Brain control of heart regulation

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Chapter 4

Slow cortical potentials

This chapter presents the slow cortical potentials measured in the experiments which were introduced in the previous chapter. The present chapter reports only the cortical slow waves; the positive slow wave (PSW), negative slow wave (NSW), and the contingent negative variation (CNV). In Chapter 5 the cardiovascular and the electrocortical results will be compared and their interrelations investigated. To avoid large amounts of redundant text, references to the preceding chapter are given for extensive descriptions of the task and the experimental manipulations. In this chapter only a short description is given. In section 1.2.2 an introduction to the slow waves was given, as well as a review of the relevant literature.

4.1 Experiment 1: Memory Load and KR

Three task manipulations were used. First, the memory search task at S1 was either easy or difficult. The size of the memory set was varied to examine the amount of processing required for the information presented at S1. In the difficult condition a smaller PSW and larger NSW were expected. Second, to investigate the effects of response preparation, the response was required either immediately after S2 (fast), or after a one-second delay (delayed). A larger CNV was expected after the instruction to give a fast response. Furthermore, since the NSW might reflect the consequence of S1 for upcoming events, the response instruction may affect the NSW as well. Third, the information given about the performance (knowledge of results, KR) was manipulated to influence the state of the subject, in terms of motivation and emotion. Either neutral KR (performance information) or noise (after an incorrect response) was given to affect the subject's motivation to perform. This manipulation was expected to induce lateralization of the slow waves, particularly at the frontal derivations. In a negative reward condition, lateralization was expected in the right hemisphere.

4.1.1 Method

Subjects Fifteen of the 26 subjects with complete cardiovascular datasets also had acceptable complete EEG data. The data of the remaining subjects were rejected, mainly because of excessive eye-movement artifacts. All subjects had normal or corrected-to-normal vision.

Apparatus The subjects were seated in a soundproof, electrically shielded room, at a table on which a monochrome monitor and two pushbuttons were placed. The EEG was measured with an Electrocap from positions F3, F4, C3, C4, P3, and P4, referred to the right earlobe (A2). Vertical eye movements measured with mini Beckman silver-silver chloride electrodes. The EEG-signals were amplified with an eight-channel Nihon-Kohden electroencephalograph (time constant 10 s, low pass filter 35 Hz). All data were sampled on-line with a frequency of 100 Hz, and stored for further analysis.

Task For a detailed description of the task and procedure, see section 3.1.1. The S1-S2 interval was six seconds. A memory set of either two (easy) or five (difficult) letters was memorized. S1 was a spoken letter, of which the subject had to decide whether it belonged to the memorized set. The result of this memory search task indicated the response instruction at S2; either a fast or a delayed response was required after S2. The S2 indicated whether the response had to be given with the left or with the right hand. There were two types of KR: neutral and noise. In the neutral KR condition a vertical bar was presented after each response, which indicated the speed of the response. In the noise KR condition aversive auditory noise was presented after each incorrect response.

Procedure Before the experiment started, the subjects were trained until they made less than 10 % errors. Subjects were instructed to perform the task as fast and accurately as possible, and to minimize eye-blinks. The subjects performed four task blocks, consisting of 80 trials each. Memory load and KR were varied between blocks, and response instruction was varied within each task block. The order of the task blocks was easy–difficult–easy–difficult, with half the subjects starting with two noise KR blocks, and the other half with neutral.

Data analysis A trial consisted of the period from one second before S1 until the presentation of S2. Before analyzing the data the number of datapoints was reduced by taking the mean of five successive samples, yielding one value for every 50 ms. In this way, there were 140 datapoints for every trial. The one second before S1 was used as a baseline. Trials with eye movement artifacts (EOG exceeding 100 μV) and trials with incorrect responses were removed. The interval between S1 and S2 was divided into twelve epochs. The average amplitude was taken for each epoch. The first epoch, from 200 to 500 ms after S1, was used as a measure for the PSW. The second epoch, between 500 and 1000 ms after S1, was the measure for the NSW. The nine subsequent 500 ms epochs were used to indicate the slow negative shift; i.e. the epoch from 1 to 1.5 s. after S1 is called epoch 1, between 1.5 and 2 seconds epoch 2, etc. The last epoch, which consisted of the last 500 ms before S2, was used as a measure for the CNV.

Statistical analysis MANOVAs were used to test the slow waves. Each epoch was tested separately for the factors position (frontal, central and parietal), hemisphere (left, right), KR (neutral, noise), memory load (easy, difficult), and response instruction (fast, delayed). By using a multivariate analysis problems concerning sphericity and compound symmetry are avoided (StatSoft Inc., 1996). The MANOVA command gives univariate (ANOVA) results for factors with two levels. When interactions occurred, they were examined with Newman-Keuls post-hoc tests; only the significant differences are described. F-values with $p < 0.05$ were regarded significant.

4.1.2 Results and discussion

Figures 4.1 and 4.2 present the slow waves in the easy and the difficult condition, respectively. Tables 4.1 gives an overview of the significance levels of the MANOVAs; for the PSW, NSW, and CNV the F-values are presented in the text. For the nine intermediate epochs only the significance level is indicated. Since more delay-trials were rejected, because of the many responses which were given prematurely, the average number of trials used for each subject was about 20 for the delay instruction, and 24 for the fast.

The anterior-posterior distribution of the slow waves, examined by the position factor, showed that there was a larger overall negativity at the frontal positions. The PSW was slightly negative at the frontal positions (-0.6 μV), and more positive at the central (0.8 μV) and parietal (2.0) positions (effect of position: $F(2, 13) = 6.8$). Also, the NSW was negative at the frontal (-4.6 μV) and central (-1.8 μV) positions, whereas a prolonged positivity (1.8 μV) was present at the parietal electrodes (effect of position: $F(2, 13) = 42.8$). This negative–frontal–to–positive–parietal distribution that was found by others as well (Donchin, Ritter, & McCallum, 1978; Ruchkin & Sutton, 1983). The frontal maximum of the NSW was also found by Gaillard & Perdok (1980) and Gaillard & van Beijsterveldt (1991), and the latter also found the prolonged parietal positivity in this latency range. These results show that the present slow waves match those normally found in S1-S2 paradigms. The negative shift, represented by the nine successive epochs between the NSW and the CNV, was maximal at the frontal positions. The frontal dominance lasted until about four seconds after S1 (epoch 6), and then gradually shifted to a (non-significant) central dominance.

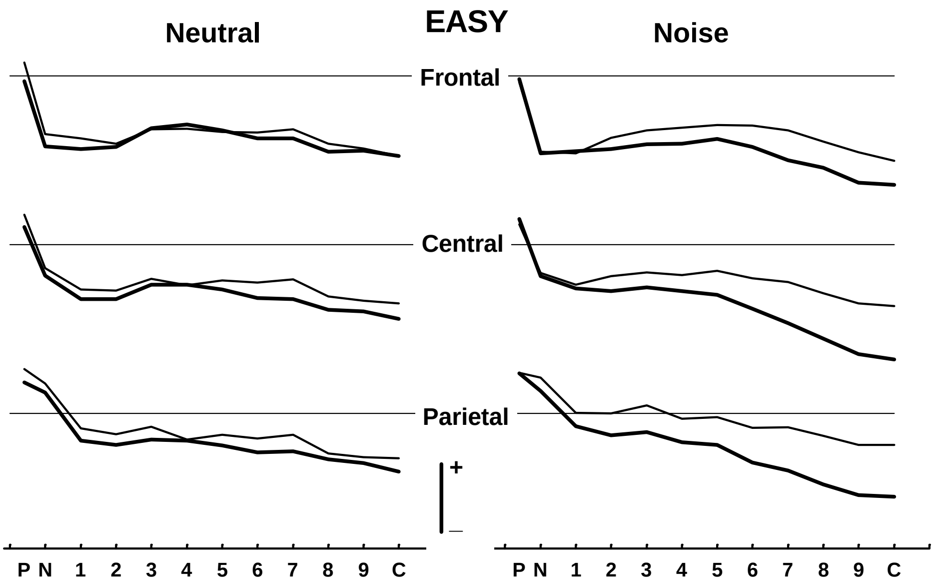

Figure 4.1: *Cortical slow waves in the easy condition of Experiment 1. Bold line: fast instruction, thin line: delay instruction. The horizontal lines indicate the baseline level; the vertical line represents 3 μV.*

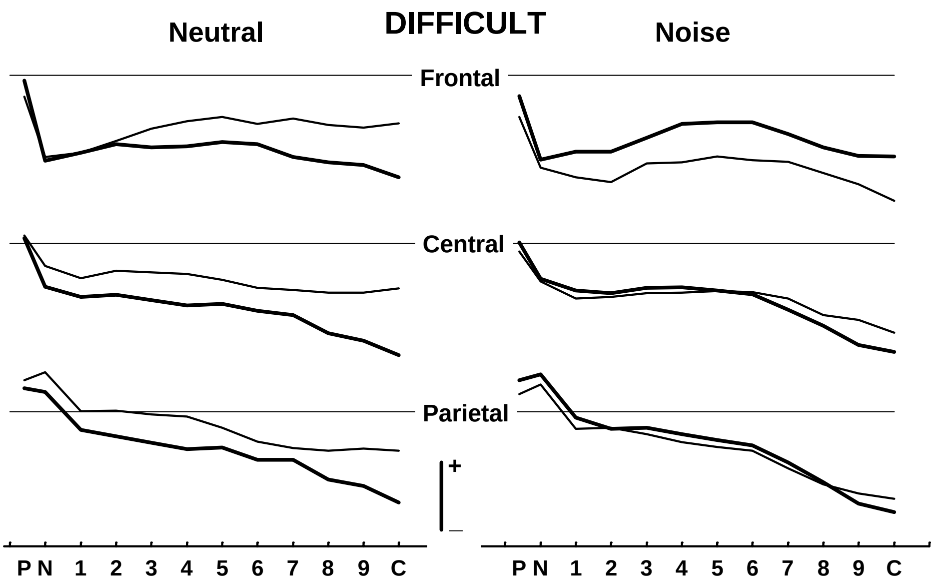

Figure 4.2: *Cortical slow waves in the difficult condition of Experiment 1. Bold line: fast instruction, thin line: delay instruction. The horizontal lines indicate the baseline level; the vertical line represents 3 μV.*

effect	P 0.2	N 0.5	1 1.0	2 1.5	3 2.0	4 2.5	5 3.0	6 3.5	7 4.0	8 4.5	9 5.0	C 5.5
Position	**	***	***	***	***	**	**	*				
Hemisphere			*	*	**	**	*	*	*			
KR												
MemoryLoad	*											
Instruction												*
P × H						*	*	*	*	*	*	*
P × ML		*										
P × I												*
H × KR		*										
H × ML				*	*	*	**	*	*			
P × ML × I	*											

Table 4.1: *Overview of the* MANOVA *significance levels of the cortical slow waves in Experiment 1. The F-values for* PSW, NSW, *and* CNV *are presented in the text. Epoch-numbers (top row) and their start-time in seconds after S1 (below) are indicated.* * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

Between one and 4.5 seconds after S1 (epochs 1 to 7) the negative shift was larger in the left than in the right hemisphere. The position × hemisphere interaction starting in epoch 4 showed that there was no lateralization at the central electrode positions, whereas at the frontal and parietal positions the negative shift was larger in the left hemisphere. This frontal and parietal lateralization lasted until S2 (for the CNV: $F(2, 13) = 4.4$).

The memory load manipulation, which was assumed to affect the PSW and NSW measures, successfully induced a reduction of the PSW in the difficult condition (effect of memory load: $F(1, 14) = 5.2$). This is in accordance with the view that positivity in the 300 ms latency range reflects the task relevance, and evaluation of the information presented (e.g. Donchin et al., 1978; Gaillard & Lawson, 1984). There was a position × memory load interaction on the NSW ($F(2, 13) = 6.6$), which showed that at the frontal positions the NSW was larger in the difficult (-5.2 μV) than in the easy condition (-4.2 μV). At the central and the parietal positions there was no difference between easy and difficult. Such a result was also found by Gaillard & van Beijsterveldt (1991), who used an easy and a hard tone discrimination at S1. This result supports the assumption that the NSW reflects the continued processing of information revealed by the stimulus, even if the task demands are rather different. However, no effect of response instruction was found on the NSW, so the second part of the expectation regarding the NSW is not supported, i.e. that the NSW should reflect the consequences of S1 for subsequent (response) behavior.

The hemisphere × memory load interaction between 1.5 and 4.5 seconds after

S1 (epochs 2 to 7) showed that in the left hemisphere the negative shift was larger in the difficult condition, whereas in the right hemisphere there was no difference between the easy and the difficult condition. This effect could be related to the nature of the memory search task. Since letters of the alphabet were used, it may be argued that the task is language-related. Thus, the memory search process might involve the left (language-related) hemisphere. Since the difficult condition requires more processing, the larger negativity may be related to the larger claim for the left hemisphere.

It was expected that the two KR conditions would induce different emotional and/or motivational processing, which should result in differential lateralization of the slow waves. Negative emotions are assumed to result in a more right lateralized activity, and positive emotions in a predominant left hemisphere activation. The results appear to confirm this hypothesis. There was a hemisphere $\times$ KR interaction on the NSW ($F(1, 14) = 5.0$) which revealed that in the right hemisphere the NSW was larger in the noise KR (-1.8 μV) than in the neutral KR condition (-1.4 μV), whereas in the left hemisphere the difference was not significant (-1.6 and -1.4 μV). This result gives an indication that the right hemisphere is more sensitive to the emotional/motivational aspects of the task.

The CNV is mostly regarded as an index of response preparation (Rohrbaugh & Gaillard, 1983). This view is supported by the present results. The CNV was larger after the fast (-5.6 μV) than after the delay instruction (-4.0 μV, effect of instruction: $F(1, 14) = 4.8$), i.e. the CNV was larger when the response had to be given immediately after S2. The position $\times$ instruction interaction on the CNV ($F(2, 13) = 4.8$) revealed that there was no difference between fast and delayed at the frontal positions, and that the effect of response instruction was most prominent over the motor cortex (central electrode positions). This gives further support for the relation with motor preparation.

The negative shift towards the CNV gradually developed in the S1-S2 interval. At first this negativity was most prominent at the frontal positions, which is most likely due to the NSW being maximal at those positions. After about four seconds the maximal negativity moves towards the central positions, i.e. over the motor cortex where the response is being prepared. Thus, a gradual transition from negative slow wave to contingent negative variation occurred. In the middle of the S1-S2 interval the negative shift was larger in the left hemisphere, but mainly at the frontal and parietal positions. The absence of lateralization at the central positions might indicate that no specific response with either the left or the right hand was being prepared. Since the S2 indicated whether a left- or right-hand response was required, with equal probability, the preparation of a specific hand was useless.

Finally, the PSW had a three-way position $\times$ memory load $\times$ instruction interaction ($F(2, 13) = 4.5$), which revealed that at the frontal positions the negativity after the delay instruction was larger than after the fast instruction, but only in the difficult condition. At the other positions there were no differences.

The conclusions from Experiment 1 are: (1) The memory load manipulation was successful: in the difficult condition the PSW was smaller, and the NSW larger. (2) The instruction manipulation successfully induced stronger motor preparation after the instruction to give a fast response, as indicated by the larger CNV. (3) The noise KR condition successfully induced an NSW which was lateralized in the right hemisphere. Although this effect of KR was only small, it does give an indication that the right hemisphere is more sensitive to the emotional or motivational aspects of a task.

4.2 Experiment 2: Reward

The manipulations in the second experiment were aimed at optimizing the cardiovascular results (see section 3.2.1). The memory load manipulation in Experiment 1 was quite successful for the slow waves, but in the cardiovascular data the results were less clear (see the previous chapter). Therefore, only an easy memory search condition was used in the second experiment. The KR manipulation was altered; instead of neutral versus noise KR there were a positive reward condition (monetary reward), and a negative reward condition (aversive noise). The larger difference between these types of reward was expected to cause stronger lateralization of the slow waves. The response instructions were the same as in Experiment 1. In addition, a reference condition is presented, in order to compare the complex experimental conditions with a simple task.

The manipulations are expected to have the following effects; the task at S1 is more difficult in the experimental conditions than in the reference condition. Therefore, a larger PSW and smaller NSW are expected in the reference condition. The response instructions are the same as in Experiment 1; the CNV is expected to be larger after the instruction to give a fast response. In the reference condition, a relatively small CNV is expected, since there is no requirement of a speeded response. The response instruction may affect the NSW, since the NSW is assumed to reflect the consequences of S1 for later events; due to this assumption, a difference between the experimental conditions and the reference condition may occur as well, since in the reference condition the S1 does not contain differential information. The KR-manipulation is expected to induce lateralization effects, with the negative reward condition resulting in larger right hemisphere negativity.

4.2.1 Method

Subjects and apparatus Fourteen subjects had complete EEG-datasets; two of these were not included in the cardiovascular analyses of Chapter 3. All subjects had normal or corrected-to-normal vision. The same equipment was used as in Experiment 1.

Task For a detailed description of task and procedure, see section 3.2.1. The S1-S2 interval was six seconds. A fixation stimulus was presented continuously, in the middle of the screen. Two sets of two letters were presented (AB and YZ), one set indicating a fast response instruction, the other a delayed. S1 was the auditory presentation of one letter, which indicated the response instruction at S2. The S2 was a visual stimulus, presented either to the left or to the right of the fixation stimulus, which indicated whether to respond with the left or the right hand. The fast responses were required within 600 ms after S2, and the delayed between 1000 and 1600 ms. Responses which were given too early, too late, or with the wrong hand, were incorrect. There were two types of reward: positive and negative. In the positive reward condition, correct responses were rewarded with money. In the negative reward condition noise was presented after an incorrect response. In addition, a reference condition was presented in which S1 had to be ignored, and only a simple, non-speeded, button press was required within one second after S2.

The subjects performed two experimental blocks consisting of eighty trials each, and a reference block of forty trials. The order of presentation was varied between subjects. Type of reward was varied between blocks, and response instruction within each block. Half the subjects responded fast to A and B, and delayed to Y and Z, whereas the other half did the reverse.

Analyses The EEG was analyzed from one second before S1 until S2. The pre-S1 period served as a baseline. Trials with eye-movement artifacts (EOG exceeding 100 μV), trials in which amplifier saturation occurred, and trials with incorrect responses were removed. The same epochs were used as in Experiment 1.

The slow waves were tested for each epoch separately with a MANOVA with the factors position (frontal, central, and parietal), hemisphere (left, right), reward (positive, negative), and response instruction (fast, delayed). The difference between the experimental conditions and the reference condition was tested in a MANOVA with the factors position, hemisphere, and condition (reference versus experimental). Interactions were examined with Newman-Keuls post-hoc tests. Results with $p < 0.05$ were considered significant.

4.2.2 Results and discussion

The grand averages of the slow waves are presented in Figure 4.3. An overview of the significance levels of the MANOVAs is given in Table 4.2 for the experimental conditions, and in Table 4.3 for the comparison with the reference condition. The average number of trials was about 32 after the fast instruction, about 26 after the delay instruction, and about 32 in the reference condition.

The anterior-posterior distribution of the slow waves was similar to Experiment 1. There was a prominent negativity at the frontal positions, and an initial positive wave at the parietal positions. The NSW was maximal at the frontal

	P	N	1	2	3	4	5	6	7	8	9	C
effect	0.2	0.5	1.0	1.5	2.0	2.5	3.0	3.5	4.0	4.5	5.0	5.5
Position		***	**	*	*	*		*				*
Hemisphere		*										
Reward												
Instruction									*	*	*	*
P × R × I	**								*		*	

Table 4.2: MANOVA *significance levels of the cortical slow waves in Experiment 2. The F-values for PSW, NSW, and CNV are presented in the text. Epoch-numbers (top row) and their start-time in seconds after S1 (below) are indicated.* * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

positions (-4.8 μV), but showed a prolonged positivity at the parietal positions (1.5 μV) (effect of position: $F(2, 12) = 28.9$). The subsequent negative shift was maximal at the frontal positions until about four seconds after S1 (epoch 6), after which the negativity became larger at the central positions. The CNV was maximal at the central positions (-5.2 μV, effect of position: $F(2, 12) = 4.4$). The NSW was lateralized in the right hemisphere (-2.3 against -1.5 μV in the left; effect of hemisphere: $F(1, 13) = 6.0$). Such a lateralization was also reported by for instance Rohrbaugh, Newlin, Varner, & Ellingson (1984).

The response instruction again successfully induced a larger negativity after the fast instruction, which began at about four seconds after S1 (epoch 7). The CNV was larger after the fast (-5.5) than after the delay instruction (-2.8 μV, effect of instruction: $F(1, 13) = 7.3$). However, as can be seen in the figure, the difference between the fast and delayed instruction was more prominent in the positive reward condition; there was a three-way position × reward × instruction interaction which revealed that only in the positive reward condition the negativity was larger after the fast instruction at all positions. In the negative reward condition there was no difference between fast and delayed at the frontal positions. Thus, the effect of response instruction was present mainly in the positive reward condition. This shows that the subjects were more motivated to perform the task in this condition; the small CNV after the delay instruction appears to reflect cautious behavior which was also reflected in the reaction times (see section 3.2.2). The subjects waited longer before giving the response, and therefore the preparation was not yet maximal. The CNV in the reference condition was in between those for the fast and delayed instruction in the experimental conditions. This, too, supports the idea that the CNV is related to motor preparation; the reaction times were in between the fast and delayed as well (see section 3.2.2).

There was a position × reward × instruction interaction ($F(2, 12) = 9.9$) on the PSW; at the frontal positions there was a larger negativity after the fast (-2.0 μV) than after the delay instruction (-0.2 μV) in the positive reward

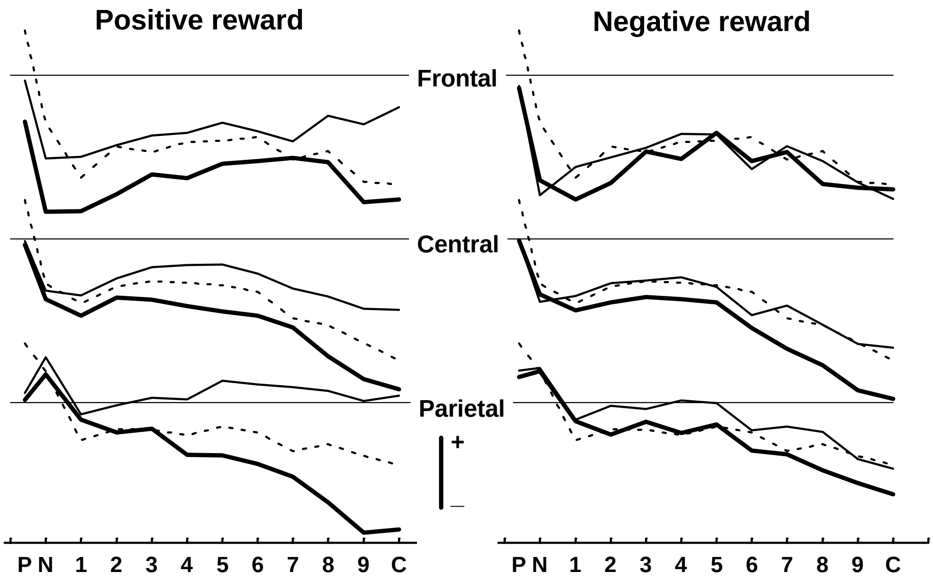

Figure 4.3: *Grand average of the slow waves of Experiment 2. Bold line: fast instruction, thin line: delay instruction, dotted line: reference condition. The horizontal lines indicate the baseline level; the vertical line represents* 3 μV.

condition, and no difference in the negative reward condition (-0.6 and -0.5 μV). At the central positions there was no difference at all (all about -0.2 μV), and at the parietal positions the PSW was larger in the negative reward condition (1.2 μV) than in the positive reward condition (0.2 μV).

The reference condition was added to compare the relatively complex experimental conditions with a simple task. There was a larger PSW in the reference condition (2.0 vs. -0.1 μV, effect of condition: $F(1, 13) = 5.9$), and the position $\times$ condition interaction on the NSW ($F(2, 12) = 12.0$) revealed that the NSW was smaller in the reference condition (-2.0 vs. $-4.8 \mu V$), but only at the frontal positions. Both these results are consistent with the view that the PSW and the NSW reflect aspects of stimulus processing (see section 4.1.2), with more processing requirements resulting in a smaller PSW and larger NSW.

Finally, there was a hemisphere $\times$ condition interaction between 0.5 and 2.5 seconds after S1, which showed that in the reference condition there was no lateralization of the NSW (for the NSW: $F(1, 13) = 8.3$), and subsequent epochs, whereas in the experimental conditions the negativity was lateralized in the right hemisphere. Thus, the presence of either positive or negative reward in the experimental conditions, versus the absence of reward in the reference condition, was sufficient to induce lateralization.

The conclusions from the second experiment are: (1) The larger CNV after the fast instruction indicates that the CNV reflects motor preparation. Only the positive reward condition was motivating enough to induce this effect. (2) A larger processing demand induced a smaller PSW and larger NSW, as was shown by the difference between the experimental conditions and the reference. (3) Although the lateralization of the slow waves did not differentiate the positive and negative reward condition, the absence of lateralization in the reference condition indicated that the presence of a reward is sufficient to induce lateralization.

4.3 Experiment 3: Control

Like in Experiment 2, the changes made in the third experiment were mainly aimed at optimizing the cardiovascular results. Because the reward manipulation used in Experiment 2 proved successful for the cardiovascular results, a different kind of feedback manipulation was used in the third experiment to further investigate the effect of different feedback structures; the level of control was varied. In the *Control* condition, there was continuous information about task performance. Good performance was coupled to a monetary reward. Noise presentation after an error could be prevented by making a number of successive correct responses. Successful avoidance of noise presentation was rewarded with money. In the *NoControl* condition no information about the performance was presented, except that sometimes after an incorrect response aversive noise was presented, depending upon the number of correct responses. This manipulation was expected to affect the state of the subject, and likewise to induce lateralization effect in the slow wave data. The same response instructions were used as in Experiments 1 and 2. The reference condition was slightly altered; only one letter was used as an S1, and a neutral S2 was presented. Furthermore, subjects were instructed to give a speeded response after S2.

The following results were expected for the cortical slow waves. First, due

effect	P 0.2	N 0.5	1 1.0	2 1.5	3 2.0	4 2.5	5 3.0	6 3.5	7 4.0	8 4.5	9 5.0	C 5.5
Position		***	*	*								
Hemisphere												
Condition	*											
P × C		**										
H × C		*	**	*	*							

Table 4.3: *Significance levels of the difference between experimental conditions and reference in Experiment 2. The F-values for* PSW*,* NSW*, and* CNV *are presented in the text. Epoch-numbers (above) and their start-time in seconds after S1 (below) are indicated.* * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

to the absence of the memory search task at S1, the PSW was expected to be larger in the reference condition, and the NSW smaller. Second, the CNV was expected to be larger after the fast than after the delay instruction, whereas due to the speed instruction, the CNV in the reference condition was expected to be comparable to the fast instruction. Third, the NoControl condition was expected to induce a larger right hemisphere activity than the Control condition.

4.3.1 Method

Subjects and apparatus Sixteen right-handed males had complete datasets; fifteen of these subjects were also included in the cardiovascular analyses of Chapter 3. All subjects had normal or corrected-to-normal vision. The same equipment was used as in Experiments 1 and 2.

Task For a detailed description of the task, see section 3.3.1. The memory search task at S1 and the response instruction were the same as in Experiment 2. The level of control was varied. In the Control condition, the number of errors that could be made before noise was presented was indicated. Subjects could compensate for earlier incorrect responses, by giving a number of successive very fast responses. In the NoControl condition, the same compensating structure was present, but invisible. In addition to the experimental conditions there was a reference condition, in which a simple speeded response was required after S2.

Procedure Training and preparation were similar to Experiment 2. The subjects performed two experimental blocks consisting of eighty trials each, and a reference block consisting of forty trials. Control conditions were varied between blocks, and response instruction was varied within each task block. Half of the subjects responded fast to 'AB' and delayed to 'YZ', whereas the other half did the reverse. The subjects could earn a financial bonus of 10 Dutch guilders maximally, depending on the number of errors, the number of successful 'avoidances' (bingos), and the mean RT.

Analyses The data acquisition and reduction procedures were the same as in Experiment 2. The slow waves were derived in the same way as in Experiments 1 and 2. The slow potentials were tested for each epoch separately with a MANOVA with the factors position (frontal, central, parietal), hemisphere (left, right), control (Control, NoControl), and response instruction (fast, delayed). The difference between the slow waves in the reference condition and those after the fast instruction in the experimental conditions were tested with a MANOVA with the factors position, hemisphere, and condition (experimental vs. reference). Interactions were examined with Newman-Keuls post-hoc tests. Results with $p < 0.05$ were considered significant.

	P	N	1	2	3	4	5	6	7	8	9	C
effect	0.2	0.5	1.0	1.5	2.0	2.5	3.0	3.5	4.0	4.5	5.0	5.5
Position		***	***	**	*							
Hemisphere												
Control		*		*								
Instruction												
P × C											*	*
P × I		*							*	*	*	*
H × C		*										
P × C × I			*	*		*						

Table 4.4: MANOVA *significance levels of the cortical slow waves in Experiment 3. The F-values for PSW, NSW, and CNV are presented in the text. Epoch-numbers and their start-time in seconds after S1 are indicated.* * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

4.3.2 Results and discussion

The grand averages of the slow waves are presented in Figure 4.4. Table 4.4 gives an overview of significance levels of the MANOVAs for the experimental conditions, and Table 4.5 for the comparison with the reference condition. The average number of trials for each subject was about 26 after the fast instruction was about 26, about 22 after the delay instruction, and in the reference condition about 28.

The anterior-posterior distribution of the slow waves was similar to the other experiments. Until about 2.5 seconds after S1 (epoch 3) there was a frontal predominance of the negativity; the NSW was largest at the frontal positions (-1.7 μV), and showed a prolonged positivity at the parietal positions (1.9 μV, effect of position: $F(2, 14) = 44.2$). The subsequent negative shift remained slightly positive at the parietal positions, and negative at the frontal and central positions. Towards S2 the negativity shifted (nonsignificantly) to the central and parietal positions. There were no main effects of hemisphere.

The NSW and subsequent negativity were larger in the NoControl condition (for the NSW, effect of control: $F(1, 15) = 4.6$). This difference lasted until 2 seconds after S1. In Experiment 1 a larger NSW was found when the task at S1 was more difficult. The present result might thus indicate that in the NoControl condition, where the subjects were not given direct information about their performance, more effort was invested in the task. In the Control condition, the NSW was lateralized in the right hemisphere (hemisphere × control interaction: $F(1, 15) = 5.4$). In Experiment 2 a lateralized NSW was found in both experimental conditions, whereas in Experiment 1 the NSW was lateralized only in the noise KR condition. It was expected that the control manipulation would induce

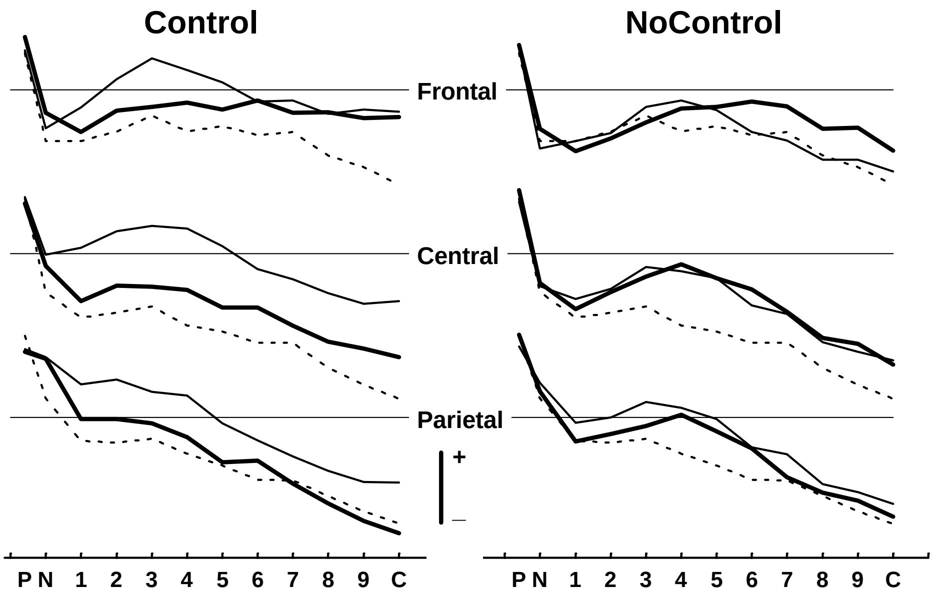

Figure 4.4: *Grand average of the slow waves of Experiment 3. Bold line: fast instruction, thin line: delay instruction, dotted line: reference condition. The horizontal lines indicate the baseline level; the vertical line represents* 3 μV.

lateralization, but particularly in the NoControl condition.

The CNV was larger after the instruction to give a fast response, but only at the central and parietal positions (position × instruction interaction, $F(2,14) = 6.1$). This again confirms that the motor preparation was larger after the fast instruction. There was a position × instruction interaction on the NSW as well ($F(2,14) = 5.0$); at the frontal positions the NSW was larger after the delay instruction, whereas there was no difference at the central and parietal positions.

Towards S2 the frontal negativity was larger in the NoControl condition (position × control interaction, for the CNV: $F(2,14) = 5.7$), whereas at the central and the parietal positions there was no difference. In combination with the three-way position × control × instruction interaction between one and three seconds after S1, it appears that the NoControl condition induced uncertainty in the subjects. In order to try and make a correct response the motor preparation was large not only after the fast, but also after the delay instruction. Early in the S1-S2 interval this caused the negativity to be equally large after the fast and delay instruction in the NoControl condition, whereas in the Control condition the delay instruction did not yet cause negativity. This effect persisted in the entire S1-S2 interval, particularly at the frontal positions.

In the comparison between the experimental and the reference condition (see Table 4.5) the effect of position was highly significant (PSW: $F(2,14) = 3.9$;

effect	P 0.2	N 0.5	1 1.0	2 1.5	3 2.0	4 2.5	5 3.0	6 3.5	7 4.0	8 4.5	9 5.0	C 5.5
Position	*	***	***	**	**	***	***	***	***	***	**	**
Hemisphere												
Condition		*										

Table 4.5: *Difference with reference: cortical slow waves in Experiment 3. The F-values for Psw, Nsw, and Cnv are presented in the text. Epoch-numbers and their start-time in seconds after S1 are indicated.* * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

NSW: $F = 38.8$; CNV: $F = 8.5$; the F-values in epochs 1 to 9 were between 10.4 and 33.8). Whereas in the experimental conditions the slow negative shift was initially larger at the frontal positions, in the reference condition the negativity was always maximal at the central positions. It appears that the speed instruction which was given for the reference condition caused the motor preparation to start immediately. This is reflected in the central dominance throughout the S1-S2 interval. The PSW was similar in the reference and the experimental conditions. This result is different from Experiment 2, where a larger PSW was found in the reference condition. The speed instruction which was presently given for the reference condition probably caused the S1 to have a rather high impact, which caused an attenuation of the PSW. The subsequent NSW was larger in the reference condition than in the experimental conditions (effect of condition: $F(1, 15) = 4.7$). This too, is probably related to the high impact of the stimulus.

The conclusions from Experiment 3: (1) The PSW is more related to general processing of the stimulus, whereas the NSW is related to the meaning and implications of stimulus content. (2) The CNV is related to motor preparation. (3) The frontal activity reflects the motivational or emotional aspects of the task (control).

4.4 General discussion

The results of the three experiments are largely in agreement with each other. The effect of the difficulty of the memory search task at S1 was reflected in the early slow waves, the PSW and the NSW. In the first experiment, where the task was either easy or difficult, the PSW was larger and the NSW smaller in the easy condition. When in the second experiment a reference condition was added which did not require a memory search, this further enhanced the PSW and reduced the NSW. These results are in agreement with the view that these components reflect the evaluation of the stimulus and reflect the amount of processing required. The result that in Experiment 3 the NSW was larger in the condition where no information was given about the subjects' performance (NoControl condition), then indicates that the subjects had to invest more effort to adequately perform this task.

The one result which appeared not in agreement with the above results is that in the third experiment the PSW was the same in the experimental and the reference condition. This was probably caused by the instruction to give a speeded response in the reference condition, which enlarged the impact of the S1 stimulus. The maximum negativity in this condition was found at the central positions, in the entire S1-S2 interval, whereas in the other conditions the maximum negativity was initially found at the frontal positions, and then gradually shifted towards the central positions. The central maximum appears to indicate that due to the speed instruction the subjects started preparing the response immediately.

The central maximum negativity before S2 is related to activity in the motor cortex. In all experiments, a larger CNV was found after the instruction to give a fast response than after the delay instruction, particularly at the central positions. This shows that when the response was required immediately after S2, the preparation was already maximal when S2 was presented. The delayed responses were required at least one second after S2, so that the subjects could first wait for the instruction with which hand to respond (S2), and then start preparing the response. In the reference condition of the second experiment the response instruction did not stress the requirement of speed; the response only had to be given within one second after S2. This caused the CNVs to have intermediate amplitudes; comparing the CNV between the reference condition and the average of the experimental conditions indicated that they were the same. Likewise, in Experiment 3, the CNV in the reference condition was the same as the CNV after the fast instruction in the experimental conditions.

The third class of manipulations involved feedback, which was expected to induce lateralization of the slow waves due to asymmetrical processing of emotion-related processes in the right hemisphere. In Experiment 1 the NSW was lateralized in the noise KR condition only; this condition was assumed to have the most negative impact and indeed caused right hemisphere dominance of the NSW. In Experiment 3, however, the NSW was lateralized only in the Control condition, and in Experiment 2 the NSW was lateralized in both the positive and the negative reward condition. Thus, the lateralization effects of the KR manipulations are inconclusive. The result of the Experiment 2 that in the reference condition the NSW was not lateralized could indicate that emotional value of the task in itself may cause lateralization of the NSW. Birbaumer, Elbert, Canavan, & Rockstroh (1990) argued that the intensity, but not the different qualities of emotional processing may play a role in determining slow waves. This implies that positive or negative feedback structures might cause similar effects, depending on their intensity. The positive and negative reward conditions in Experiment 2 may have been equally intense, and thus both caused the same lateralization, whereas the reference condition was less intense and lacked lateralization.