

Posterior and Anterior Contribution of Hand-Movement Preparation to Late CNV

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Abstract The late part of the Contingent Negative Variation (CNV) is assumed to be a composite potential, reflecting both movement preparation and several other processes. To assess the contribution of hand-motor preparation to overall CNV, three S1–S2 experiments were performed. Replicating earlier results that have been interpreted as demonstrating hand-motor preparation, experiment 1 showed that CNV gets larger centro-parietally under speed instruction. Experiments 2 and 3 compared preparation for hand responses (key-press) to preparation for ocular responses (saccades) varying the effector system either between blocks (exp. 2) or between trials (exp. 3) and also comparing these preparation situations to no preparation (exp. 3). Hand-motor preparation was reflected in CNV getting larger fronto-centrally, with this topography being significantly different from the effect in experiment 1. Thus, two different kinds of motor preparation appear to be reflected by CNV. One kind may consist of assembling and maintaining the stimulus-response links appropriate to the expected S2 patterns, the other is for activating the hand-motor area. These two motor contributions to CNV might reflect the two aspects of the parieto-frontal motor system.

Introduction

The contingent negative variation (CNV, Walter, Cooper, Aldridge, McCallum, & Winter, 1964) is a slow negative EEG shift which develops in the temporal interval between two stimuli. The first stimulus, the “S1” or “cue” is a warning signal and may also provide information about the required response; the second, “imperative stimulus” or “S2” signals to the subject to make (or withhold) a response. The phase of the CNV that immediately precedes S2 is largest at the vertex, similar to the Bereitschaftspotential (BP) that precedes self-paced movements. Therefore, this “late CNV” has been assumed to indicate preparation of the response and to reflect activity of the hand-motor areas (Gaillard, 1977; Rohrbaugh & Gaillard, 1983; Rohrbaugh, Syndulko, & Lindsley, 1976). However, more recent data has supported the view that the late CNV is brought about by a diversity of cortical generators. This suggestion is based both on intracranial recordings (Ikeda et al., 1996; Lamarche, Lou-

vel, Buser, & Rektor, 1995) and on source modeling of scalp-recorded potentials (Böcker, Brunia, & van den Berg-Lenssen, 1994) or of magnetic fields (Elbert, Rockstroh, Hampson, Pantev, & Hoke, 1994; however, see Hultin et al., 1996). This is in contrast to the BP which has well-delimited generators in the primary hand-motor cortex and in the supplementary motor area, shown both by intracranial recordings (Ikeda et al., 1996; Lamarche et al., 1995) and by source modeling of scalp-recorded potentials (e. g., Praamstra, Stegeman, Horstink, & Cools, 1996). Those diverse other sources of the late CNV might reflect several non-motoric functions like anticipation of S2 (Damen & Brunia, 1994; Van Boxtel & Brunia, 1994), working memory activity (Honda et al., 1996; Klein, Rockstroh, Cohen, & Berg, 1996; Ruchkin, Canoune, Johnson, & Ritter, 1995) and effort invested in the task (Van Boxtel, 1994; Wascher, Verleger, Jaśkowski, & Wauschkuhn, 1996). Van Boxtel (1994, p. 66) distinguished between three components of the terminal CNV, overlapping in time: “Movement-Preceding Negativity,” with its maximum at central recording sites

(Cz), “Stimulus-Preceding Negativity,” maximum at parietal sites (Pz), and a frontal component (recorded from Fz) “reflecting a process that controls task performance.” Although certainly helpful in terms of orientation, this classification is not without alternatives. Particularly relevant in the present experiments, parietal CNV-activity as measured, e. g., by Lamarche et al. (1995) from the dorsal posterior parietal cortex need not be necessarily non-motoric, but might well reflect activity of the dorsal pathway from perception to action (Milner & Goodale, 1995; Previc, 1998). This pathway has been further specified in recent conceptions of the organization of the cortical motor system (Rizzolatti, Luppino, & Matelli, 1998), which parcel this system into different modules, each consisting of two main elements, one in the posterior parietal cortex and one in the frontal cortex (including the motor cortex proper).

In the present study, we focused on the issue of motor-related components of the CNV. To this purpose, Gaillard’s (1977) study was replicated in experiment 1. It was this study that led Gaillard to make the influential proposal that “the late CNV could be regarded as that part of the readiness potential which precedes S2 in cued RT-tasks” (Gaillard, 1977; p. 568). That study used a go/no-go task, where participants had to respond to S2, 3 s after S1, whenever S2 was presented (with different probabilities of S2 presentation according to the pitch of S1). In different blocks, participants were instructed either to respond as quickly as possible, or to avoid any erroneous response, or to delay the response by 1 s. CNV was found to be larger under speed instructions than under the two other instructions. Gaillard and Van Beijsterveldt (1991) replicated this CNV difference between speed and delay instructions with a task that differed in several respects from the original study: S2 was visual, not auditory; participants had to choose between two different responses depending on S2; and speed instruction was varied trial-wise, depending on the pitch of S1. Thus, the effect proved to be stable under different experimental conditions.

Of particular interest is the topography of this CNV increase. Gaillard (1977) explicitly argued that this topography agrees with the topography of the Bereitschaftspotential (BP). Yet, both in Gaillard (1977) and in Gaillard and Van Beijsterveldt (1991), the effect on CNV was approximately equal at central (Cz) and parietal (Pz) sites and markedly smaller at frontal sites (Fz). Based on present knowledge obtained from multi-channel recordings, this argues against identification of this part of the CNV with the BP, because the BP is usually markedly larger at central than at parietal sites (e. g., Cui, Huter, Lang, & Deecke, 1999). In terms of Van Boxtel’s (1994) taxonomy, the centro-parietal increase might instead indicate an increased stimulus-related component. Based

on the physiological literature mentioned above (Milner & Goodale, 1995; Rizzolatti et al., 1998), one might, on the other hand, assume that the centro-parietal increase reflects activity of the posterior part of the motor system.

By comparing the CNV before hand movements and saccades (fast eye movements) in experiments 2 and 3, we took a different approach to delineate the hand-movement related component of the CNV. Several cortical areas are known to contribute to saccade behavior (parietal, frontal, and supplementary eye fields, e. g., Heide, Kurzidim, & Kömpf, 1996), and the BP (e. g., Klostermann et al., 1994) and the CNV (e. g., Evdokimidis et al., 1992) recorded before saccades might be interpreted to reflect activity of these areas. However, it is doubtful whether these BPs and CNVs are specific to saccades because the command impulse for saccades is generated in the pons, not in the cortex, and can therefore not be recorded from the scalp. Probably due to this reason, event-related EEG activity specific to saccades has not been unambiguously demonstrated so far (e. g., Van der Lubbe et al., 2000a; Van’t Ent & Apkarian, 1998; Wauschkuhn, Wascher, & Verleger, 1997) or was found to consist in small lateralized activity, visible only when time-locked to saccade onset (Evdokimidis et al., 1992; Wauschkuhn et al., 1998). Therefore, we reasoned (and tested in experiment 3) that the CNV before saccades would consist of an effector-unspecific part above all and as a result could serve as control measure for hand movements where activity of the hand-motor cortex would add to that unspecific part such that a hand-specific topography should become evident by the difference between hand and eye trials. Indeed, the resulting hand-specific topography corresponded much better to the fronto-central distribution of the Bereitschaftspotential than the time-pressure effect of experiment 1.

Re-averaging the data time-locked to the response did not resolve the difference between the topographies of experiments 1 and 2 but rather demonstrated that CNV is a stimulus-locked component. Therefore, it will be outlined in the General Discussion how the different topographies and the stimulus-locked nature of the CNV might fit together to reflect aspects of response preparation.

An S1–S2 interval of 1 s (stimulus-onset to stimulus-onset) was used in these experiments. This may appear rather short with regard to the well-established findings that early CNV and late CNV become well separated with long S1–S2 intervals only (2 s and more; Loveless & Sanford, 1974; Weerts & Lang, 1973). We used this interval because short S1–S2 intervals are more appropriate to human motor preparation (Niemi & Näätänen, 1981). More specifically, in pilot studies with a 3 s S1–S2 interval, participants indicated that with increasing time-on-task they had to spend undue effort on maintaining fixation and alertness during the S1–S2 interval. More-

over, CNV differences between patients with Parkinson's disease and healthy participants, as well as between schizophrenics and healthy participants, have been found to depend on the task, possibly due to different S1–S2 intervals: Group differences in the “clock task,” where the mean S1–S2 interval was 2.4 s, differed from those in the “validity task,” where the S1–S2 interval was 1 s (Verleger et al., 1999a; Wascher et al., 1997) suggesting differential deficits in maintaining alertness (in the long S1–S2 interval task) and in efficient motor preparation (in the short S1–S2 interval task). Converging evidence may be found in Lamarche et al.'s (1995) remark that although sometimes two distinct components of the CNV could be separated in their intracranial recordings with an S1–S2 interval of 3 s, “there were numerous cases where a CNV-like potential was observed with a short foreperiod [1.5 s] and none with a long one” (p. 271). Our use of a shorter S1–S2 interval made it essential to replicate Gaillard's (1977) results which were obtained with an interval of 3 s.

Experiment 1

Method

Participants

Ten medical students, 5 men and 5 women, aged 23–29 years, participated in the experiment. All participants were right-handed, as assessed by the Edinburgh Handedness Inventory, in good physical health, had normal or corrected-to-normal vision by self-report, and had no history of psychiatric or neurological disorders.

Stimuli and Procedure

Participants were seated in a comfortable armchair in a sound-proof, electrically shielded chamber and viewed a 14" Multisync monitor from a distance of approximately 120 cm.

S1 was an arrowhead (1.2×1.2 cm) placed in the center of two concentric circles. The outer circle had a diameter of 6 cm (visual angle = 3°), the inner circle of 3.7 cm (1.8°) and 3 cm (1.5°) in the conditions with and without time pressure, respectively. The arrow pointed to the left or right, indicating the probable (80%) response hand. After 1 s, S2 appeared and at the same time the space between the two circles began filling inwards. The filling speed varied from trial to trial, as described below. In the 80%-go task, S2 was a plus (go, 80%) or minus sign (no-go, 20%). In the 80%-CR task (CR = choice response), S2 was a color change of the S1 arrow from gray to blue. On the 20% “invalidly cued” trials of this task, the arrow additionally changed direction. The sub-

jects' task was to respond with the correct hand before the space was completely filled. The screen was cleared 2 s after S2 onset and a message was presented for 600 ms, informing participants whether their response was correct and fast enough. The next trial started 1.1 s after feedback onset, thus the interval between two S1 onsets was 4.1 s.

Each session was divided into two halves: one with and one without time pressure, with the order alternating between subjects. Within either half, one 80%-go and one 80%-CR block was presented, with the order likewise alternating between participants. Each block consisted of 400 stimuli, 320 (80%) trials with valid information provided by S1 and 80 (20%) trials with invalid information.

Participants were instructed to make their response during the interval when the space between the circles was filling: as soon as filling was finished, the response period was over. To keep time pressure on an individually equal level, the filling speed was changed by an adaptive “staircase” method (e. g., Jaśkowski, Verleger, & Wascher, 1994) in the blocks with time pressure, separately for each type of response (left and right, validly and invalidly cued): after two consecutive correct and fast-enough responses the filling time was reduced, making the task more difficult; after every incorrect or too slow response filling time increased, making the task easier. The steps for decreasing and increasing were 60 ms at the beginning of blocks, to reach threshold rapidly, but were then reduced to 15 ms. Participants were told that filling speed varied randomly during the session. In the condition without time pressure, filling time was held constant at 600 ms. The starting value of the filling time for the condition with time pressure was 450 ms.

Recording and Data Processing

Participants responded with their index fingers by pressing one of two response keys equipped with a mechano-to-electrical converter (force sensing elements dismounted from an electronic scale). The keys did not bend under the exerted force but a short tone was provided by the control computer when the force output exceeded 2 N, informing the participants that their response was registered. EEG was recorded from F3, Fz, F4, T7, C3', C1, Cz, C2, C4', T8, P7, P3, Pz, P4, P8, PO7, PO8, O1, and O2 (positions marked as circles in the topographical maps of Figure 2; C3' and C4' were situated 1 cm anterior to C3 and C4) using Ag/AgCl electrodes (Picker-Schwarzer) affixed at the mastoids as reference (linked by a 5 kOhm resistor) and at the forehead as ground. Vertical electrooculogram (EOG) was recorded from above vs. below the left eye, horizontal EOG from the outer canthi of both eyes. Resistance was less than 5

kOhm for all electrodes. EEG and EOG were amplified between 0.032 Hz and 35 Hz by a Nihon-Kohden 4421.

Triggered by the control computer, the data were stored on another PC and were digitized at 100 Hz for 2100 ms, from 100 ms before S1 to 1000 ms after S2. Offline, trials were excluded when there were zero lines, out-of-scale values, slow drifts larger than 60 μV , or fast shifts larger than 100 $\mu\text{V}/500$ ms. The transmission of vertical and horizontal EOG into the EEG, as ocular artifacts, was estimated separately in areas of maximum EOG variance, and was subtracted from the EEG data. Reliability and validity of such a procedure to remove the ocular artifact from the EEG have been repeatedly demonstrated (e. g., Kenemans, Molenaar, Verbaten, & Slangen, 1991; Verleger, Gasser, & Möcks, 1982). Averages were formed across all artifact-free and correctly responded trials.

Data Analysis

Response parameters. Response times were measured relative to S2, defined as the moment when response force exceeded 2 N. Trials with premature (0.5 N from S1 onset to 100 ms after S2), wrong and too slow responses were excluded from further response-time and EEG analysis, i. e., analysis included the fast-enough and correct responses only. Mean latencies of these responses and frequencies of wrong responses (arc-sin transformed to normalize the distributions) were evaluated statistically by analysis of variance (ANOVA) for repeated measurements. Analysis focused on the fast-enough trials of the valid-cue condition (because there were only few fast-enough responses after invalid cues) with the factors TIME PRESSURE (with, without) and TASK (go/no-go, CR).

EEG parameters. Trials with correct and fast-enough responses were averaged and CNV was measured as mean amplitude 100–0 ms before S2 (i. e., 900–1000 ms after S1) referred to baseline (100–10 ms before S1). The main ANOVA used the same design as for response times, with the factors TIME PRESSURE and TASK. This ANOVA was performed on the Fz, Cz, and Pz recordings separately. For comparing the topographic distribution between conditions, the CNV values from all 19 recording sites were normalized by their vector-sum (Naumann et al., 1992) separately for each subject and condition. One omnibus ANOVA was performed on these values, with the factors TIME PRESSURE, TASK (as above), and TOPOGRAPHY (19 levels). If this ANOVA resulted in interactions of topography with the experimental factors, three further ANOVAs were conducted on restricted sets of recordings to localize the effects. These were: midline (Fz, Cz, Pz), lateral-posterior sites (P7, PO7, O1, P8, PO8, O2), and lateral sites (F3, C3', P3, F4, C4', P4). In the latter two ANOVAs, topography was split into two fac-

tors: ANTERIOR–POSTERIOR and LEFT–RIGHT. Being redundant with the midline analysis, effects of anterior-posterior will not be reported from analyses of the lateral sites. Since TOPOGRAPHY and ANTERIOR–POSTERIOR were repeated-measurement factors with more than two levels, their degrees of freedom were corrected by the Huynh-Feldt ϵ coefficient. To display the topographic distribution of experimental effects on CNV, scalp maps of amplitude differences between conditions were drawn, extrapolating from measured values by spherical splines (Perrin, Pernier, Bertrand, & Echallier, 1989). Each map was individually scaled by displaying the range from its negative maximum to zero.

Results

Behavioral Results

Responses were markedly faster under time pressure ($F(1,9) = 132.6, P < .001$), by 83 ms on the average in the choice-response task (250 ms vs. 333 ms) and by 108 ms in the go/no-go task (257 ms vs. 365 ms). Due to this difference, time pressure interacted with task ($F(1,9) = 6.5, P = .03$). Wrong responses tended to be more frequent under time pressure (3.3% vs. 1.5%, $F(1,9) = 3.3, P = .10$) without difference between tasks.

CNV

As displayed in Figure 1, CNV was larger with time pressure than without, at Cz ($P = .001$), Pz ($P = .001$), and Fz ($P = .04$; see Table 1 for F -values), this effect being somewhat larger in the go/no-go task than in the choice-response task (e. g., at Cz $-4.0 \mu\text{V}$ vs. $-2.1 \mu\text{V}$; TASK \times TIME PRESSURE: $F(1,9) = 5.15, P = .049$).

Topography differed between the conditions with time pressure and without (Table 1, $P = .005$) equally for both tasks (TIME PRESSURE \times TOPOGRAPHY \times TASK: $F(18,162) = 0.3, n.s.$). The detailed topographical analyses showed that midline topography was more posterior with time pressure than without (Table 1, $P = .03$). The topography of the difference between the conditions with and without time pressure is displayed in Figure 2 (left map) and for the midline in Figure 3 (top row).

Discussion

CNV increased under time pressure. This increase was largest at Cz, with a smooth reduction towards Pz and a rather steep reduction towards Fz, such that at midline sites the increase was largest at Cz, second largest at Pz, and smallest at Fz. This appears as a satisfying replication of the centro-parietal effect of time pressure on the

Table 1 F-values and their probabilities. The first three rows are from ANOVAs separately done for Fz, Cz, Pz. The 4th and 5th row are from ANOVAs on vector-normalized amplitudes. In the 4th row, all 19 recording sites were analyzed, in the 5th row the Fz, Cz, and Pz data. This latter analysis was performed only if the omnibus ANOVA yielded a significant interaction of TOPOGRAPHY \times EFFECT OF INTEREST. Degrees of freedom (6th row) have 18 in the numerator for effects involving topography in the omnibus ANOVA, and 2 in the midline ANOVA, else 1. Degrees of freedom >2 in the numerator were corrected by Huynh-Feldt's ϵ coefficient.

	Time Pressure		Hand vs. Eye		50%-go vs. 100%-go		Partial Eye vs. No Inf.		Partial Hand vs. No Inf.		Partial Hand vs. Partial Eye	
	Exp. 1		Exp. 2		Exp. 2		Exp. 3		Exp. 3		Exp. 3	
	F	P	F	P	F	P	F	P	F	P	F	P
Fz	5.5	.04	14.1	.003	14.3	.003	1.3	.29	14.1	.004	7.4	.02
Cz	24.8	.001	13.4	.004	13.9	.003	3.9	.08	22.8	.001	7.7	.02
Pz	23.0	.001	0.3	.57	9.5	.01	0.3	.61	1.6	.23	1.1	.31
Effect \times Topogr., normalized	3.4	.005	5.9	.001	4.9	.001	1.1	.39	2.7	.04	1.1	.32
	$\epsilon = .36$		$\epsilon = .20$		$\epsilon = .15$				$\epsilon = .25$			
Effect \times Topogr., midline	6.0	.03	13.3	.001	3.7	.04	-		1.7	.21	-	
	$\epsilon = .64$		$\epsilon = .75$		$\epsilon = .96$							
df	1/9, 2/18, 18/162		1/11, 2/22, 18/198		1/11, 2/22, 36/396		1/10, 18/180		1/10, 2/20, 18/180		1/10, 18/180	

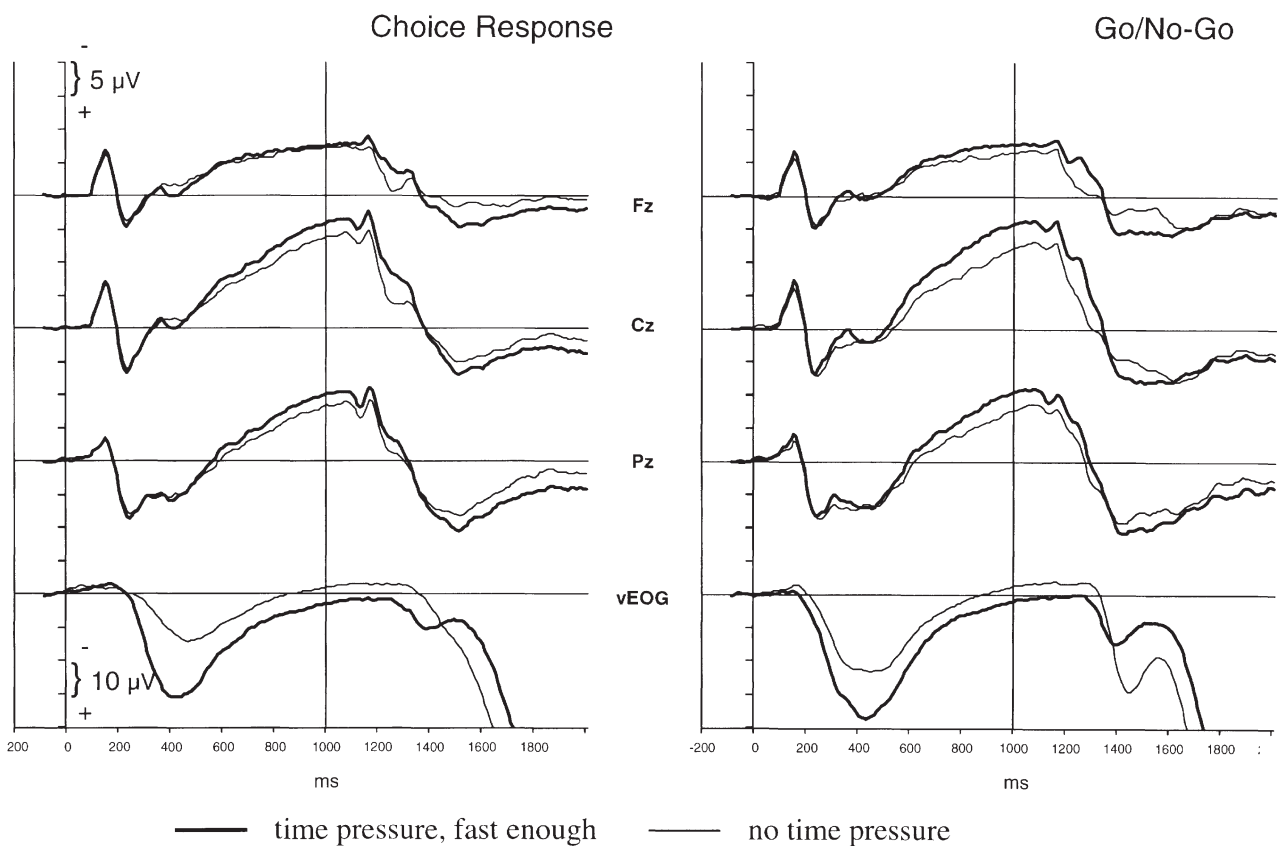


Figure 1 Grand means of midline ERPs (and vEOG for artefact control) from experiment 1. S1 was presented at 0 ms, S2 at 1000 ms.

late CNV reported by Gaillard (1977) and Gaillard and Van Beijsterveldt (1991). Since the largest effect was seen at Cz, the result is also in line with Van Boxtel's (1994) model according to which the movement-related portion of the CNV is largest at Cz. The fact that the effect was also pronounced at parietal sites might suggest, in terms of Van Boxtel's (1994) model, that there is

also more intensive preparation of perceptual processing of S2. However, other psychophysiological literature on time pressure has provided little evidence for the contribution of such non-motoric processes to the speeding of responses (Falkenstein, Hohnsbein, & Hoorman, 1994; Kutas, McCarthy, & Donchin, 1977; Pfefferbaum, Ford, Johnson, Wenegrat, & Kopell, 1983; Van der Lubbe,

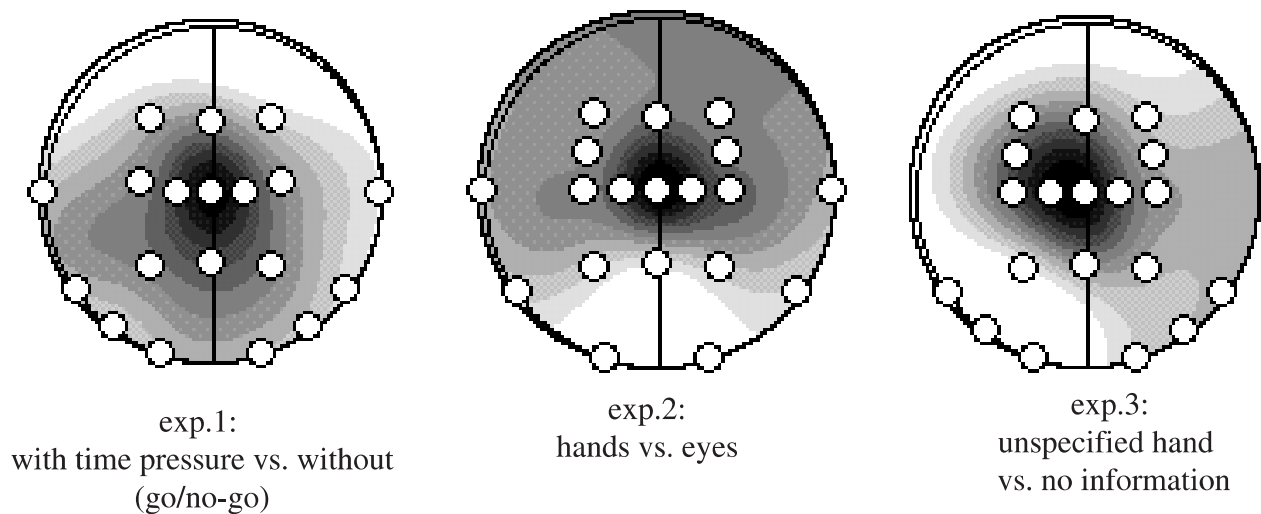


Figure 2 Spline-interpolated distribution of CNV potential differences at the scalp. Depicted are those effects from the three experiments that are assumed to reflect the influence of hand-motor preparation. Each map was individually normalized, by displaying the range from its negative maximum (black) to zero (white). Note the more posterior topography of the leftmost map compared to the two other maps.

Jaśkowski, Wauschkuhn, & Verleger, 2000b). Thus, this additional assumption does not seem probable, and we are left with the motor account for this centro-parietal effect. Lacking evidence to the contrary, one might even assume that motor effects on the CNV always have a centro-parietal signature as the present data and Gailard's studies show. Due to this, the following experiment, where hand movements are compared to eye movements, was chosen to be instructive.

Amplitudes were more increased by time pressure in the go/no-go than in the CR task. A possible reason is that movement preparation might have been more unequivocal in the go/no-go task than in the CR task, because the responding hand was unambiguously defined by S1 in the go/no-go task. However, as this differential effect is not particularly relevant to the present purpose, this matter will not be further pursued here.

Experiment 2

In this experiment, either hand movements (left or right key-press) or eye movements (saccade to the left or right) were required, block-wise separated. As argued in the Introduction, the expected increase of CNV activity in the hand-movement task should provide a pure measure of hand-movement preparation. Any activity common to both effectors should be cancelled out by this comparison, including effector-unspecific motor preparation, preparation to perceive the S2, as well as any pre-S1 and post-S1 activity. To be consistent with the results of experiment 1, at the midline this increase of amplitudes was expected to be largest at Cz, somewhat smaller at Pz, and smallest at Fz. On the other hand, to be consistent with

the topography of the Bereitschaftspotential, this increase of amplitudes was expected to be largest at Cz, somewhat smaller at Fz, and smallest at Pz.

There were three different tasks for hand-movements and eye-movements, block-wise separated. As a result, the stability of the hand-eye difference could be studied across different task requirements, and an estimate could be made about the approximate proportion of hand-movement-related CNV activity relative to the total CNV in different tasks with different total CNV amplitudes.

Method

Participants

Twelve participants were recruited from the same population as in experiment 1. They were seven men and five women, aged 23–31 years. Data of two further participants had to be discarded, one due to technical problems, the other due to failure in following the instructions.

Stimuli and Procedure

The apparatus was the same as in experiment 1. A small white fixation dot was displayed continuously in the center of the screen. In each trial, a cue (S1) and an imperative stimulus (S2) were presented, both for 200 ms, with an onset asynchrony of 1000 ms. S1 consisted of two identical red arrows, left and right of fixation (with their inner edge 0.15° from fixation), 0.9° wide and 0.6° high. Both arrows either pointed to the right or left, in random sequence across trials. Simultaneously with S1, two gray crosses ($0.7^\circ \times 0.7^\circ$) were presented at the left and right

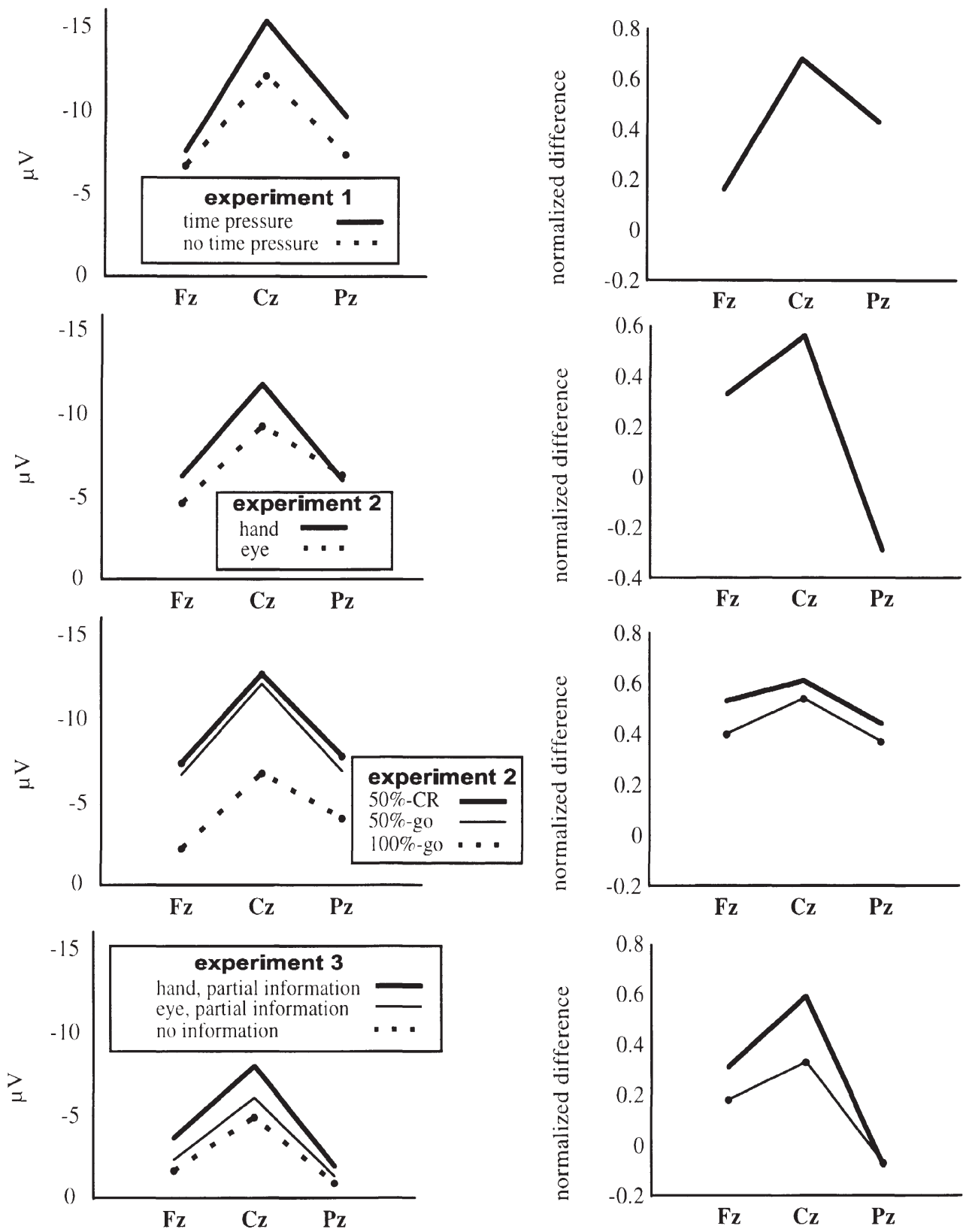


Figure 3 Illustration of relevant topographical effects on midline CNV amplitude. Left column: raw values. Right column: vector-normalized differences of the raw values (where the dotted line was subtracted from the other lines; normalization was done by reference to the vector sum of the Fz, Cz, Pz differences, not of all 19 scalp sites, to stay more closely to the data displayed in the left column). Note the posterior distribution of the time-pressure difference (1st row), the more anterior distribution of the hand-eye difference (2nd and 4th row), and the equal distribution of the task effect (3rd row).

margin of the screen, 5.4° from fixation. These crosses served as gaze targets for saccades but were also displayed in the key-press blocks. S2 was a yellow plus ($0.4^\circ \times 0.4^\circ$) or minus sign (0.4° wide), in random sequence across trials, replacing the fixation dot. The saccade targets were removed 1000 ms after S2 onset. The next S1 was presented 2200 ms after S2 onset.

Responses had to be made after S2 either by pressing the left or right key ("hand" blocks) or by making a leftward or rightward saccade ("eye" blocks). Three tasks were defined for both hands and eyes. In the "100% go" task, participants had to respond left or right according to S1, i. e., S2 had no meaning except for being the "go" signal. In the go/no-go task (50% go), left or right responses according to S1 had to be made only if S2 was a plus. In the "50% choice response" task (50% CR), responses according to S1 had to be made if S2 was a plus, and the alternative response if S2 was a minus.

Each task consisted of 300 trials, with a short break after every 100 trials. Thus, the experiment included 1800 trials, lasting 96 minutes. In 30 practice trials before each task, feedback about correct performance, in particular about the presence or absence of saccades, was provided after each trial. This was possible because response force (the output of the force-sensitive response keys) and horizontal EOG (for saccades) were fed back to the control computer. No feedback tone was produced when the manual response threshold was reached (as done in experiment 1), because there was also no feedback of this kind provided with saccades in the experiment proper.

There are six possible permutations for the order of three tasks, with each of these six orders used in two subjects. Of these two subjects, one started with a hand block in each task, the other with an eye block.

Recording and Data Processing

These methods were the same as in experiment 1, except for the following changes. Recordings were additionally made from FC3 and FC4, leaving out PO7 and PO8 instead (due to hardware constraints). Baseline before S1 was recorded for 200 ms instead of 100 ms. Triggered by the control computer, the EEG-amplifier was reset to baseline after each trial, to avoid contamination of the EEG of the following trial with residual EOG artifacts from the saccade in the eye blocks.

Data Analysis

These methods were the same as in experiment 1, except for the following.

Response parameters. Response times for saccades were defined as the moment when hEOG amplitude exceeded $40 \mu\text{V}$ (approximately corresponding to a 2° saccade, i. e., about 35% of the distance to the target, similar to the 2N keypress criterion which is likewise about 1/3 of usual keypress peak force). In addition to the errors listed with experiment 1, saccades above $40 \mu\text{V}$ before S2 and double responses (saccade plus key-press) after S2 led to exclusion of the trial from further analysis. The main ANOVA analyzed the responses in the direction of the arrow, with the factors EFFECTOR (hand vs. eye) and TASK (100% go / 50% go / 50% CR). Since task was a repeated-measurement factor with more than two levels, its degrees of freedom were corrected by the Huynh-Feldt ϵ coefficient. When effects of task were significant, the effect was further localized by ANOVAs on 100% go vs. 50% go and on 50% go vs. 50% CR.

EEG parameters. The main ANOVA used the same design as for response times. The only change from experiment 1 was due to the slightly changed recording scheme: The topographical sub-ANOVA of lateral sites included FC3 and FC4, while PO7 and PO8 were now missing from the sub-ANOVA on lateral sites.

Results

Behavioral Results

Response times. Response times are compiled in Table 2. There was a main effect of TASK ($F(2,22) = 90.8$, $\epsilon = 1.0$, $P < .001$). *Post-hoc* tests showed that responses were faster in 100% go than in 50% go ($F(1,11) = 74.0$, $P < .001$) and faster in 50% go than in 50% CR ($F(1,11) = 24.6$, $P < .001$).

There was no general difference between hand and eye response times (EFFECTOR: $F(1,11) = 1.5$, n.s.), but the difference between 50% go and 50% CR was larger in hand than in eye blocks (TASK \times EFFECTOR: $F(2,22) = 6.7$, $\epsilon = .94$, $P = .006$; *post-hoc*: TASK \times EFFECTOR for 100% go vs. 50% go: $F(1,11) = 2.3$, n.s.; for 50% go vs. 50% CR: $F(1,11) = 7.0$, $P = .02$) such that eye movements were faster than key-presses when the 50% CR task was considered separately ($F(1,11) = 7.7$, $P = .02$).

Table 2 Means and standard deviations of response times in experiment 2.

	100%-go	50%-go	50%-CR, valid	50%-CR, invalid
Hands (key-press)	241 \pm 31 ms	346 \pm 23 ms	408 \pm 49 ms	438 \pm 48 ms
Eyes (saccades)	247 \pm 47 ms	338 \pm 33 ms	377 \pm 49 ms	394 \pm 53 ms

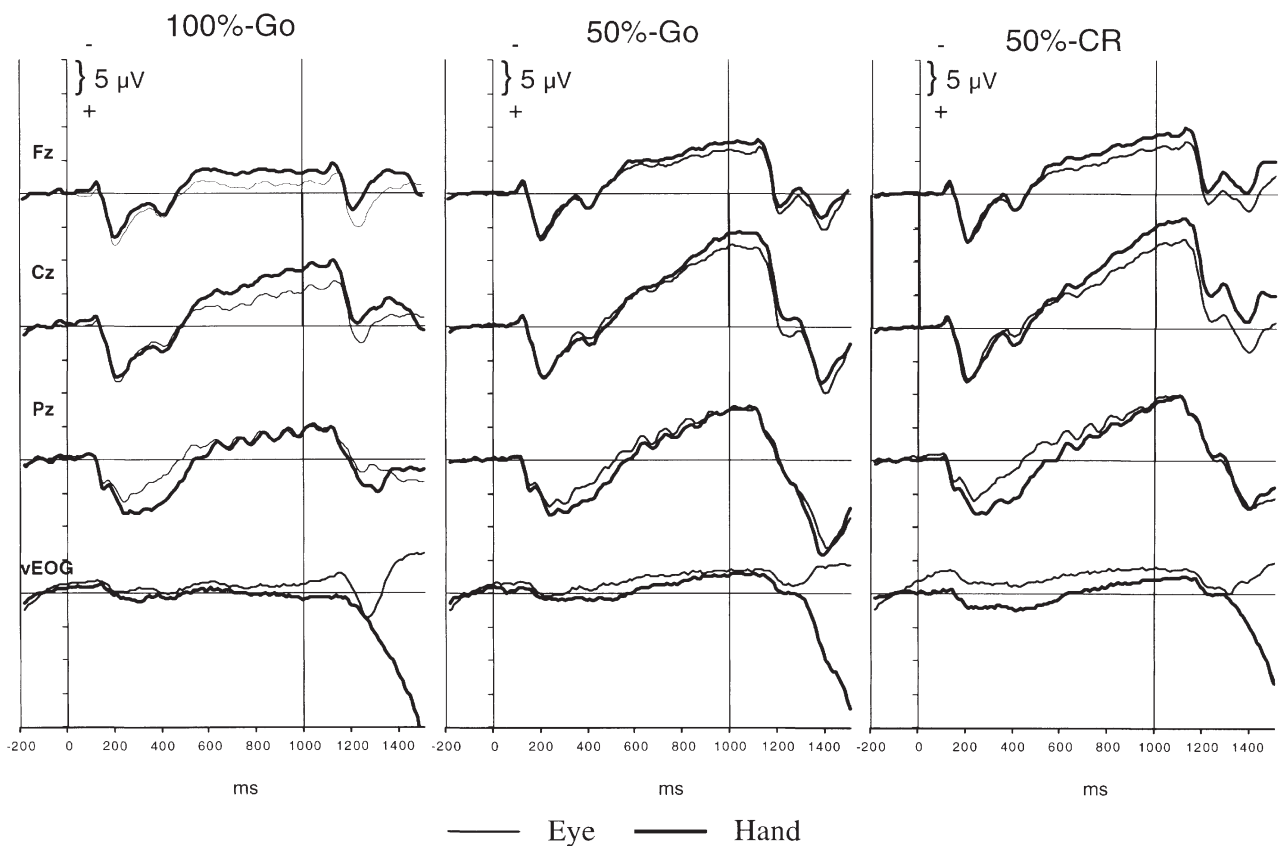


Figure 4 Grand means of midline ERPs (and vEOG for artefact control) from experiment 2. S1 was presented at 0 ms, S2 at 1000 ms.

Errors. Most errors were made in the 50% CR task (TASK: $F(2,22) = 72.3$, $\epsilon = 0.99$, $P < .001$; *post-hoc*: 100% go vs. 50% go: $F(1,11) = 0.1$, n.s.; 50% go vs. 50% CR: $F(1,11) = 88.4$, $P < .001$). A tendency for more errors in hand than in eye blocks was not significant ($F(1,11) = 3.8$, $P = .08$) nor was its interaction with task ($F(1,11) = 0.5$, n.s.).

CNV

Hand vs. eye blocks. As displayed in Figure 4 and compiled in Table 1, CNV was larger in the hand than in the eye blocks at Cz ($P = .004$) and Fz ($P = .003$), but not at Pz ($P = .57$). This effect was equal across all three tasks (TASK \times EFFECTOR for Fz, Cz, Pz: $F(2,22) \leq 0.9$, n.s.).

In line with these effects at the single recording, topography differed between hand and eye blocks ($P = .001$; EFFECTOR \times TOPOGRAPHY in Table 1), because midline topography was more anterior in the hand blocks than in the eye blocks ($P = .001$, Table 1). The topographical difference hand minus eye is displayed in Figure 2 (middle map) and for the midline in Figure 3 (2nd row).

Task effect. CNV differed between tasks at Fz, Cz and Pz, being smallest in the 100%-go task: CNV differed be-

tween 100%-go and 50%-go (at Fz, Cz, Pz: $P = .003$, $P = .003$, $P = .01$; Table 1) and did not differ between 50%-go and 50%-CR (Fz: $F(1,11) = 1.5$, $P = .25$; Cz: $F(1,11) = 0.4$, $P = .55$; Pz: $F(1,11) = 1.9$, $P = .20$).

Topography differed between tasks (TASK \times TOPOGRAPHY in Table 1: $P = .001$) due to the difference between 100%-go and the two other tasks (100%-go vs. 50%-go: $F(18,198) = 5.0$, $\epsilon = .21$, $P = .003$; but 50%-go vs. 50%-CR: $F(18,198) = 1.2$, n.s.). Because there was almost no CNV at Fz in the 100%-go task, midline topography was more posterior in this task ($P = .04$, Table 1). The midline amplitudes are depicted in Figure 3 (3rd row).

To test whether the EFFECTOR effect of this experiment differed in its midline topography from the TIME PRESSURE effect of experiment 1, a between-subjects comparison was made between the two normalized differences, i. e., with-minus-without time pressure from experiment 1 and hand-minus-eye from experiment 2, both pooled across tasks (see Figure 3, right panels of 1st and 2nd row). Indeed, this difference in topography was significant ($F(2,40) = 12.0$, $\epsilon = .83$, $P < .001$) because the TIME PRESSURE effect was more posterior than the EFFECTOR effect.

Also the TASK effect from experiment 2 (pooled over hands and eye, as in Figure 3, 3rd row, right panel) was

compared to these two effects. For this comparison, the two effects displayed in Figure 3 (50%-go minus 100%-go, and 50%-CR minus 100%-go) were averaged. Due to its rather equal midline distribution, the TASK effect differed from the EFFECTOR effect (within subjects ($F(2,22) = 9.6$, $\epsilon = .91$, $P = .002$) and tended to differ from the TIME PRESSURE effect (between subjects, $F(2,40) = 2.2$, $\epsilon = .77$, $P = .14$).

Discussion

The contribution of hand-specific preparation to late CNV was estimated by the difference between hand and eye blocks and was found to be considerable, amounting to about $3 \mu\text{V}$ at Cz. In the 100%-go task, where CNV was smallest, this amount was approximately half of total CNV amplitude. In the two other tasks, where CNV was larger, the contribution of hand-motor preparation remained constant in absolute terms and thus decreased in proportion.

Topography of this hand-motor contribution was restricted to central and frontal sites. This topography differed significantly from topography of the time-pressure effect found in experiment 1, which extended to parietal sites and was small at frontal sites. Yet both effects were assumed to serve as estimates of the topography of hand-motor contribution to CNV. A centro-parietal effect as found in experiment 1 even provided important evidence for the assumption that the late CNV is movement-related (Gaillard, 1977). How can this contradiction be resolved? There are three possibilities:

- 1) The fronto-central effect (experiment 2) is the motor effect, the centro-parietal effect (experiment 1) is not a motor effect but rather reflects stimulus-preceding negativity.

This interpretation of the fronto-central effect would fit the topography of the Bereitschaftspotential, and the interpretation of the centro-parietal effect would support Van Boxtel's (1994) classification of the parietal component of the CNV. However, previous literature does not fit well with this interpretation of the parieto-central effect from experiment 1. We already referred to psychophysiological studies on the effects of time pressure, which provided little evidence for the contribution of non-motoric processes to the speeding of responses under time pressure. Furthermore, the available evidence on stimulus-preceding negativity does not unambiguously favor this interpretation. Such negativities were found to be much larger before stimuli that provide feedback than before stimuli that give information on how to respond (Damen & Brunia, 1994; see also Kotani & Aihara, 1999), and

were therefore tentatively related to the emotional value of feedback stimuli (Chwilla & Brunia, 1991, 1992). In the present experiments, S2 did not provide feedback but rather instructed participants to respond. Being more similar to an instruction stimulus than to a feedback stimulus, this S2 cannot be expected to be preceded by stimulus-related negativities.

- 2) Both the fronto-central (experiment 2) and the centro-parietal (experiment 1) effect reflect aspects of motor preparation.

This interpretation would refer to the findings made in monkeys that the cortical motor system is made up of modules, each consisting of two main elements, one in the posterior parietal cortex and one in the frontal cortex (Rizzolatti et al., 1998). Apart from the studies on time pressure, there is little evidence from CNV studies in favor of such a proposal, but there is also hardly any evidence against it. Thus, if true, this suggestion would be the original contribution made by the present study.

- 3) The centro-parietal effect does represent the motor effect on the CNV, while the fronto-central effect of experiment 2 is due to some irregularity of the pre-saccadic CNV.

This is to say that, it might be possible that the hand-eye comparison is biased by some saccade-specific potential, contrary to the assumptions made in the Introduction. If this hypothetical potential was relatively large at Pz, any hand-specific activity at parietal sites would be canceled in the hand-eye difference and would thus be made artificially invisible. Whether the assumption of "motor-neutrality" is justified for the saccade blocks, which served as reference for the hand blocks, will be further investigated in experiment 3, after the following response-locked analysis of experiments 1 and 2.

Response-Locked Analysis

One referee of this paper suggested that more insight into the nature of these CNV components might be gained by analyzing the potentials time-locked to the response. We will turn to this analysis now to see whether it helps to decide among the three alternatives.

Method

Artifact-edited and correctly responded trials of experiments 1 and 2 were averaged anew, time-locked to response onset. The pre-S1 baseline was subtracted from the data in each trial, and data were averaged from

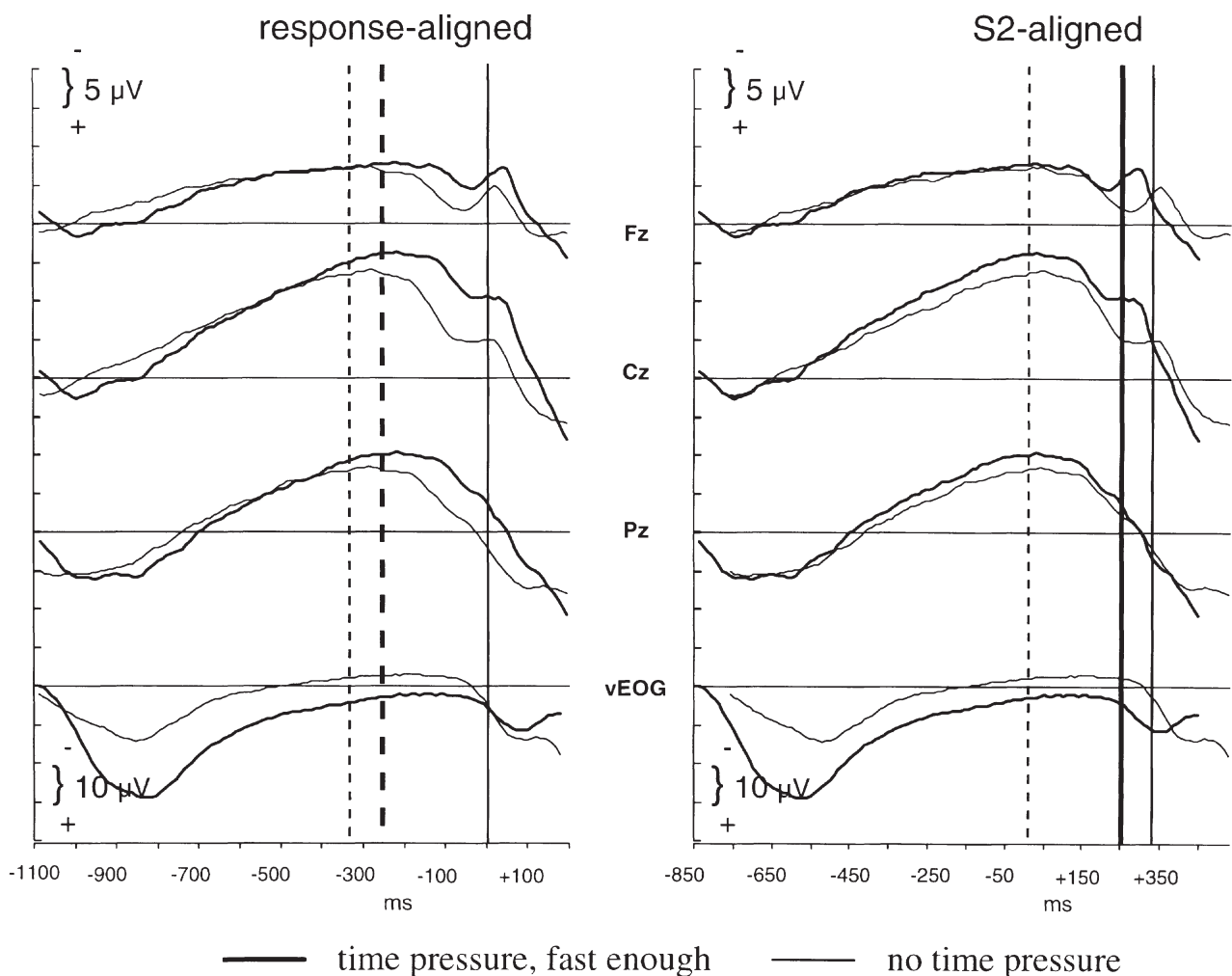


Figure 5 Grand means of midline ERPs (and vEOG for artefact control) of the choice-response task from experiment 1. Different from Figure 1, trials were averaged time-locked to response onset, from 1100 ms before to 200 ms after response. *Left panel:* Data from the two conditions are graphically aligned at response onset (thin solid line). Mean time points of S2 onset are shown as dashed lines, bold for time-pressure, thin for without time pressure. *Right panel:* Data are graphically aligned at mean time point of S2 onset (thin dashed line), by shifting the without-time-pressure data of the left panel by 80 ms rightwards. Solid lines denote response onset, bold for time-pressure, thin for without time pressure.

1100 ms before until 200 ms after response onset. This analysis could, of course, not be made for the no-go trials (in the go/no-go tasks of experiments 1 and 2) as there was no response time in these trials. The time point of response was defined as detailed above: 2 N for the key-press responses, 40 μ V for saccades.

Results

Grand means of the choice-response condition of experiment 1 are displayed on the left-hand side of Figure 5. The solid vertical line marks time of response onset, the two dashed lines mark the average times of S2 onset (which were necessarily spread in time, due to response-locked averaging), with the bold line for the condition with time pressure, the thin line for the condition without time pressure.

At first sight, the general waveshape of these potentials might suggest that response-locked averaging is not appropriate: Evidently, negativity does not rise until response onset but decreases some time before, most probably in response to S2 onset, even crossing baseline at Pz at the time of responding. The only consistent response-related component appears to be the negative peak shortly after response onset (possibly related to somatosensory reafference reflecting the perception of the moving finger, Bötzel, Ecker, & Schulze, 1997).

However, it is of interest that potentials are consistently more negative under time pressure than without, approximately from stimulus onset onwards, not only at Cz and Pz, as in the stimulus-locked averages before S2 (Figure 1), but also at Fz. One might assume that here is some fronto-central contribution to the time-pressure effect, which only becomes apparent through response-

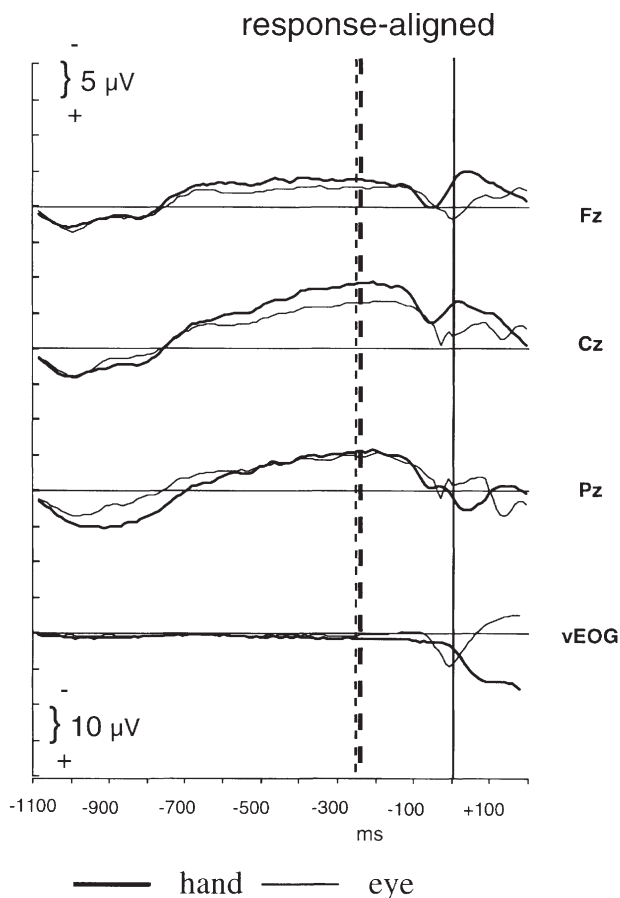


Figure 6 Grand means of midline ERPs (and vEOG for artefact control) of the 100%-go task from experiment 2. Different from Figure 4, trials were averaged time-locked to response onset, from 1100 ms before to 200 ms after response. Mean time points of S2 onset are shown as dashed lines, bold for time-pressure, thin for without time pressure.

locked averaging. However, this difference is only an apparent one: On the right-hand side of Figure 5, the same potentials are displayed as on the left-hand side. The only difference is that the condition without time pressure is shifted by 83 ms in time. This way, the average times of S2 onset overlap (dashed line). It is clearly shown that the anterior difference has disappeared. Therefore, it was obviously only due to an inappropriate shifting backward of the stimulus-locked slow potential in the response-aligned graph.

In principle, the same findings were made in the go/no-go data of experiment 1 (not illustrated in a figure) and in experiment 2. Figure 6 shows the response-locked data from the 100%-go task. Again, CNV returns towards the baseline before response onset, and again the difference between conditions (here the fronto-central increase of CNV with hand movements) appears to be time-locked to S2. Because response times were almost identical in this task (Table 2), these data do not need to be shifted to be stimulus-aligned for further inspection.

Discussion

The CNV before S2 onset does not continue until the response, but returns to less negative values before the response, obviously triggered by S2 onset (cf. also Figure 8 of Van't Ent & Apkarian, 1999). In particular, both the centro-parietal increase under time-pressure in experiment 1 and the fronto-central increase with hand movements in experiment 2 were not artificially produced by some inappropriate stimulus-locked averaging of a response-locked phenomenon, and no new feature of the CNV became visible to be characteristic for response preparation in the response-locked data.

Of course, it is puzzling that CNV, which is undoubtedly related to response preparation, is time-locked to the stimulus that evokes the response but not to the response itself. That is, CNV appears to reflect stimulus-locked response preparation. We will come back to this apparent paradox later.

Experiment 3

The estimate made in experiment 2 about the hand-motor contribution to CNV is valid only if its reference condition, the eye-movement block, has no CNV signature of its own. To further test this assumption, we used a trial-wise variation of saccades and key-press responses that included a no-information condition as the reference condition: All four responses of experiment 2 (press right, press left, look right, look left) were possible responses in any trial, and S1 provided either no information or information that a hand-movement or an eye-movement would be required. In case of no information (and of partial information, cf. below) S2 gave the information that was still needed to select the response. We predicted that CNV would not differ between lack of information and eye-information and, similar to experiment 2, that CNV would be larger at Fz and Cz with hand-information than both with eye-information and without information.

One might try to make this comparison by just using three different types of S1: full information about hand movement (press left or right), about eye movement (look left or right), or no information. However, we reasoned that the full-information conditions would differ from no-information not only by making movement preparation possible, but perhaps also by prolonged processing of the S1 or by less intense expectation of S2 (which was uninformative when S1 provided full information). In fact, full information turned out to evoke a parietally enhanced protracted positivity following S1, similar to the positive slow wave reported by Ruchkin et al. (1997) and to the positive wave visible in Leuthold, Sommer, and Ulrich's

(1996) full information condition (their Figure 9). Therefore, we made the comparison between no-information and partial information, using the paradigm of Wauschkuhn et al. (1997): In addition to no- and full-information trials, there were trials in which S1 provided partial information about the effector ("press" or "look," without specifying left or right). These partial-information trials were more similar to the no-information trials in the two features that might interfere with full information: Processing of S1 was about as simple as with no information (the letter "X" meant no information, while "H" and "A" meant hand and eye, respectively), and the information provided by S2 had to be expected in all these trials to finally select the response. To balance the design completely, S1 could also provide partial information about the direction of responding ("right" or "left," without specifying the effector system).

In the present report, for brevity's sake, we will only deal briefly with the effects of this paradigm that are not related to the present question. (A full account of the effects on behavior and on lateralized EEG activity, contra- minus ipsilateral to the response, is given in Van der Lubbe et al., 2000a). Rather, we will focus on comparing the no-information trials to the partial-information trials in which S1 gave the unspecified information about the effector system (either hand or eye). The prediction was exactly the one made above: CNV will not differ between no information and eye-information and will be larger at Fz and Cz with hand-information than both with eye-information and without information.

Method

Participants

Twelve healthy right-handed participants from the same population as in experiments 1 and 2 performed this experiment (6 male, mean age 26 years). Data from one participant were lost due to technical failure.

Stimuli and Procedure

The apparatus was the same as in experiments 1 and 2. Upon the arrival of S2, participants either had to move their eyes to the left or right, or to press the left or right key. Trials started with a white fixation cross ($0.75^\circ \times 0.65^\circ$) displayed in the center of the screen for 1500 ms. Next, S1 was presented in the center for a duration of 300 ms. S1 consisted of a white frame ($1.4^\circ \times 0.7^\circ$) enclosing a yellow letter (A, H, or X; $0.3^\circ \times 0.45^\circ$) and two red arrowheads ($0.4^\circ \times 0.5^\circ$), one at either side of the letter. The letter provided information about the required effector. An A indicated a saccade (A denoting Auge, German for eye), an H (hand) indicated a key-press, and an X

indicated that this information would be given by S2. The arrowheads gave direction information, by pointing either to the right or to the left. If the arrowheads pointed inwards then only S2 indicated the required response direction. Thus, S1 provided either full information (e. g., >H<), direction information (e. g., <X<), effector information (e. g., >A<), or no information (>X<). The provided information was 100% valid. Simultaneously with S1, two gray crosses ($0.75^\circ \times 0.65^\circ$) were presented, one to the left and one to the right of the center (6.0°). These crosses indicated the potential target location when a saccade would be required, and remained present until the end of the trial. After S1, the fixation cross was presented for 700 ms. Then, S2 was displayed in the center for 200 ms, providing the information not given by S1. That is, S2 indicated the required response direction, the required effector, or both, but only when S1 lacked this information. For example, after <H< as S1, S2 was a meaningless >X<, after >H< as S1, S2 still had to indicate the direction, e. g., left: <X<, etc. Finally, after S2 the fixation cross was again presented until the next trial started. Total trial duration amounted to 4000 ms. There was also a second session with auditory S2 instead of visual S2, but this condition will not be reported here, since only visual stimuli were used in experiments 1 and 2.

Participants were instructed to respond as fast as possible upon the arrival of S2 with a 6° saccade or a flexion of the index finger, and were instructed to avoid errors such as double responses (finger movement plus saccade) and premature responses. A total of 1280 trials were presented in random sequence, 160 of each condition (saccade/finger with 4 types of S1 information: no, partial effector, partial direction, full). A practice block of 200 trials was run before the experimental session to get participants adjusted to the experimental procedure and to the criteria needed for an overt response.

Recording and Data Processing

These methods were the same as in experiment 2, except for including PO7 and PO8 again (as in experiment 1), leaving out T7 and T8 instead (due to hardware constraints).

Data Analysis

These methods were the same as in experiment 2, except for the following.

ANOVA on mean response times and proportions of correct responses had the factors EFFECTOR (hand vs. eye), EFFECTOR INFORMATION (given by S1 or S2), and DIRECTION INFORMATION (given by S1 or S2).

The ANOVA used for CNV analysis compared no-information (pooled over hand- and eye-movement trials, because participants could not know this in advance) to

trials either with unspecified hand information or with unspecified eye information. Topography was optionally included as an additional factor.

Results

Behavioral Results

Response times are compiled in Table 3.

Saccades were faster than finger movements ($F(1,10) = 43.4$, $P < 0.001$), similar to the difference in the 50%-CR task of experiment 2. This effect did not interact with the effects of information, to be described next. Responses were faster when S1 gave information about the required effector system ($F(1,10) = 145.7$, $P < 0.001$), and about the required direction ($F(1,10) = 97.0$, $P < 0.001$). In addition, these two effects interacted ($F(1,10) = 16.5$, $P = 0.002$), reflecting the large benefit of full information.

Percentages of correct responses are not detailed here, for brevity's sake. Altogether, there was no indication for a speed-accuracy trade-off.

CNV

The grand means from the three conditions entering analysis are displayed in Figure 7.

No information vs. unspecified-eye information. S1 information that the response should be performed by eyes did not reliably change CNV amplitudes at midline compared to no information (Table 1, $P = .08$ at best; right graph of Figure 7, and thin vs. dotted lines in lower left panel of Figure 3). Likewise, there was no difference in topography (Table 1: $P = .39$; the normalized midline difference is displayed as the thin line in the lower right panel of Figure 3).

No information vs. unspecified-hand information. In contrast, S1-information that the response should be performed by hands enhanced CNV at Cz and Fz ($P = .001$ and $.004$; Table 1; left graph of Figure 7, and bold vs. dashed line in the lower left panel of Figure 3) and not at Pz ($P = .23$).

Also topography differed between unspecified hand and no information ($P = .036$; Table 1). However, this effect was not due to a more anterior midline topography for unspecified hand ($P = .21$ only, Table 1; although this

pattern can be discerned, see Figure 3, lower right panel), but rather referred to a changed left-right asymmetry in the lateral analysis (INFORMATION \times LEFT/RIGHT: $F(1,10) = 19.8$, $P = .001$), CNV being larger over the left hemisphere than over the right with unspecified hand information. The topographical difference is displayed in the rightmost map of Figure 2.

Unspecified-eye information vs. unspecified-hand information. Comparing the two effector-information conditions directly against one another resulted again (similar to experiment 2) in increased CNV amplitudes for hand at Cz and Fz (both $P = .02$, Table 1) and not at Pz ($P = .31$).

These differences did not, however, lead to a significant effect on topography ($P = .32$; Table 1).

Discussion

First, importantly, eye information indeed did not change CNV amplitude and topography relative to no information. The use of eye blocks as a reference condition in experiment 2 is supported by this result.

Second, hand information had principally the same effect as in experiment 2, increasing CNV at Fz and Cz, but not at Pz. Unfortunately, the change in midline topography did not become significant for the hand-eye comparison, in contrast to experiment 2. We are inclined to consider this outcome as a type 2 error, made more probable by the fact that, due to the very complex task, participants might have not been able to prepare in the same highly specific manner as with the block-wise presentation in experiment 2.

Thus, by and large, experiment 3 confirmed the results of experiment 2.

General Discussion

Two different movement-related CNV effects were obtained, one (Exp. 1) with a centro-parietal topography, and one (Exp. 2 and Exp. 3) with a fronto-central topography.

The two experiments 2 and 3 provided independent evidence that the fronto-central effect is hand-specific. Therefore, we can assume that this effect indeed reflects

Table 3 Means and standard deviations of response times in experiment 3.

	Full information	Partial information about effector	Partial information about direction	No information
Hands (key-press)	452 \pm 75 ms	590 \pm 96 ms	612 \pm 68 ms	654 \pm 69 ms
Eyes (saccades)	359 \pm 78 ms	489 \pm 54 ms	519 \pm 42 ms	561 \pm 45 ms

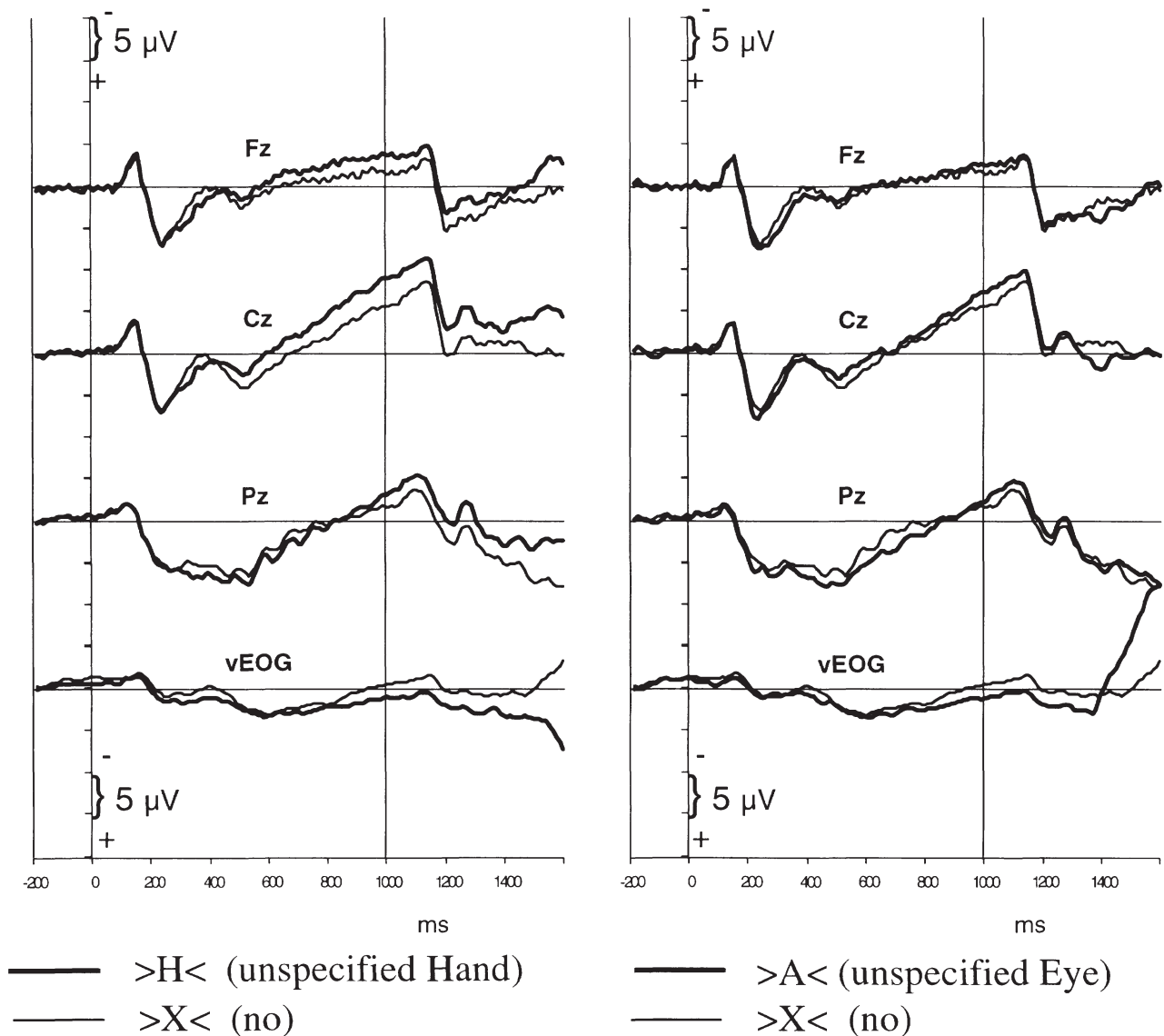


Figure 7 Grand means of midline ERPs (and vEOG for artefact control) from experiment 3, comparing the trials in which S1 gave partial information to no information. S1 was presented at 0 ms, S2 at 1000 ms. The thin line is the same in both panels, evoked by trials in which S1 gave no information.

activation of cortical hand-motor areas and is not artificially produced by some peculiarity of the saccade conditions of experiments 2 and 3 or of the no-information condition of experiment 3. Because of the fronto-central topography of this effect, which was more anterior than the second, centro-parietal effect, these hand-motor areas are probably the ones situated anterior to the central sulcus in the frontal lobe, i. e., some or all of the primary motor area and of the premotor and supplementary motor areas.

The centro-parietal component is more difficult to interpret. What can be said with certainty is that this component is more posterior than the hand-specific fronto-central component, thus might well reflect activity of the parietal cortex, posterior to the central sulcus. As de-

scribed in the Introduction, recent concepts of the organization of the motor system argue that the cortical motor system is made up of modules, each consisting of two main elements, one in the posterior parietal cortex and one in the frontal cortex (including the motor cortex proper) (Rizzolatti et al., 1998). This conception might well fit the conclusion drawn above from the response-locked data that CNV reflects *stimulus-locked* response preparation, due to the following consideration. In S1–S2 tasks like the present ones, only some part of the preparation to respond consists of direct motor activation. Much more important appears to be the assembly of stimulus-response rules of the form: If S2 will be *x*, then response *a*. If S2 will be *y*, then response *b*, etc., such that as little time as possible will have to be spent with response selection after presen-

tation of S2. The presentation of S2 then serves as a trigger for executing the response rule, like a pulse that releases a tensed spring. CNV might well be seen as reflecting the tensing of the spring, binding together the expected stimulus patterns and the appropriate responses. The dorsal parietal cortex probably has an important function in this binding of stimuli to responses (Milner & Goodale, 1995), thus forming a part of the parieto-frontal motor system (Rizzolatti et al., 1998) and so the present results suggest that the CNV might help in delineating the contribution of the parietal and the frontal component of this system in humans.

One source of evidence besides experimental manipulation in healthy subjects can be data from patient groups. For example, in a monotonous task with a relatively long S1–S2 interval we found smaller CNV amplitudes in Parkinson patients at Cz, and as a tendency at Pz, but not at Fz (Wascher et al., 1997, Fig. 5). Thus, the ability to maintain an S-R association in readiness appeared to be affected, whereas the hand-motor activation remained unimpaired. In contrast, in a more demanding task with a short S1–S2 interval, similar to the present experiments, the Parkinson patients had a general deficit in CNV amplitude (Wascher et al., 1997, Fig. 8), suggesting that with short intervals both the readiness to respond and hand-motor activation were impaired.

A similar reasoning can be made with CNV data of schizophrenic patients. In an acute state, these patients had a general reduction of CNV amplitude, but in a chronic state, their Fz amplitudes were close to normal (Verleger et al., 1999a). Thus, the ability to maintain an S-R association in readiness appeared to remain impaired in chronic schizophrenics, whereas hand-motor activation returned to the normal range.

Patients with cerebellar atrophy, on the other hand, had reduced amplitudes at Cz and Fz, but close-to-normal values at Pz (Verleger et al., 1999b). So it might be argued that these patients' ability to maintain an S-R association in readiness is normal, whereas their hand-motor activation is deficient due to the lack of cerebellar input.

Before drawing firm conclusions, however, the validity of the present data and suggestions has to be discussed further. For example, one puzzling problem is posed by the data of Ulrich, Leuthold, and Sommer (1998) who used a design similar to the present experiment 3, except for requiring manual responses only, no eye movements. In their data, CNVs were non-existent at Fz (equally large at Cz and Pz) and also increases of CNV with S1 information were non-existent at Fz (largest at Cz, somewhat smaller at Pz). One wonders why a study that used only hand responses did not obtain the fronto-central CNV part that was found to be hand-specific in the present study (exp. 2 and 3). However, it may be argued that this pattern of results fits the above distinction between

the two main elements of the motor system: In our experiment 3, specification of the response by S1 referred to the selection between the effectors hand and eye. Therefore, in case of hand information, the hand-motor cortex became specifically activated, but not so in case of eye information. In contrast, in Ulrich et al. (1998) specification of the response by S1 referred to the selection between different types of movement within the hand-motor system. Therefore, this information did not imply a *selective* activation of the hand-motor cortex but the selection between different motor programs. It may be speculated that this selection implies activation within the parietal parts of the motor system. Furthermore, the hand-motor system might have been tonically activated in their experiment, due to the combination of two features: a complex partial priming design, similar to the present experiment 3, putting great demands on participants' capacity, and the use of the hands as the only effectors, in contrast to the present experiment 3. Perhaps this unique combination made participants activate their hand-motor areas in a tonic way. Such tonic activation might have been visible in DC recordings or in fMRI, but not in the phasic changes recorded within trials.

Notwithstanding these problems, which merit further discussion, the new contribution of the present data is in the delineation of the fronto-central hand-specific part to the CNV and in its distinction from the centro-parietal part, while other work, from Gaillard (1977) to Ulrich et al. (1998) described movement-related variation in the centro-parietal part only.

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