001$), and centro-temporal ($F(1, 9) = 12.48$, $P < 0.01$) sites (see Figs. 5 and 7, rows FC3/4, C1/2 and C3/4 in rectangles). Adaptation (early versus late) reduced the ERL at frontal ($F(1, 9) = 5.80$, $P < 0.05$), central ($F(1, 9) = 14.93$, $P < 0.01$), and at centro-temporal sites ($F(1, 9) = 22.35$, $P < 0.001$, see also Fig. 10). This anterior effect of adaptation was indicated by the adaptation by site interaction in the ANOVA ($F(6, 54) = 3.67$, $P < 0.05$) and the main effects of factors site ($F(6, 54) = 34.18$, $P < 0.001$) and adaptation ($F(1, 9) = 28.58$, $P < 0.001$).

Movement ERL: The movement ERL (see Fig. 6 and 8, rectangles) did not reach significance in the overall mean ($F(1, 9) = 4.28$, $P > 0.05$). However, lateralization during the movement varied significantly with adaptation ($F(1, 9) = 5.22$, $P < 0.05$) and showed reduced arm-contralateral negativity during late compared to early adaptation. This ERL varied with factor site ($F(6, 54) = 7.88$, $P < 0.001$) and reached significance over motor and sensory sites (central: $F(1, 9) = 10.20$, $P < 0.05$, centro-temporal: $F(1, 9) = 12.22$, $P < 0.01$, centro-parietal: $F(1, 9) = 7.27$, $P < 0.05$). There was no significant main effect of factor condition, i.e., lateral displacement on the ERL ($F(1, 9) = 0.49$, $P >$

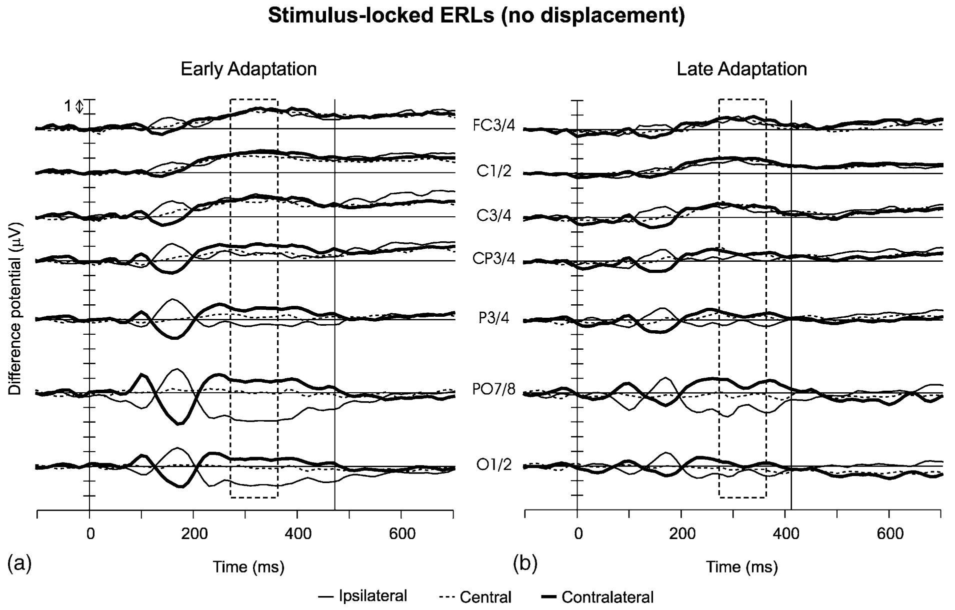

Fig. 5. ERLs in Experiment 2 in the no-displacement condition. Stimulus-locked ERLs. (a) Early adaptation and (b) late adaptation. Electrode sites are exemplary for the frontal to occipital electrode groups. The measurement interval for the intermediate ERL is marked by dashed rectangles. Lateralizations are plotted relative to the response side, i.e., the arm used for pointing (upwards: increased negativity contralateral to response side, downwards: increased negativity ipsilateral to response side). Thin lines: target perceived on response side (ipsilateral targets), broken lines: central targets, bold lines: targets perceived opposite to the response side (contralateral targets). Zero on the time scale is the onset of the target on the screen. The average response times are indicated by vertical lines. The intermediate ERL decreased with adaptation.

0.05). Nevertheless, at parietal sites, a condition by adaptation interaction ($F(1, 9) = 5.22$, $P < 0.05$) indicated that during early adaptation, this ERL increased with the lateral displacement (illustrated in Fig. 9). This effect was, however, not evident in a significant main effect of factor condition when the ANOVA was performed on the early adaptation data only ($F(1, 9) = 2.49$, $P > 0.05$). The adaptation by condition interaction at the parietal electrode group did not result in a significant interaction with factor site in the ANOVA ($F(6, 56) = 1.19$, $P > 0.05$). However, since we hypothesized that parietal cortex was involved in the adaptation, we evaluated the parietal effect without the corresponding interaction with factor site.

The LRP (see Figs. 6 and 8) decreased during adaptation ($F(1, 9) = 6.91$, $P < 0.05$), but was not affected by the lateral displacement ($F(1, 9) = 0.79$, $P > 0.05$).

3.2.2.2. Target-oriented ERL. Posterior intermediate ERL—target-oriented lateralization in the posterior intermediate ERL was evident in the effect of factor position ($F(2, 18) = 4.96$, $P < 0.05$) and its interaction with factor site ($F(12, 108) = 7.0$, $P < 0.05$). Factor position resulted in a significant effect at temporo-parietal ($F(2, 18) = 8.47$, $P < 0.05$) and occipital sites ($F(2, 18) = 5.95$, $P < 0.05$). The posterior ERL was also reduced by

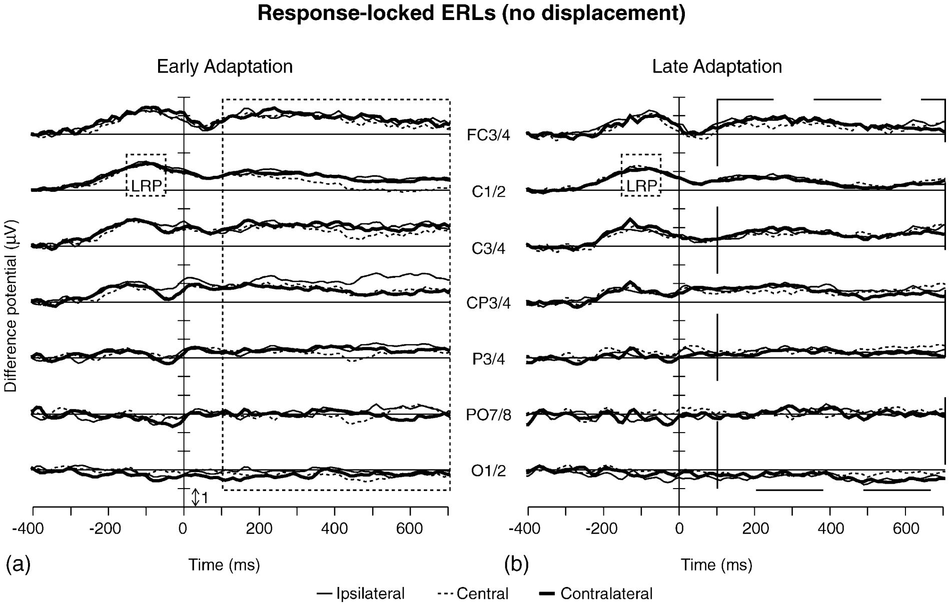

Fig. 6. ERLs in Experiment 2 in the no-displacement condition. Response-locked ERLs. (a) Early adaptation and (b) late adaptation. Electrode sites are exemplary for the frontal to occipital electrode groups. The measurement intervals for the motor ERL as well as for the LRP are marked by dashed rectangles. Lateralizations are plotted relative to the response side (upwards: increased negativity contralateral to response side, downwards: increased negativity ipsilateral to response side). Thin lines: target perceived on response side (ipsilateral targets), broken lines: central targets, bold lines: targets perceived opposite to the response side (contralateral targets). Zero on the time scale is the onset of the movement. The LRP was significantly reduced by adaptation. During the movement, arm-related lateralization decreased with adaptation.

adaptation (see Figs. 5 and 7, rows PO7/8 and O1/2 in rectangles, and Fig. 10). The main effects of factors adaptation ($F(1, 9) = 28.58$, $P < 0.001$) and site ($F(6, 54) = 34.18$, $P < 0.001$) were significant (see also the anterior intermediate ERL). The decrease in target-oriented lateralization with adaptation in the posterior ERL was indicated by the adaptation by position interaction at temporo-parietal ($F(2, 18) = 5.59$, $P < 0.05$) and occipital ($F(2, 18) = 7.89$, $P < 0.01$) sites. The posterior localization of the adaptation by position interaction was evident in the ANOVA in the interaction with factor site ($F(12, 108) = 4.13$, $P < 0.01$). There was no significant effect of the lateral displacement in the posterior intermediate ERL (condition by position interaction: $F(2, 18) = 0.27$, $P < 0.05$).

No other effects reached significance ($P > 0.06$).

3.3. Discussion

Overall, Experiment 2 could not provide strong evidence for increased arm-oriented parietal activity with the lateral displacement. During the movement in the early adaptation period, activity contralateral to the arm in parietal cortex increased when participants pointed with the lateral displacement. However, this effect was only evident in an interaction

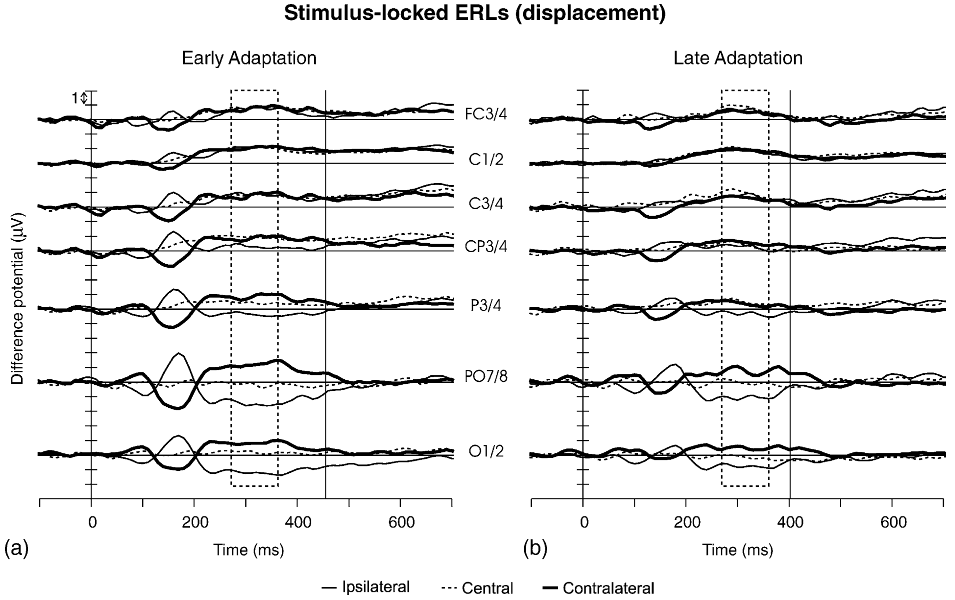

Fig. 7. ERLs in Experiment 2 in the displacement condition. Stimulus-locked ERLs. (a) Early adaptation phase and (b) late adaptation phase. Electrode sites are exemplary for the frontal to occipital electrode groups. The measurement interval for the intermediate ERL is marked by dashed rectangles. Lateralizations are plotted relative to the response side, i.e., the arm used for pointing (upwards: increased negativity contralateral to response side, downwards: increased negativity ipsilateral to response side). Thin lines: target perceived on response side (ipsilateral targets), broken lines: central targets, bold lines: targets perceived opposite to the response side (contralateral targets). Zero on the time scale is the onset of the target on the screen. The average response times are indicated by vertical lines. The intermediate ERL decreased with adaptation.

of factors condition and adaptation. The main effect of factor condition did not reach significance when tested in the early adaptation data. The recalibration of visuomotor control during the movement probably elicited the increased parietal ERL in the early adaptation phase. This effect thus seems to reflect the involvement of parietal cortex in the recalibration of visual to motor mapping with displaced vision.

On the other hand, the displacement had no effect on the ERLs in the movement-preceding phase. Before the onset of the movement, the displacement condition perceptually equaled the no-displacement condition. Participants observed the effect of the displacement only after they started pointing. However, processes that map the target position in visual space on the spatial parameters of the movement had to be suppressed, since the physical target was always displayed in the center of the screen. Thus, the visually perceived target position was irrelevant for the spatial parameters of the reach. Nonetheless, this implication of the displacement was not reflected in a change in the ERLs before the start of the pointing movement.

Although the movement requirements differed in the no-displacement and in the displacement condition, no effect of the displacement was evident in the behavioral data. In the displacement condition, only straightforward movements were required if the target

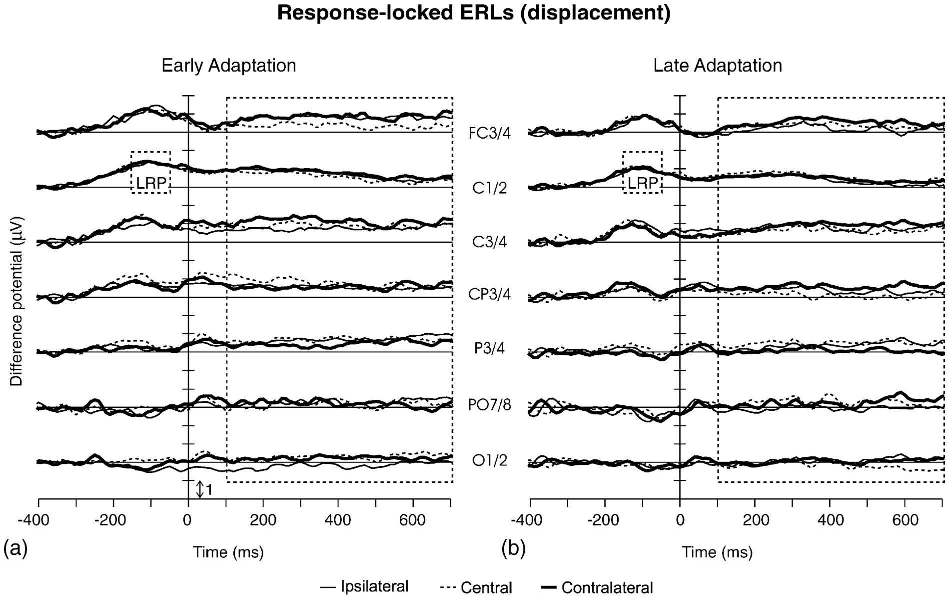

Fig. 8. ERLs in Experiment 2 in the displacement condition. Response-locked ERLs. (a) Early adaptation phase and (b) late adaptation phase. Electrode sites are exemplary for the frontal to occipital electrode groups. The measurement intervals for the movement ERL and the LRP are marked by dashed rectangles. Lateralizations are plotted relative to the response side (upwards: increased negativity contralateral to response side, downwards: increased negativity ipsilateral to response side). Thin lines: target perceived on response side (ipsilateral targets), broken lines: central targets, bold lines: targets perceived opposite to the response side (contralateral targets). Zero on the time scale is the onset of the movement. The LRP was reduced by adaptation. During the movement, arm-related lateralization also decreased with adaptation.

was visually perceived as ipsi- or contralateral. Neither response times, nor accuracy or movement duration were effected by this discrepancy. This suggests that the displacement did not distort visuomotor behavior markedly, which probably also accounts for absence of stronger effects of the displacement on the ERLs.

The degree of displacement was restricted by the field of view through the prisms and by the need to minimize eye movements towards the target. Participants needed to be able to observe pointing errors in both directions from the target, which further restricted the degree of displacement. In the Clower et al. study Clower et al. (1996), which found adaptation-related activity in posterior parietal cortex during pointing with a lateral displacement, the prisms displaced the target by 17° or 7 cm. It might be the case that the lateral displacement used in the present experiment was too small to yield stronger displacement effects.

Effects of adaptation were seen in both behavior and ERLs. Responses became faster and more accurate with repeated pointing direction. Adaptation also resulted in a decrease of arm-oriented as well as target-oriented ERLs. Decreased activation of task-related cortical areas with practice has been found in non-motor and motor learning tasks (Deiber et al., 1997; Poldrack et al., 1998; Kassubek et al., 2001). Deiber et al. found reduced regional cerebral blood flow in task-related frontal and parietal areas during learning of

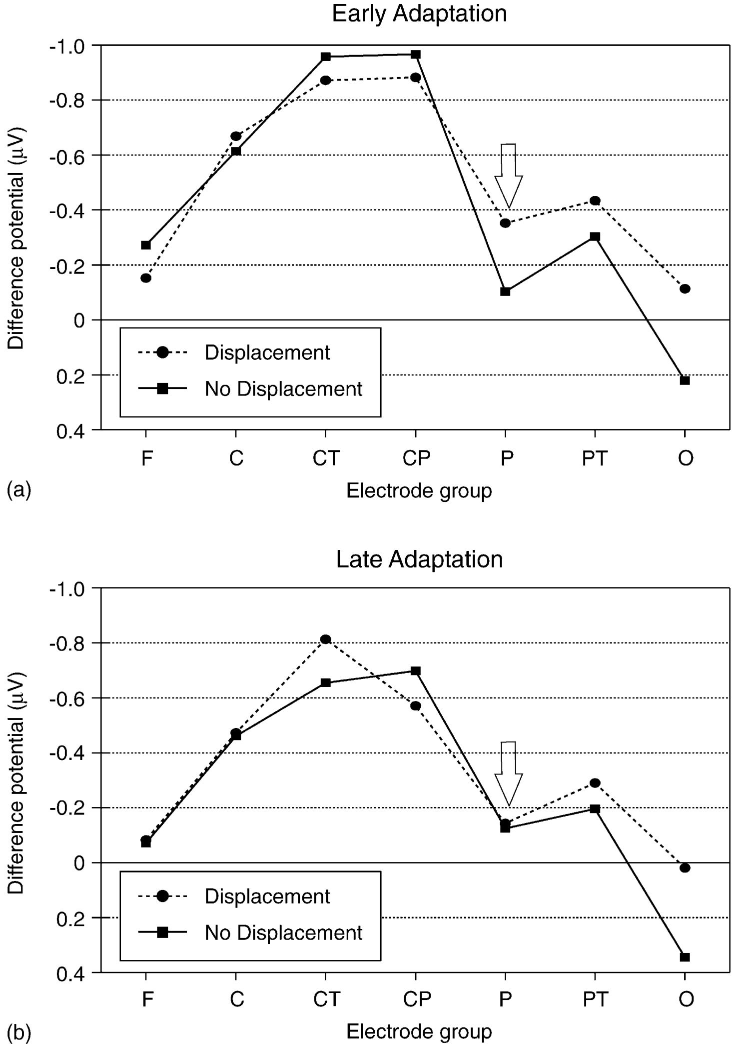

Fig. 9. Movement ERL in Experiment 2. Mean amplitudes at frontal (F), central (C), centro-temporal (CT), centro-parietal (CP), parietal (P), temporo-parietal (PT), and occipital (O) electrode groups. (a) Early and (b) late adaptation phase. Note the relative increase in parietal lateralization (arrow) in the displacement condition compared to the no-displacement condition in the early adaptation period.

stimulus-response mapping tasks. They concluded that a broad frontoparietal network may show decreased activity as stimulus-response mapping rules become more familiar. Similarly, the familiarity of the visual to motor transformation in the present experiment might explain the decrease in ERL amplitudes with adaptation. Moreover, with increased familiarity of visuomotor codes motor preparation might have been more efficient resulting in the decreased LRP amplitude with adaptation (Chiarenza, 1998) and a general improvement in performance.

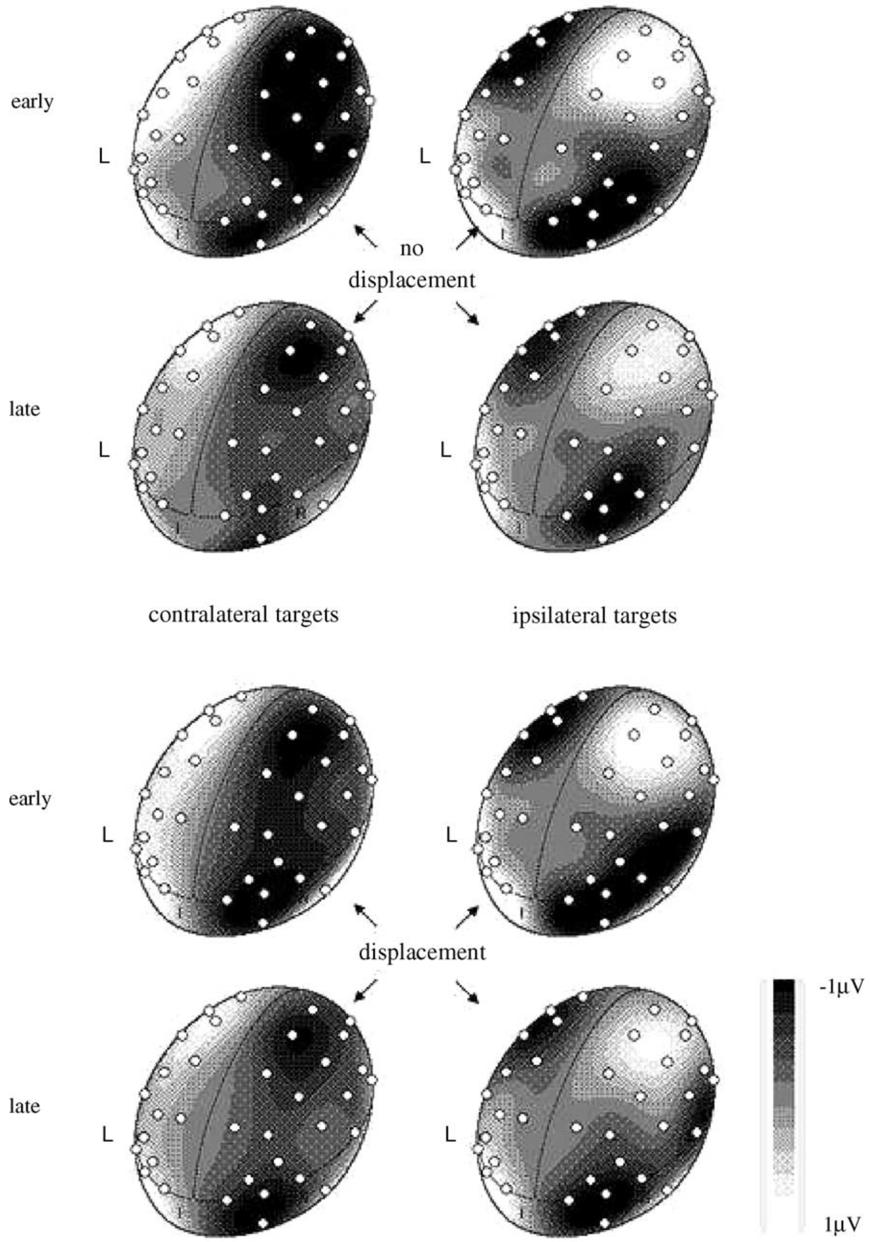

Fig. 10. Voltage maps of the intermediate ERL (at 300 ms after target onset) in Experiment 2. The right hemisphere shows the hemisphere ipsilateral to the target. The left hemisphere is the mirror image of the right hemisphere. Note that the anterior and posterior intermediate ERLs can be seen on opposite hemispheres when the target was perceived on the response side (ipsilateral targets) and and on the same hemisphere with targets opposite the response side (contralateral targets) since the anterior and ERLs is response-oriented. Adaptation (early vs. late) reduced the ERL.

Certainty about the movement parameters reduces the activity of multimodal neurons that code the direction of the response. This has been shown by Battaglia-Mayer et al. (2000) who recorded from neurons in the parietooccipital cortex while the monkey performed different kinds of target directed eye and arm movements. The activity of most of the recorded neurons reflected a combined influence of visual signals, as well as eye and arm position and movement-related signals. Many cells had receptive fields in the contralateral hemispace. The neurons' preferred directions across the different tasks clustered in a limited segment of space, the field of global tuning. Interestingly, they found decreased responses in a delayed reach task (when reaching was performed under directional certainty) compared to a reaction time reach task (when response direction was uncertain). The authors suggested that the properties of the recorded parietal neurons could be a common property of the frontoparietal network underlying reaching.

During the five trials of the adaptation phase in the present experiment, the position of the target was constant. Therefore, participants could be certain as to where the target would appear in the next few trials. This predictability of target position might have decreased the importance of directional encoding upon onset of the target. This might have resulted in reduced responses of multimodal neurons in the frontoparietal network as described in the Battaglia et al. study (Battaglia-Mayer et al., 2000).

4. General discussion and conclusions

This study used the event-related lateralization of EEG activity (ERLs) to study visuomotor processing with conflicting visual and proprioceptive information. We measured ERLs during pointing movements with normal and reversed vision. The reversal of vision modified the inter-hemispheric distribution of reach-related activity and especially reduced arm-oriented lateralizations. The adaptation to an additional displacement of the visual field increased arm-contralateral activity in parietal cortex during the movement.

ERLs were sensitive to the visuomotor discrepancy caused by the reversed visual field. With reversed vision, arm-related lateralization in the frontoparietal network for reaching decreased, whereas lateralization related to the target increased.

We found reduced arm-oriented ERLs with reversed vision before and during the movement. This might be due to the inconsistency of visual feedback and motor activity. We suggest that the reversal of vision resulted in simultaneous activity of left arm and right arm specific neurons. Neurons in the hemisphere contralateral to the observed action were activated by visual feedback from the moving arm. Neurons in the hemisphere contralateral to the response side were activated by the somatomotor feedback.

On the other hand, target-oriented lateralization over parietal areas increased with reversed vision. This finding might be explained by the fact that visual to motor transformation in parietal cortex required additional time and resources due to the reversed spatial codes.

When participants were able to adapt to pointing in a given direction within a series of five trials, ERLs decreased. Additionally, responses were faster as well as more accurate. This might be attributable to the increased familiarity of the visuomotor codes for pointing.

It probably reduced the importance of visual to motor transformation upon target onset, movement preparation, and execution.

The decoupling of visual and proprioceptive information in the displacement condition was reflected in increased lateralization in parietal cortex. During early adaptation, arm-contralateral activity during the movement in parietal cortex increased when participants pointed with lateral displacement. However, the effect was rather small, which might be attributable to the small displacement that was used in the present study. ERLs in the movement-preceding phase showed no significant effects of displacement. Nonetheless, the effect on the parietal ERL during the movement is in agreement with the study of Clower et al. (1996), which showed that adaptation to a displacement of the visual field is reflected in increased parietal involvement during pointing.

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