Spatial Frames of Reference in Hemispatial Neglect Patients

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Abstract

The coordinate systems that the human brain uses to represent objects in space are still under debate. They can be studied by analyzing patients with a lesion in the parietal lobe, since these patients fail to respond to stimuli that are presented contralateral to the brain lesion: a lesion in the right hemisphere leads the subject to ignore the left side of the space. But what is *left*? We analyze an experiment where neglect patients perform visually guided saccades under different experimental conditions. Determining where neglect patients have longer reaction time and higher probability of errors helps to identify the dominant coordinate system that the brain uses.

1 Introduction

The parietal lobe is the part of the brain responsible for processing and coding spatial information in humans: patients with a lesion in the parietal lobe fail to report, respond or orient to stimuli that are presented contralateral to the brain lesion. For example, patients with a lesion in the right hemisphere tend to ignore the left side of the space. Manifestations of right hemisphere neglect depend on the severity of the lesion: they might vary from drawing only the right side of objects, when asked to copy some objects, to ignoring the left side of the body when lesions are more severe.

In this context, in order for *left* and *right* to be well defined, we have to specify the coordinate system that the human brain uses to locate objects in the space; *left* and *right* are not absolute concepts, but they have to be defined with respect to some reference system, often called frame of reference. Frames of reference can be classified as follows: *egocentric*, if spatial information is coded with respect to viewer-centered coordinates, and *allocentric*, if instead spatial information is coded independently on the viewer. We can further distinguish egocentric frames of reference when the coordinate system is centered on the line of sight (in this case we say *retinotopic* frame of reference), the midline of the head (*craniotopic*), and the midline of the trunk (*trunk-centered*). Analogously allocentric frames of reference can be classified as *environment-centered* if the coordinate system is centered on the midline of the environment, or as *object-centered* if the coordinate system is based on the midline of objects.

Evidence on the nature of spatial representation may be obtained by studying humans who have sustained a lesion in the parietal lobe, in particular in the right hemisphere since in this case neglect is more frequent and severe than neglect following left hemisphere lesions. Noting the midline with respect to which information is ignored gives an indication of the underlying reference frame of internal visuospatial representation: if the frame of reference is retinotopic, for example, patients with a right hemisphere lesion will be impaired when stimuli appear on the left of the line of gaze.

At present, there is no agreement on the coordinate system with which spatial representations are defined in humans: many experiments have been performed comparing groups of normal subjects and neglect patients, with contradictory results. However the experiments did not always allow for discrimination among the coordinate systems. Behrmann (1998) performed an experiment in which frames of reference (retinotopic, craniocentric and trunk-centered) are decoupled from each other as well as decoupled from the environmental frame of reference. In Section 2 the experiment is described.

The specific aim of this paper is to analyze the data from that experiment in order to determine in which part of the space, in terms of frame of reference, targets are neglected when subjects perform visual tasks. Patients exhibit various effects of neglect, which can be evident in the reaction time, the error trials, velocity, acceleration, etc. In Section 3 of this paper we focus on the reaction time. When neglect patients respond to stimuli appearing in the contralateral hemifield, they might tend to have a longer reaction time; this means that the time since the target appears and eyes start moving gets longer in neglect patients. We therefore try to determine where the reaction time gets longer for patients. In Section 4 we analyze the error trials. Knowing in which part of the space neglect patients make more errors helps to identify the dominant frame of reference: if a target appears in the contralateral hemifield, neglect patients might perceive the stimuli, but move eyes in a wrong direction or miss the target. Section 3 and 4 are each divided in three parts: in the first, the patients are analyzed as a group, in the second they are analyzed individually to understand how individual subject relates to the group, and in the last part comparisons between the patient group and the control group are made. In Section 5, we present some comments on the design of experiment, and, finally, in Section 6 we present the conclusions.

2 Experiment and Data

The experiment consists of visually guided saccades (rapid eye movements) in two groups of subjects: 10 normal subjects with no evidence of clinical neglect, and 5 patients with lesions of the parietal lobe in the right hemisphere. Subjects are seated 1 meter from a circular array, which contains targets at positions $-15°$, $-10°$, $-5°$, $0°$, $+5°$, $+10°$, $+15°$ (expressed in degrees of visual angle). Targets consist of light emitting diodes (LED's). The task of the experiment is to fixate on a particular target position, after a random time, from 500 to 1.500 m-sec, a target is presented by illuminating a LED, and subjects have to look at the target and return to the original position.

In order to isolate single frame of reference contributions, seven experimental conditions are considered.

a) *Baseline* condition: the midlines of eyes, head, trunk and environment are aligned. Subjects have to fixate position $0°$. A target appears at one of positions $-15°$, $-10°$, $-5°$, $+5°$, $+10°$, $+15°$. In this condition, if patients are impaired at targets on the left, we cannot distinguish with respect to which coordinate system the deficit is occurring since *left* is the same with respect to all frames of reference. In the following conditions, eyes, head and trunk are systematically decoupled.

b) *Eyes left* condition: the head and the trunk are aligned with the midline of the environment-centered frame of reference, while the retinotopic frame is decoupled making subjects keep the fixation on $-15°$. In this case all targets appears on the right of the line of gaze.

c) *Eyes right* condition: the setting is the same as condition b), but the retinotopic frame is decoupled by making subjects keep fixation on $+15°$. In this case all targets appear on the left of the line of gaze.

d) *Head left* condition: the eyes and the trunk are aligned with the midline of the environment, while the head-centered coordinate is decoupled by aligning the midline of the head to $-15°$.

e) *Head right* condition: the setting is the same as condition d), but the head-centered frame of reference is decoupled by aligning the midline of the head to $+15°$.

f) *Trunk left* condition: the eyes and the head are aligned with the midline of the environment, while the trunk-centered coordinates are decoupled by aligning the midline of the trunk to $-15°$.

g) *Trunk right* condition: the setting is the same as condition f), but the trunk-centered frame of reference is decoupled by aligning the midline of the trunk to $+15°$.

The experimental conditions are depicted in Figure 1. The dashed line indicates where which part of the body is aligned with which target angle. Note that the eyes keep fixation on $0°$ in all experimental condition but *eye-left* and *eye-right* conditions.

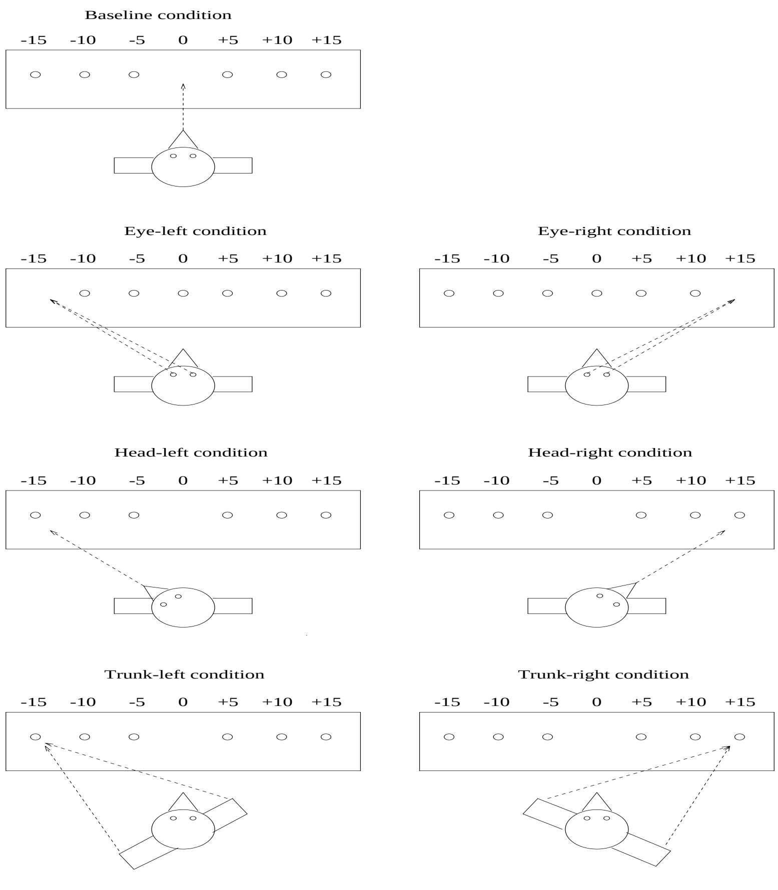

Figure 1: Experimental conditions.

To prevent unwanted movement during trials, subjects are seated in a heavy chair on a carpet and, to stabilize the head position, a chin rest is used. The eye movements are recorded with infra-red monitoring, and analyzed off line by the WINSAC software (McCurtain, 1997), which extracts traces measurements characteristic of the eye movement from the voltage. We analyzed the measurements obtained by WINSAC.

Initially the experiment was designed to have one replication of trials for each subject, where a replication is intended to be a set of 9 trials for each target position and each experimental condition (for a total of $9 \times 6 \times 7 = 378$ trials for each subject). In practice, the number of successful trials was much smaller due either to technical failures or subject's errors. Therefore the number of replications was different for each subject.

We analyzed two sets of data: one contains, for each subject, eight measurements on trials successfully performed. These measurements are: peak velocity, peak acceleration, peak deceleration, target position, starting position, experimental condition, reaction time, and number of saccades.

The second data set we analyzed contains for each subject the number of trials that were not successfully performed. These trials were further classified as missed trials (when subject missed the target), wrong direction trials (when subject moved the eyes in the wrong direction), and invalid trials (when some technical failures happened). Missed and wrong direction trials are considered subject errors. This data set contains, for each subject, the number of missed trials, wrong direction trials, invalid trials and total number of trials performed on that subject.

3 Analysis of Reaction Time

In this section we focus the analysis on the reaction time. In Section 3.1, we present the analysis of the reaction time in the patient group to characterize common pattern. In Section 3.2, we analyze each patient individually and compare how individual behavior relates to the group. Finally, in section 3.3, we compare the patient group with the control group.

3.1 Patient group analysis

We present in this section two models we used to analyze the reaction time. Both models capture different aspects of the phenomena and help to identify dominant frames of reference. The order of presentation does not correspond to the order of importance. As we will see in detail in the next sections, the head position and trunk position do not have significant effects on the reaction time, meanwhile the eyes and the environment position do. Due to the experimental design, it is hard to isolate the single effects of the environmental angle and retinotopic angle. In section 3.1.1 and 3.1.2 we emphasize different interpretations.

We excluded one subject from the analysis of reaction time on the patient group. The analysis is based on four patients. The reasons for this will be more clear in section 3.2, when we analyze each subject individually.

3.1.1 Environmental Angle

Since the experiment has repeated measurements on the same subject, we used a Normal linear mixed effect model (Laird and Ware, 1982) to model the log-reaction time. We used a logarithmic transformation of the reaction time to adjust for unequal error variances and non-normality of the error terms. The explanatory variables are the target position and the experimental condition. Note that the target position is expressed as degrees from the midline of the array, which also corresponds to the midline of the environment. In the rest of the paper we refer to the target position in terms of the environmental angle.

As suggested by the observed means of log-reaction time, see Appendix A, we assume that the relation between log-reaction time and environmental angle is polynomial. We choose the order of the polynomial based on the Bayesian Information Criteria, BIC, (Schwarz, 1978), adjusted for the right sample size as suggested by Pauler (1998):

$$BIC = -2 \log p(y|\hat{\theta}) + \sum_{k=1}^{p_0} \log N_k$$

where $p(y|\hat{\theta})$ is the likelihood of data y evaluated at the MLE, $\hat{\theta}$, of $\theta = (\theta_1, \ldots, \theta_{p_0})' \in I\!R^{p_0}$ and $N_k = I$ (number of subjects) if θ_k has an associated random effect, or $N_k = \sum_{i=1}^{I} n_i$ (total number of observation) otherwise. The model with the smallest value of BIC is chosen.

Table 1 shows the Log-likelihood and BIC value associated to polynomials of different order (where we assume only a random intercept).

Table 1

Order	**likelihood**	**BIC**
1	-1342.18	2795.81
2	-1320.44	2760.19
3	-1320.11	2767.39
	N=2596	I=4

From the table it is clear that a second order polynomial is preferred. We test for a random slope using a likelihood ratio test, which suggests that we do not have enough evidence to include in the model a random slope ($p = .87$).

Finally we fit the following model:

$$y_{ikj} = \alpha + \alpha_i + \gamma_k + \beta X_{ikj} + \beta_k X_{ikj} + \tau X_{ikj}^2 + \epsilon_{ikj} \tag{1}$$

where

y_{ikj}	log-RT for subject i, $i = 1, .., 4$; condition k, $k = 1, ..., 7$; replication j, $j = 1, ..., n_{ik}$;
X_{ikj}	environmental angle;
α	grand mean assumed to be the *baseline* condition;
α_i	random effects $\sim N(0, \sigma_\alpha^2)$;
γ_k	effects of the experimental conditions;
	expressed as deviation from *baseline* condition, $\gamma_1 = 0$;
β	common slope;
β_k	interaction of X and experimental condition;
	expressed as deviation from *baseline* condition;
τ	quadratic effect of the environmental angle;
ϵ_{ikj}	error term assumed $\sim N(0, \sigma_\epsilon^2)$.

Note that this model is parameterized in such a way that the coefficient for experimental condition and its interaction with the environmental angle represent increases in intercept and slope from the *baseline* condition.

The model parameter estimates are obtained using the procedure **proc mixed** in SAS (1994) using Restricted Maximum Likelihood, REML, method. The estimates of the fixed effects of the model are in Table 2, where we highlight the significance level according to the standard notation: $*$ denotes 0.05 significance level, $** = 0.01$ and $*** = 0.001$.

Table 2

parameter	description		estimate ± sd
α	grand mean	**	-1.3001 ± 0.1497
γ_2	incr. in intercp. in EL	***	-0.2294± 0.0288
γ_3	incr. in intercp. in ER		0.0269 ± 0.0361
γ_4	incr. in intercp. in HL		0.0543 ± 0.0296
γ_5	incr. in intercp. in HR		-0.0188 ± 0.0293
γ_6	incr. in intercp. in TL		0.0291 ± 0.0288
γ_7	incr. in intercp. in TR		0.0120 ± 0.0294
β	common slope	***	-0.0200 ± 0.0019
β_2	incr. in slope in EL	***	0.0173 ± 0.0029
β_3	incr. in slope in ER	**	0.0116 ± 0.0038
β_3	incr. in slope in HL		0.00001± 0.00269
β_3	incr. in slope in HR		0.0007 ± 0.0027
β_3	incr. in slope in TL		0.0015 ± 0.0026
β_3	incr. in slope in TR		0.0030 ± 0.0027
τ	quadratic effect	***	0.0008±0.0001
σ_α^2	between subj. var.		0.0874 ± 0.0715
σ_ϵ^2	within subj. var.		0.1538 ± 0.0043

In the experimental conditions *head-left, head-right, trunk-left* and *trunk-right*, the log-reaction time does not behave significantly differently from the *baseline* condition, since in each of those experimental conditions the deviations in slope and intercept from *baseline* are not significantly different from zero. This suggests that no matter where the head and trunk are aligned, the log-reaction time behaves the same.

Figure 2 shows the fitted model for those experimental conditions which are significantly different from the *baseline* condition in either intercept or slope. The corresponding observed means are plotted too.

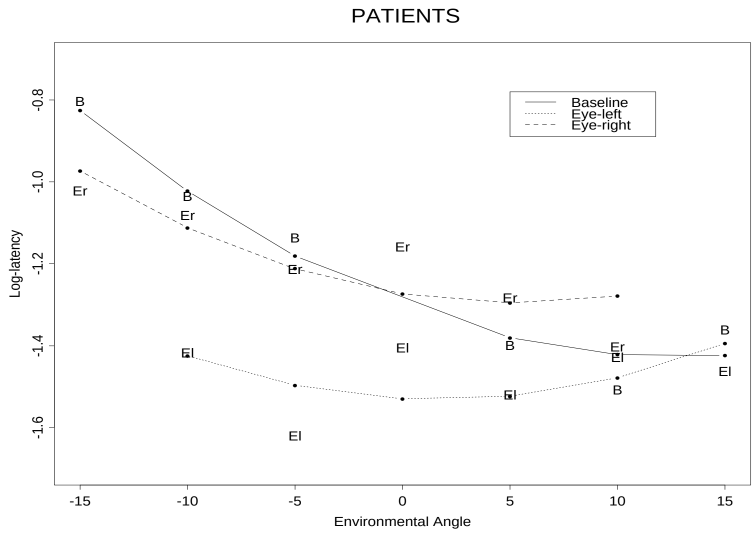

Figure 2: The fitted model is plotted together with the observed means for *baseline*, *eye-left*, and *eye-right* condition, denoted with “B”, “El” and “Er” respectively.

In Figure 2, we see that the log-reaction time is consistently smaller in *eye-left* condition than in *eye-right* condition for all targets. Furthermore in those experimental conditions the linear effect of the environmental angle is not significantly different from zero.

3.1.2 Retinotopic angle

In the previous section we modeled how the log-reaction time changes with the environmental angle and the experimental condition. As the target moves to the left of the environment, the log-reaction time gets longer, and the effect of the environmental angle, in terms of slope, gets smaller if targets appear on the left (in *eye-right* condition) and on the right (*eye-left* condition) of the line of gaze.

In this section we model the log-reaction time with the retinotopic angle and experimental condition. In this way, once the effect of the retinotopic angle is considered, we can isolate the environmental angle's effect. The retinotopic angle is the position of the target relative to fixation. In order to convert the environmental coordinates to the retinotopic ones, let X' be the new coordinates, and, as before let X be the environmental position of the target. Then we set:

$$X' = \begin{cases} X & \text{in } \textit{baseline, head-left head-right, trunk-left and trunk-right} \text{ condition;} \\ X + 15^\circ & \text{in } \textit{eye-left} \text{ condition;} \\ X - 15^\circ & \text{in } \textit{eye-right} \text{ condition.} \end{cases}$$

As in the previous section, we use a Normal linear mixed-effect model. After we selected the order of the polynomial regression based on the BIC value, and we tested for random slope, we fit the following model:

$$y_{ikj} = \alpha + \alpha_i + \gamma_k + \beta X'_{ikj} + \beta_k X'_{ikj} + \tau X'^2_{ikj} + \epsilon_{ikj} \tag{2}$$

where

y_{ikj}	log-reaction time for subject i, $i = 1,..,4$; condition k, $k = 1,...,7$; replication j, $j = 1,...,n_{ik}$;
X'	retinotopic angle;
α	grand mean assumed to be the *baseline* condition;
α_i	random effects $\sim N(0, \sigma^2_\alpha)$;
γ_k	effects of the experimental conditions; expressed as deviation from *baseline* condition, $\gamma_1 = 0$;
β	common slope;
β_k	interaction of X' and experimental condition; expressed as deviation from *baseline* condition;
τ	quadratic effect of the retinotopic angle;
ϵ_{ikj}	error term assumed $\sim N(0, \sigma^2_\epsilon)$.

The REML estimates of the fixed effects are in the next table:

Table 3

parameter	description	estimate ± sd	
α	grand mean	**	-1.3001 ± 0.1497
γ_2	incr. in intercp. in EL		-0.0137 ± 0.0606
γ_3	incr. in intercp. in ER		0.0775 ± 0.0787
γ_4	incr. in intercp. in HL		0.0543 ± 0.0296
γ_5	incr. in intercp. in HR		-0.0188 ± 0.0293
γ_6	incr. in intercp. in TL		0.0291 ± 0.0288
γ_7	incr. in intercp. in TR		0.0120 ± 0.0294
β	common slope	***	-0.0200 ± 0.0019
β_2	incr. in slope in EL		-0.0061 ± 0.0045
β_3	incr. in slope in ER	***	0.0350 ± 0.0053
β_3	incr. in slope in HL		0.00001± 0.0027
β_3	incr. in slope in HR		0.0007 ± 0.0027
β_3	incr. in slope in TL		0.0015 ± 0.0026
β_3	incr. in slope in TR		0.0030 ± 0.0027
τ	quadratic effect	***	0.0008 ± 0.0001
σ^2_α	between subj. var.	***	0.0874 ± 0.0715
σ^2_ϵ	within subj. var.	***	0.1538 ± 0.0043

As before, there is no significant effect of the head and the trunk position, since both intercept and slope in these experimental conditions are not significantly different from the *baseline* condition.

Figure 3 displays the fitted model together with the observed means for *baseline*, *eye-left*, and *eye-right* condition, even though, in *eye-left* condition, the log-reaction time does not behave differently from *baseline* condition.

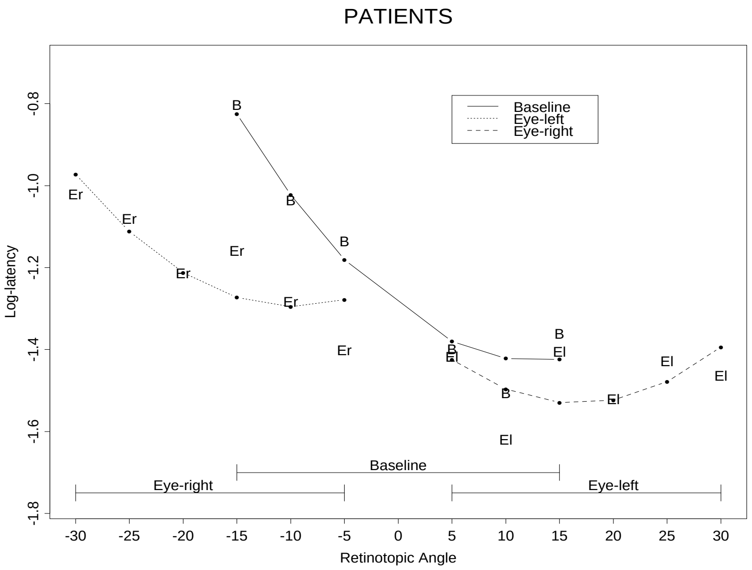

Figure 3: The fitted model is plotted together with the observed means for *baseline*, *eye-left*, and *eye-right* condition, denoted with “B”, “El” and “Er” respectively.

If we compare the log-reaction time in the *baseline* and *eye-right* condition at position $-15°$, $-10°$, and $-5°$ relative to fixation, we see that the log-reaction time gets significantly shorter in the *eye-right* condition. This is due to the fact that, in the *eye-right* condition, those targets are on the right of the environment, while in the *baseline* condition they are on the left. This suggests that when targets are on the left of the line of gaze, the log-reaction time gets even longer if they are also on the left of the environment.

The environment effect is not evident, instead, when targets appear on the right of the line of gaze. Comparing the log-reaction time at position $5°, 10°$, and $15°$ relative to fixation, in *baseline* and *eye-left* condition, we do not see any significant difference. We present a 95% simultaneous confidence interval, using the Bonferroni correction, for the pairwise comparison of the mean log-reaction time for *baseline* and *eye-right* condition and for the comparison of the mean log-reaction time for *baseline* and *eye-left* condition in the next table. We denote with $\mu_{(x,y)}$ the mean log-reaction time in experimental condition x and retinotopic angle y.

Table 4

	estimate	sd	95% CI
$\mu_{(er,-15)} - \mu_{(b,-15)}$	-0.355	0.088	(-0.566, -0.144)
$\mu_{(er,-10)} - \mu_{(b,-10)}$	-0.248	0.062	(-0.396, -0.100)
$\mu_{(er,-5)} - \mu_{(b,-5)}$	-0.265	0.098	(-0.500, -0.030)
	estimate	sd	95% CI
$\mu_{(el,5)} - \mu_{(b,5)}$	-0.018	0.065	(-0.174, 0.138)
$\mu_{(el,10)} - \mu_{(b,10)}$	-0.113	0.062	(-0.261, 0.035)
$\mu_{(el,15)} - \mu_{(b,15)}$	-0.044	0.060	(-0.188, 0.100)

In summary, there is a tendency in neglect patients to have a slower log-reaction time when targets are on the left of the line of gaze, and this is modulated by the target position relative to the environment. If targets appear both on the left of the midline of gaze and of the environment, the log-reaction time is longer than when targets appear on the left of the line of gaze, but on the right of the environment.

3.2 Individual analysis

In this section we analyze each subject individually, and compare the individual behavior of log-reaction time with the model described in the previous section. Although we analyzed individual behavior in both environmental and retinotopic coordinate systems, for the sake of simplicity we report the results of individual subjects' analyses of model (2), where we model the log-reaction time with the retinotopic angle. It is obvious that in comparing individual and group behavior, the conclusions are analogous if we use model (1) instead.

We mentioned before that one patient, we denote it as p3437, was excluded from the analysis. There were two reasons related to each other, for excluding this subject: first, there were many missing observations when targets appeared on the left of line of gaze; second, the few observations remaining were very influential, so that the overall behavior of log-reaction time was very different from the rest of the patients. Instead of including this subject in the analysis, we preferred to analyze it individually. In Figure 4 we can see observed data for patient p3437 and its observed means.

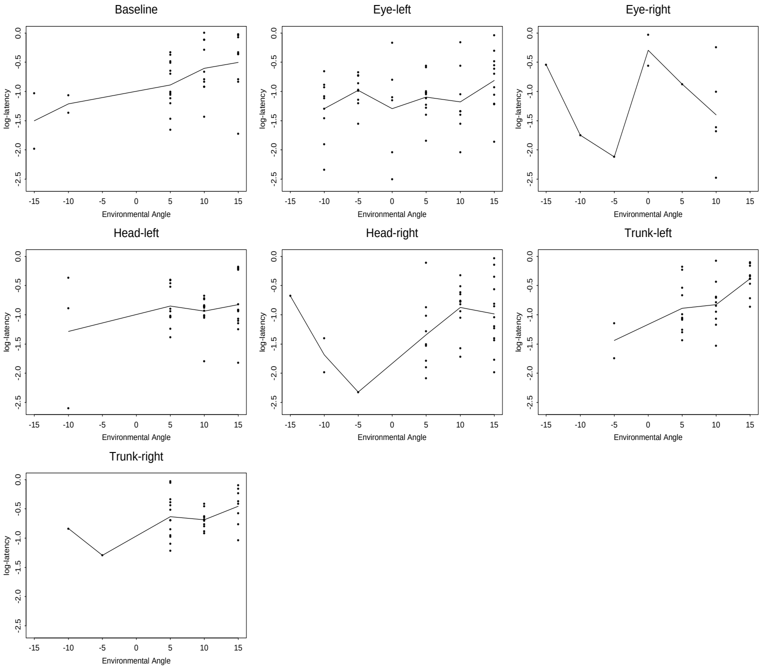

Figure 4: Observed means, connected with a solid line, and data for patient p3437.

For each patient we fit the following linear model:

$$y_{kj} \quad = \quad \alpha + \gamma_k + \beta X'_{kj} + \beta_k X'_{kj} + \tau X'^2_{kj} + \epsilon_{kj}$$

where

y_{kj}	log-reaction time in the experimental condition k, $k = 1, ..., 7$ and replication j, $j = 1, ..., n_{ik}$;
X'	retinotopic angle;
α	grand mean assumed to be the *baseline* condition;
γ_k	effects of the experimental conditions; expressed as deviation from *baseline* condition, $\gamma_1 = 0$;
β	common slope;
β_k	interaction of X' and experimental condition; expressed as deviation from *baseline* condition;
τ	quadratic effect of the retinotopic angle;
ϵ_{kj}	error term assumed $\sim N(0, \sigma^2)$.

Table 5 shows the maximum likelihood estimates of the parameters of the model above for each patient, and estimates of the fixed effects for the whole group.

Table 5

	lme	Patients				
	on 4 subj.	p3359	p3382	p3433	p3405	p3437
α	*** -1.3001	*** -1.6885	*** -1.3366	*** -0.9781	*** -1.5396	*** -1.0301
γ_2	-0.0137	-0.1162	-0.1197	0.1938	* 0.3960	-0.1877
γ_2	0.0775	0.1535	-0.1338	0.0607	* 0.8495	* -0.8978
γ_2	0.0543	* 0.1545	-0.0296	0.0281	** 0.4490	-0.0190
γ_2	-0.0188	-0.0572	0.00003	-0.0736	** 0.4982	-0.2177
γ_2	0.0291	0.1070	0.0325	-0.0447	0.0721	-0.1591
γ_2	0.0120	0.1003	0.0396	-0.0343	0.0538	0.2264
β	*** -0.0200	*** -0.0223	*** -0.0201	*** -0.0218	0.0148	** 0.0321
β_2	-0.0061	-0.0025	0.0048	-0.0070	*** -0.0528	-0.0333
β_3	*** 0.0350	*** 0.0442	** 0.0296	*** 0.0293	-0.0031	** -0.1350
β_4	0.00001	0.0020	-0.0039	0.0075	* -0.0344	-0.0207
β_5	0.0007	-0.0028	0.0037	0.0006	* -0.0378	-0.0169
β_6	0.0015	0.0044	-0.0007	0.0045	-0.0064	0.0125
β_7	0.0030	0.0017	0.0062	0.0074	-0.0190	-0.0159
τ	*** 0.0008	*** 0.0008	*** 0.0006	*** 0.0007	* 0.0009	0.0004

The first three patients in the table, namely p3359, p3382, and p3433, seems to be very homogeneous: all of them have a highly significant negative slope ($p < 0.001$) in the *baseline* condition, a highly significant quadratic term ($p < 0.001$), and a highly significant positive increment in slope ($p < 0.001$) when eyes are aligned at $+15^\circ$. From Table 5 it would seem that subject p3405 behaves differently from the others. The model is parameterized in such a way that the intercept and slope are deviations from the *baseline* condition. This means that if baseline is for some reason different, then the estimates of the coefficients in the other conditions will be influenced by that. Patient p3405, in particular, has only one observation at the left of 0° in the *baseline* condition (which has been removed from the analysis), and the slope seems positive, but the overall behavior of the log-reaction time of patient p3405 is consistent with the other three patients. This is confirmed by the fact that if we base the linear mixed-effect model only on the first three patients, the estimates of the fixed effects do not change.

The patient who was excluded from the analysis of reaction time, p3437, has a highly significant positive slope ($p < 0.01$) in the *baseline* condition as well as in *head-left*, *head-right*, *trunk-left* and *trunk-right*, and this is exactly the opposite to what happens for the other patients. There might be some reason why this patient is so different from the other three patients, maybe a more severe lesion.

Figure 5 shows the observed means for patients p3359, p3382, p3433, and p3405 in each experimental condition. We see that there is a very similar pattern in the mean log-reaction time in each experimental condition.

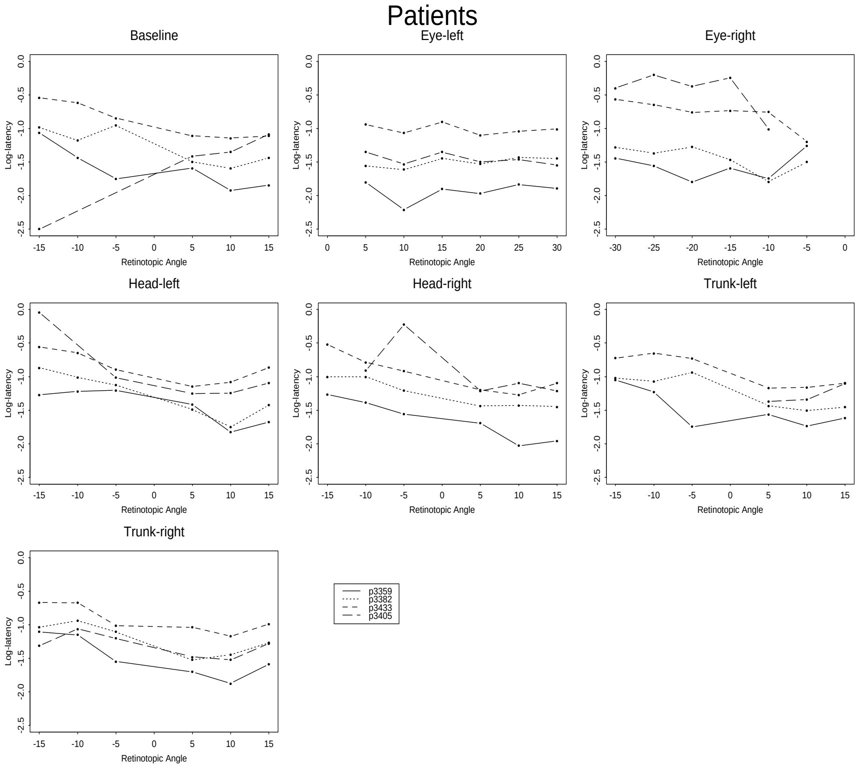

Figure 5: Individuals observed means of log-reaction time.

3.3 Comparison of patients versus controls

So far we have focused the interpretation of the model on the patient group only. It is also interesting to compare how different the reaction time behaves in the patient and control groups as the retinotopic angle changes. We refer to Appendix B for the details of the model selection for the control group. We report in Table 6 the REML estimates of the fixed effects in the two groups:

Table 6

	description		Controls		Patients
α	grand mean	***	-1.2850 $\pm$ 0.0416	**	-1.3001 $\pm$ 0.1497
γ_2	incr. in intercp. in EL		0.0603 $\pm$ 0.0383		-0.0137 $\pm$ 0.0606
γ_3	incr. in intercp. in ER	***	0.1270 $\pm$ 0.0370		0.0775 $\pm$ 0.0787
γ_4	incr. in intercp. in HL	***	-0.0636 $\pm$ 0.0155		0.0543 $\pm$ 0.0296
γ_5	incr. in intercp. in HR	**	-0.0484 $\pm$ 0.0153		-0.0188 $\pm$ 0.0293
γ_6	incr. in intercp. in TL	**	-0.0390 $\pm$ 0.0152		0.0291 $\pm$ 0.0288
γ_7	incr. in intercp. in TR		-0.0192 $\pm$ 0.0153		0.0120 $\pm$ 0.0294
β	common slope		-0.0023 $\pm$ 0.0011	***	-0.0200 $\pm$ 0.0019
β_2	incr. in slope in EL	***	-0.0108 $\pm$ 0.0026		-0.0061 $\pm$ 0.0045
β_3	incr. in slope in ER	***	0.0147 $\pm$ 0.0026	***	0.0350 $\pm$ 0.0053
β_3	incr. in slope in HL		0.0015 $\pm$ 0.0014		0.00001$\pm$ 0.0027
β_3	incr. in slope in HR		-0.0008 $\pm$ 0.0014		0.0007 $\pm$ 0.0027
β_3	incr. in slope in TL		0.0006 $\pm$ 0.0014		0.0015 $\pm$ 0.0026
β_3	incr. in slope in TR		-0.0025 $\pm$ 0.0014		0.0030 $\pm$ 0.0027
τ	quadratic effect	***	0.0005 $\pm$ 0.00005	***	0.0008 $\pm$ 0.0001

The main difference between patients and controls is in the linear coefficient, β, of the retinotopic angle, X', in the *baseline* condition, which represents the linear trend in the log-reaction time. In the patient group there is a significant negative slope (-0.020 ± 0.002): this means that as targets move to the left of the line of gaze, the log-reaction time gets longer. In the control group, instead, the slope is not significantly different from zero, (-0.002 ± 0.001): this suggests that there is a symmetry in the log-reaction time for targets on the left and on the right of the line of gaze. Both groups have a significant quadratic term, but in the patient group it is much bigger: (0.0008 ± 0.0001) for patients versus (0.0005 ± 0.00005) for controls. This means that as target angle increases in either directions from fixation, the log-reaction time gets much longer for patients than for controls. Figure 6 shows the fitted models for patients (solid line) and controls (dashed line) for each experimental condition together with the observed means.

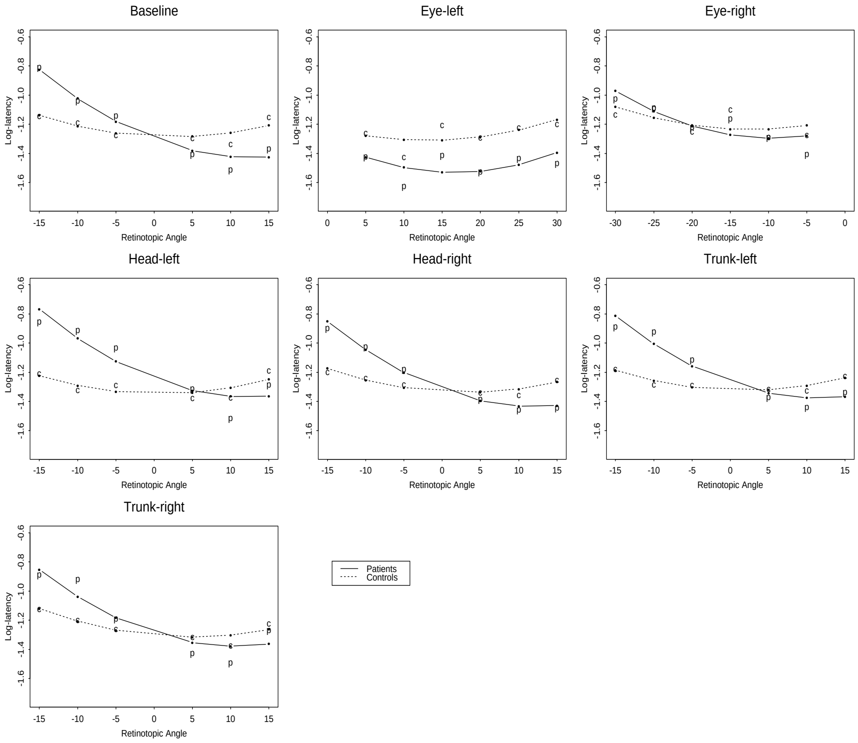

Figure 6: Fitted models for patients and controls with the corresponding observed means, denoted with p and c respectively.

From Figure 6 we see that these patients, compared to the controls, have longer log-reaction time on the left of the fixation, but on the right the log-reaction time is shorter. This might suggest a compensation mechanism in neglect patients, such that if they lose ability on the contralateral hemifield, they improve it in the ipsalteral one.

4 Error Trials Analysis

As we mentioned before, analyzing the error trials helps to identify the dominant frame of reference used by the brain to locate objects in the space. If the dominant frame of reference is centered on the eyes, we would expect not only an increase in the reaction time when targets appear on the left of fixation point, but we would also expect that patients are more likely to make errors there.

The error trials data contain for each subject the number of missed trials, wrong direction trials, invalid trials and the total number of trials, for each target and experimental condition. We refer to the end of Section 2 for details on this classification. Both missed trials and wrong direction trials are considered subject errors. The invalid trials, defined to be errors caused by a machine failures, were independent of the subjects. We, therefore, adjusted the total number of trials by excluding the invalid trials due to technical errors.

In Section 4.1 we analyze the error trials in the patient group. In Section 4.2 we analyze each subject individually and compare it to the group. Finally in Section 4.3 we compare the patient group with the control group.

4.1 Patient group analysis

We analyze the error trials using a mixed effect logistic regression. We assume that the number of errors for subject i, condition k, follows a Binomial distribution with parameters p_{ik} and n_{ik}, where n_{ik} is the total number of valid trials, and p_{ik} is the probability of making an error in one trial. We model the error probability p_{ik} as follows

$$\text{logit}(p_{ik}) = \log\left(\frac{p_{ik}}{1-p_{ik}}\right) = \alpha + \beta_i + \gamma_k + \tau_k X'_{ik} \tag{3}$$

where

p_{ik} probability of making an error of subject i, in condition k, $k = 1, .., 7$;
α intercept;
β_i random intercept assumed to be $N(0, \sigma^2_\beta)$;
γ_k main effect of experimental condition as deviation from baseline, $\gamma_1 = 0$;
X' retinotopic angle;
τ_k interaction of experimental condition and X'.

Model (3) allows each subject to have different intercept. We fit this model using the macro **glimmix** in SAS (1994), which estimates the the model parameters using REML methods. We also use Bayesian methods to estimates the model parameters. Table 7 shows the REML estimates of the fixed effects obtained using SAS, and the Bayesian estimates obtained using BUGS (Spiegelhalter et al. 1995).

Table 7

	description	SAS		BUGS	
α	grand mean		-1.912 ($\pm$ 0.818)	***	-1.930 ($\pm$ 0.143)
γ_2	incr. in intercp. in EL		-0.999 ($\pm$ 0.629)		-0.971 ($\pm$ 0.389)
γ_3	incr. in intercp. in ER	**	1.760 ($\pm$ 0.535)	**	1.777 ($\pm$ 0.345)
γ_4	incr. in intercp. in HL		-0.206 ($\pm$ 0.340)		-0.214 ($\pm$ 0.220)
γ_5	incr. in intercp. in HR		-0.051 ($\pm$ 0.317)		-0.056 ($\pm$ 0.207)
γ_6	incr. in intercp. in TL		-0.074 ($\pm$ 0.323)		-0.078 ($\pm$ 0.211)
γ_7	incr. in intercp. in TR		0.267 ($\pm$ 0.299)		0.269 ($\pm$ 0.197)
τ_1	slope in B	***	-0.125 ($\pm$ 0.020)	***	-0.127 ($\pm$ 0.013)
τ_2	slope in EL		0.001 ($\pm$ 0.029)		-0.001 ($\pm$ 0.018)
τ_3	slope in ER		0.015 ($\pm$ 0.024)		0.015 ($\pm$ 0.016)
τ_4	slope in HL	***	-0.158 ($\pm$ 0.025)	***	-0.160 ($\pm$ 0.017)
τ_5	slope in HR	***	-0.139 ($\pm$ 0.022)	***	-0.140 ($\pm$ 0.015)
τ_6	slope in TL	***	-0.172 ($\pm$ 0.024)	***	-0.174 ($\pm$ 0.016)
τ_7	slope in TR	***	-0.115 ($\pm$ 0.020)	***	-0.116 ($\pm$ 0.014)
σ^2_β	between subj. var.		3.112 ($\pm$ 2.244)		2.807 ($\pm$ 3.248)

Note that the model is parameterized in such a way that γ_i are deviation in intercept from the *baseline* condition, and β_i are not expressed as deviation in slope.

The Bayesian estimates are the means of the posterior distributions of the parameters. The posterior distributions are simulated via Gibbs sampling, assuming the following priors for the model parameters:

$$
\begin{array}{rcl}
\alpha & \sim & N(0,10) \\
\gamma_k & \sim & N(0,10) \quad k=2,..7 \\
\tau_k & \sim & N(\xi,\sigma^2_\tau) \\
\xi & \sim & N(0,10) \\
1/\sigma^2_\beta & \sim & \Gamma(1.44,.45) \\
1/\sigma^2_\tau & \sim & \Gamma(1.44,.45)
\end{array}
$$

The simulation is based on 5000 iterations, and had a burn in of 1000 iterations, see Appendix D for more details on the code in BUGS. Note that the estimates of the fixed effects are very similar, but the standard error are much smaller using BUGS.

As we observed in the reaction time analysis, for the error trials the experimental conditions *head-left, head-right, trunk-left*, and *trunk-right* are not different from the *baseline* condition: in all those conditions the intercepts and slopes are not significantly different from the ones in the *baseline* condition. There is a significant negative slope in the *baseline* condition ($\hat{\tau}_1 = -0.127 \pm 0.013$). This suggest that as the target moves to the left of the line of gaze, the log odds increases and so does the probability of making an error. Instead, in *eye-left* and *eye-right* condition there is no significant slope, which suggests that when all targets are on the left (or right) of the fixation point, the probability of errors is the same for all targets, and this probability is much larger when eyes are aligned at $+15°$ ($\hat{\gamma}_3 = 1.777 \pm 0.345$).

Figure 7 shows the fitted model together with the individual proportion of errors.

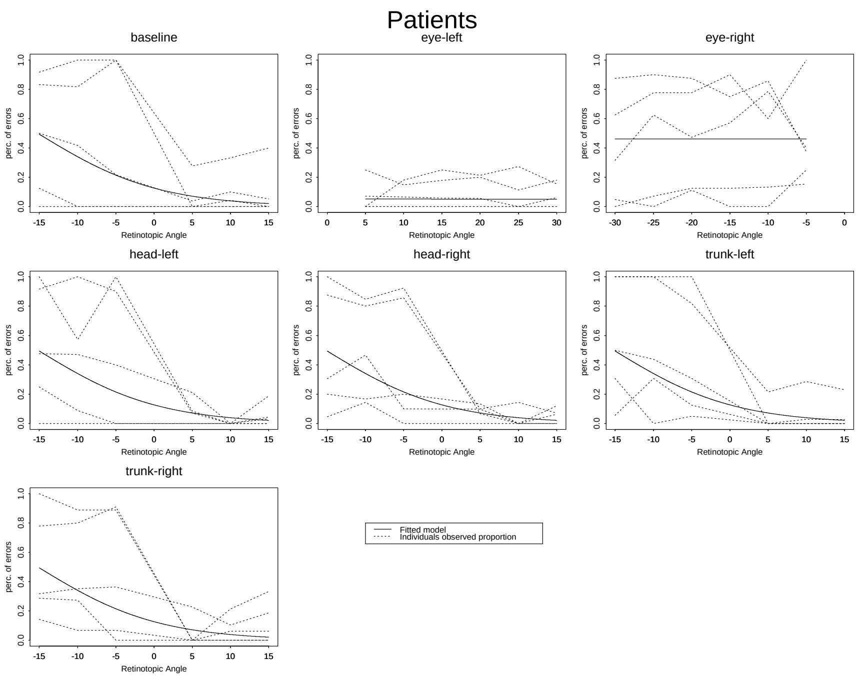

Figure 7: Fitted model for patients and individuals observed proportion.

In order to see if there is any effect of the environment, we computed the mean proportion of errors across subjects and compared it in the experimental conditions *baseline* and *eye-right* at targets $-15°$, $-10°$, $-5°$ relative to fixation, and in *baseline* and *eye-left* condition for targets at 0°, 5°, 10° from fixation. For each experimental condition and target angle, the mean proportion of errors across subjects was computed as weighted mean of individual error proportion $\hat{p}_i$, $i = 1,..,5$. The weights are the adjusted total number of trials n_i. In Table 8 we report the group error proportion, $\overline{p} = \sum_i n_i \hat{p}_i / \sum_i n_i$, for each condition and target angle (expressed in environmental degrees), with standard deviation $sd(\overline{p}) = \left(\sum_i n_i \hat{p}_i (1-\hat{p}_i)/(\sum_i n_i)^2\right)^{1/2}$, where $\hat{p}_i$ is the observed proportion of errors out of n_i trials for subject i.

Table 8

	Patients						
	-15	-10	-5	0	5	10	15
B	0.42 (0.04)	0.39 (0.03)	0.35 (0.03)		0.06 (0.02)	0.09 (0.03)	0.07(0.02)
EL		0.08 (0.03)	0.08 (0.03)	0.09 (0.03)	0.10 (0.03)	0.07 (0.02)	0.09(0.03)
ER	0.27 (0.04)	0.41 (0.04)	0.39 (0.05)	0.40 (0.04)	0.37 (0.04)	0.40(0.06)	
HL	0.45 (0.04)	0.31 (0.04)	0.33 (0.04)		0.08 (0.03)	0.00 0.00	0.05(0.02)
HR	0.38 (0.04)	0.44 (0.05)	0.33 (0.03)		0.08 (0.03)	0.02 (0.01)	0.06(0.02)
TL	0.43 (0.04)	0.46 (0.04)	0.35 (0.04)		0.03 (0.01)	0.05 (0.02)	0.04(0.02)
TR	0.38 (0.05)	0.37 (0.05)	0.35 (0.04)		0.06 (0.02)	0.07 (0.02)	0.11(0.03)

Using the Normal approximation to the distribution of $\hat{p}_i$, and assuming independence between subjects and across trials, we can compute the 95% simultaneous confidence interval for the difference in error proportions in *baseline* and in *eye-right* condition for targets at $-5°$, $-10°$, $-15°$ from fixation. The 95% simultaneous confidence intervals are obtained using the Bonferroni correction.

Table 9a

	estimates	sd	95% CI
$\overline{p}_{(b,-5)} - \overline{p}_{(er,-5)}$	0.02	0.06	(-0.12, 0.17)
$\overline{p}_{(b,-10)} - \overline{p}_{(er,-10)}$	0.02	0.05	(-0.10, 0.15)
$\overline{p}_{(b,-15)} - \overline{p}_{(er,-15)}$	-0.06	0.06	(-0.22, 0.10)

where $\overline{p}_{(x,y)}$ denotes the mean error proportion in experimental condition x and retinotopic angle y. The difference in error proportions in *baseline* and in *eye-left* condition for targets at 0°, 5°, 10° from fixation is shown in the next table:

Table 9b

	estimates	sd	95% CI
$\overline{p}_{(b,5)} - \overline{p}_{(el,5)}$	-0.02	0.04	(-0.10, 0.07)
$\overline{p}_{(b,10)} - \overline{p}_{(el,10)}$	0.01	0.04	(-0.09, 0.10)
$\overline{p}_{(b,15)} - \overline{p}_{(el,15)}$	-0.02	0.04	(-0.11, 0.06)

When targets appear on the left of fixation, there is no difference in the error proportion whether or not those targets are on the left or right of the environment. The same holds when targets appear on the right of fixation. This can be clearly seen in Figure 8, where the observed group error proportions are plotted for the comparisons above.

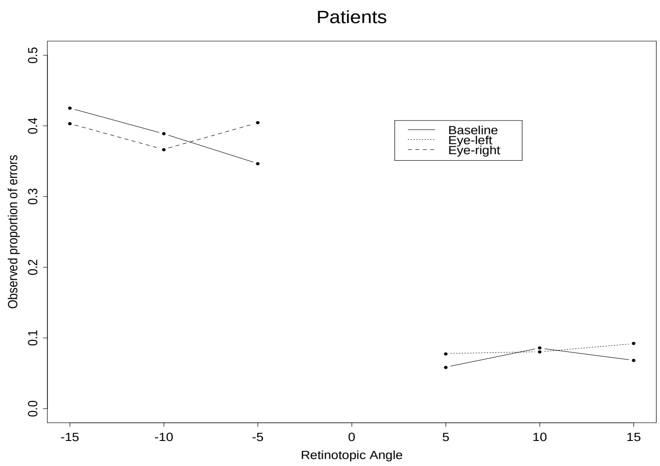

Figure 8: Observed proportion of errors for *baseline, eye-left* and *eye-right* condition.

Analogously to the log-reaction time, patients make more errors when targets appear on the left of the line of gaze, but there is not a modulation due to the position of the target relative to the environment, as we see in Figure 8.

4.2 Individual analysis

In this section we analyze each subject individually by fitting a logistic model; we then compare how individual behavior relates to the group. For each subject we fit the following model:

$$\mathrm{logit}(p_k) = \alpha + \gamma_k + \tau_k X'_k$$

where

p_k	probability of making an error in condition k;
α	intercept;
γ_k	main effect of experimental condition as deviation from baseline, $\gamma_1 = 0$;
X'	retinotopic angle;
τ_k	interaction of experimental condition and X'.

For each patients, the estimates of the coefficients are presented in the next table together with the estimates of the fixed effects for the whole group:

Table 10

	BUGS	Patients				
		p3359	p3382	p3433	p3405	p3437
α	*** -1.930	*** -3.713	*** -1.477	*** -3.154	-0.335	0.422
γ_2	-0.971	-0.022	0.259	1.037	* -2.932	** -2.239
γ_3	** 1.777	1.590	** 1.971	* 2.003	* 2.384	-0.690
γ_4	-0.214	1.063	0.133	-0.299	-0.057	-0.761
γ_5	-0.056	0.616	-0.102	* 1.338	-0.045	-0.649
γ_6	-0.078	0.641	-0.340	0.713	0.064	0.021
γ_7	0.269	0.965	0.422	0.379	-0.104	-0.281
τ_1	*** -0.127	-0.003	*** -0.097	-0.060	*** -0.295	*** -0.091
τ_2	-0.001	-0.003	-0.014	-0.020	-0.006	0.025
τ_3	0.015	0.024	0.024	0.047	0.047	-0.081
τ_4	*** -0.160	* -0.079	*** -0.107	-0.006	*** -0.254	*** -0.141
τ_5	*** -0.140	-0.063	** -0.067	-0.046	*** -0.271	*** -0.150
τ_6	*** -0.174	** -0.127	*** -0.135	* -0.069	*** -0.348	*** -0.143
τ_7	*** -0.116	** -0.132	-0.037	-0.072	*** -0.166	*** -0.129

There are three patients, p3382, p3405, and p3437, who seem very homogeneous: they all have significant negative slopes for *baseline, head-left, head-right, trunk-left* and *trunk-right*. This suggests that, as target moves to the left of fixation, the logit increases for all them. Note that all three patients have the highest intercepts in the group. They made on average more errors. Note in particular that patient p3437 has the highest intercept, and this is the patient excluded from the reaction time analysis.

The log-odds seems to be constant for almost all the experimental conditions for patients p3433 and p3359. Maybe these patients had a less severe lesion to the parietal lobe. The proportion of errors for each patients are in Figure 9.

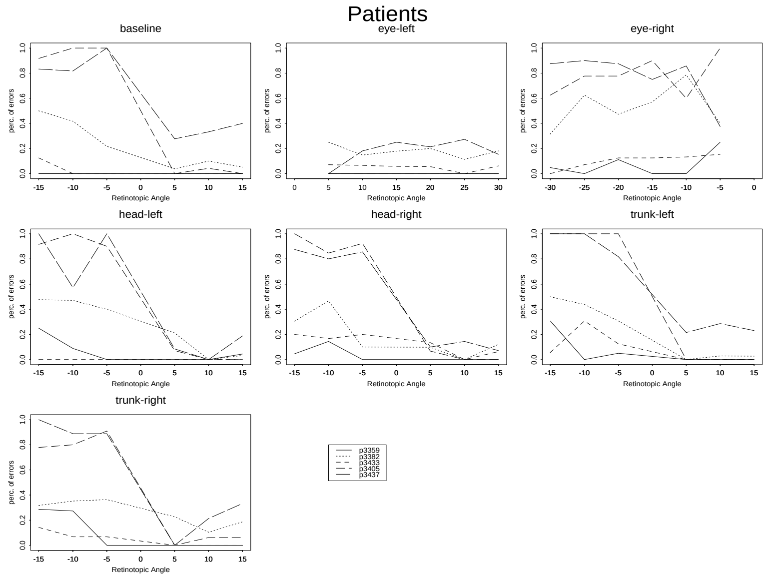

Figure 9: Individual observed proportion of error in the patient group.

4.3 Comparison of patients versus controls

As we did for the reaction time analysis, it is important to compare patients' behavior with that of controls. As we can see from the comparison of the observed error proportion in the control group and in the patient group in Figure 10, patients make on average more errors than control subjects, in particular when targets appear on the left of fixation (see for example condition *eye-right*). The observed mean error proportion for the control group can be found in Appendix C.

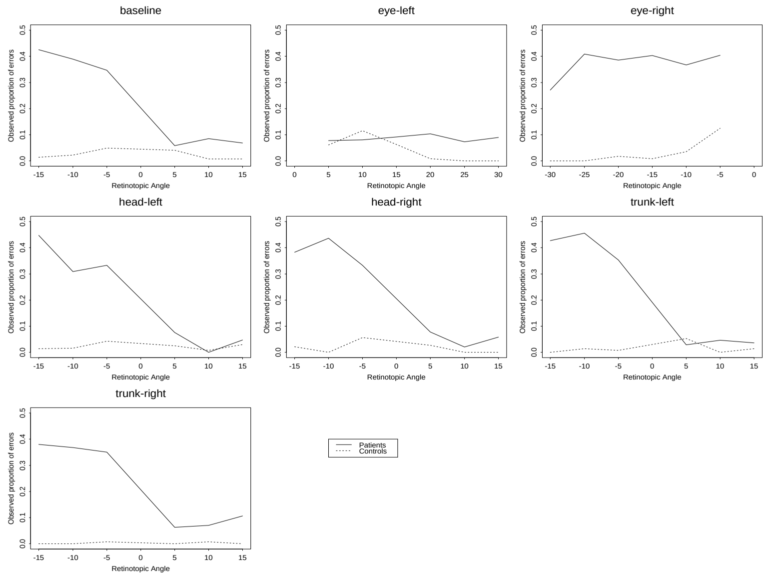

Figure 10: Comparison of the observed proportion of error in the control and patient group.

As we did for the patient group, we estimate the parameters of model (3) both using **proc glimmix** in SAS, and simulating the posterior distribution of the parameters, via Gibbs sampling, in BUGS. Since the estimates are very similar, for sake of simplicity, in Table 11 we report only the Bayesian estimates to compare the control group compare with the patient group.

Table 11

		Bugs			
		Patients		Controls	
α	grand mean	***	-1.930 (± 0.143)	***	-3.823 (± 0.238)
γ_2	incr. in intercp. in EL		-0.971 (± 0.389)	***	2.244 (± 0.425)
γ_3	incr. in intercp. in ER	**	1.777 (± 0.345)	***	2.393 (± 0.511)
γ_4	incr. in intercp. in HL		-0.214 (± 0.220)		0.005 (± 0.313)
γ_5	incr. in intercp. in HR		-0.056 (± 0.207)		-0.286 (± 0.351)
γ_6	incr. in intercp. in TL		-0.078 (± 0.211)		-0.385 (± 0.356)
γ_7	incr. in intercp. in TR		0.269 (± 0.197)	**	-1.196 (± 0.422)
τ_1	slope in B	***	-0.127 (± 0.013)		-0.014 (± 0.019)
τ_2	slope in EL		-0.001 (± 0.018)	***	-0.127 (± 0.028)
τ_3	slope in ER		0.015 (± 0.016)	***	0.177 (± 0.043)
τ_4	slope in HL	***	-0.160 (± 0.017)		0.004 (± 0.020)
τ_5	slope in HR	***	-0.140 (± 0.015)		-0.030 (± 0.023)
τ_6	slope in TL	***	-0.174 (± 0.016)		0.020 (± 0.023)
τ_7	slope in TR	***	-0.116 (± 0.014)		0.003 (± 0.033)
σ^2_β	between subj. var.		2.806 (± 3.248)		0.45 (± 0.24)

The simulation was based on 5000 iteration and a burn in of 1000 iteration, and under the following priors:

$$
\begin{aligned}
\gamma_k &\sim N(0,1) \\
\tau_k &\sim N(0,\sigma_\tau^2) \\
1/\sigma_\tau^2 &\sim \Gamma(1.44,.45) \\
1/\sigma_\beta^2 &\sim \Gamma(1.44,.45)
\end{aligned}
$$

Overall patients have a much smaller grand mean compared to normal subjects: this means that overall they have greater log-odds, and therefore a greater probability to make errors. Normal subjects have non significant slope for the experimental condition *baseline*, *head-left*, *head-right*, *trunk-left*, and *trunk-right*.

It seems odd the presence in the control group of significant slopes in *eye-left* and *eye-right* condition. Also looking in Figure 10, it seems that when targets are closer to fixation the probability of error increases.

5 Discussion on the experimental design

In this section we discuss strengths and limitations of the experimental design. In particular we focus our attention on isolating main effects of the environmental and retinotopic frames of reference, since the cranio-centered and trunk-centered frames do not have significant effect either on reaction time or on the error trials.

If we assume there was no distance effect, and we were interested in isolating dichotomous effects of the environmental and retinotopic frame of reference, then we find the experiment to be well planned. Let us consider the environment frame as factor 1 which can be either L (left) or R (right). Analogously let the retinotopic frame of reference be factor 2 which take levels L and R. Then we can think the experiment in the following way:

targets:	-15, -10, -5	5, 10, 15
baseline	(L,L)	(R,R)
eye-left	(L,R)	(R,R)
eye-right	(L,L)	(R,L)

where $(\cdot,\cdot)$ stands for (level factor 1, level factor 2). All main effects of the two factor could be isolated as well as their interaction. BUT as target moves away from fixation, we expect a longer reaction time due to the further distance. We then have to control for the "distance effect", and design a simpler experiment (always if we are interested in the left/right effects only). For example, we could have the following experiment, where we have four experimental conditions: in the first two, the eyes are aligned at 0° and at random time targets appear at any position on the LED, but we keep measurements only when targets appear at $\pm 5^\circ$. In the third condition, the eyes are keeping fixation at $+10^\circ$ relative to the environment, and we keep measurements only when targets appear at $+5^\circ$. In the last condition, the eyes keep fixation on -10° and measurements are kept only when targets appear at -5°. Figure 11 shows the four experimental conditions.

This experiment controls for the position of the target relative to the environment (targets are always at $\pm 5^\circ$ from the midline of the LED), and for the position of the target relative to fixation (targets are always at $\pm 5^\circ$ from the fixation point). In this experiment main effects and interaction could be computed.

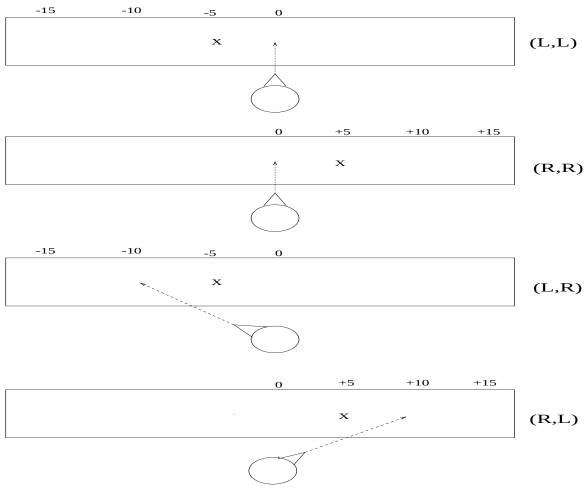

Figure 11: Design of experiment where the "distance" effect is controlled.

However the experiment we analyzed in this paper was designed in such a way that the "distance effect" of targets could be estimated. Unfortunately the design is not orthogonal with respect to the quantitative variables environmental and retinotopic angle. In fact as we can see in Figure 12, observations were measured only on the points on the grid which are highlighted.

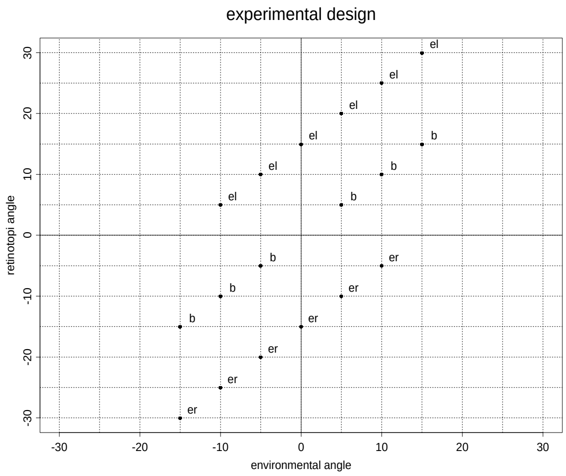

Figure 12: Actual design of the experiment.

This could (maybe) be avoided choosing the experimental design as suggested in Figure 13 where the position of target relative to the environment is orthogonal to the position of target relative to the eyes. In this case we could model the reaction time with two quantitative explanatory variables: environmental and retinotopic angle.

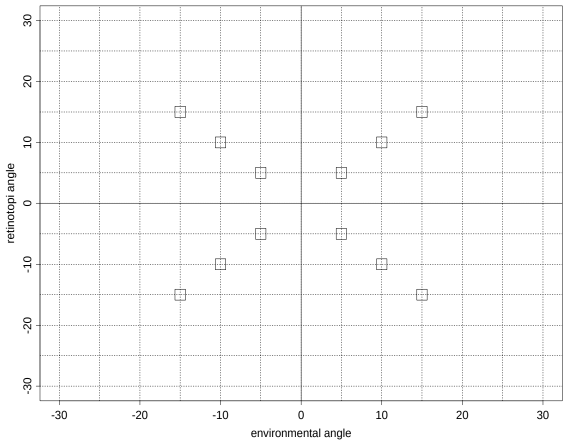

Figure 13: Proposed design of the experiment.

6 Conclusions

The objective of this paper was to isolate the dominant frame of reference within which spatial representations are defined. In both the reaction time and error trials analyses, it does not seem that the head and the trunk position effects the reaction time or the error probability. Both reaction time and error probability remain the same when targets appear on the left or right of the head and the trunk.

In the reaction time analysis, we isolated two frames of reference, environmental and retinotopic, which play a role in explaining the change in reaction time. Due to the particular design of the experiment, it is hard to isolate single contributions.

For the patients, considered as group, we see that for any target, expressed in degree from the midline of the array, the log-reaction time is significantly shorter in the *eye-left* condition than in the *eye-right* condition (see Figure 2).

Another key to interpret the change in the log-reaction time is to consider the retinotopic angle as explanatory variable instead of the environmental angle. In Figure 3, we see that as the target moves to the left of the line of gaze, the log-reaction time increases of $0.02(\pm 0.002)$ log-msec per visual degree. Furthermore when the targets are on the left of fixation, the log-reaction time is significantly longer when the targets appear also on the left of the environment, than when they are on the right of the environment. When the targets appear on the right of fixation, instead, it does not seem that the target position relative to the environment matters. In fact the mean log-reaction time is not significantly different when targets, appearing on the right of fixation, are also on the left or on the right of the environment. The comparison above are shown in Table 4.

In the analysis of the individual patients, we see that the log-reaction time behaves consistently for four patients. For one patient the log-reaction time showed a different behavior. As we can see in Figure 4, this patient had very few observation on the left of fixation.

In the error trials analysis, we found that, in the patient group, the probability of making an error increases when the target moves to the left of fixation. Contrarily to the results of the reaction time analysis, for the error probability there is not a modulation of the environment. In fact if target is on the left of fixation, the error probability is not different whether or not the target is also on the right or the left of the environment, see Table 9.

From the analyses above, it seems that the dominant frame of reference is centered in the eyes.

There is a modulation due to the coordinates of the targets relative to the environment, but this is evident only in the reaction time: the error probability changes only according to the position of the target relative to fixation.

A Appendix: Observed means of log-reaction time

In this appendix we present the tables with the observed means (and standard error) of the log-reaction time for each condition and each target angle for patients and control. For the patient group, the means are based only on the four subjects for which the analysis of reaction time has been done.

In order to keep track of the correlation structure of the data, we computed the group means as REML estimates of the fixed effects in the following model:

$$y_{il} = \alpha_i + \tau_l + \epsilon_{il}$$

where $\alpha_i \sim N(0, \sigma_\alpha^2)$, $\epsilon_{il} \sim N(0, \sigma_\epsilon^2)$, and τ_l, for $l = 1, .., 42$ is a factor with 42 levels each of which corresponds to one cell in the table below.

	Patients (5th patient excluded)						
	-15	-10	-5	0	5	10	15
B	-0.80 (0.16)	-1.03 (0.16)	-1.14 (0.16)		-1.40 (0.15)	-1.51 (0.15)	-1.36 (0.15)
EL		-1.42 (0.16)	-1.62 (0.16)	-1.40 (0.16)	-1.52 (0.15)	-1.43 (0.15)	-1.46 (0.15)
ER	-1.02 (0.16)	-1.08 (0.16)	-1.21 (0.16)	-1.16 (0.16)	-1.28 (0.16)	-1.40 (0.17)	
HL	-0.85 (0.16)	-0.90 (0.16)	-1.03 (0.16)		-1.31 (0.16)	-1.51 (0.15)	-1.28 (0.15)
HR	-0.89 (0.16)	-1.02 (0.16)	-1.17 (0.16)		-1.38 (0.16)	-1.45 (0.15)	-1.44 (0.15)
TL	-0.88 (0.16)	-0.92 (0.16)	-1.11 (0.16)		-1.36 (0.15)	-1.43 (0.15)	-1.33 (0.15)
TR	-0.91 (0.16)	-0.88 (0.16)	-1.18 (0.16)		-1.42 (0.16)	-1.49 (0.15)	-1.26 (0.15)

	Controls						
	-15	-10	-5	0	5	10	15
B	-1.14 (0.03)	-1.18 (0.03)	-1.27 (0.03)		-1.29 (0.03)	-1.33 (0.03)	-1.15 (0.03)
EL		-1.25 (0.03)	-1.42 (0.03)	-1.20 (0.03)	-1.29 (0.03)	-1.22 (0.03)	-1.19 (0.03)
ER	-1.13 (0.03)	-1.08 (0.03)	-1.24 (0.03)	-1.09 (0.03)	-1.28 (0.03)	-1.27 (0.03)	
HL	-1.21 (0.03)	-1.32 (0.03)	-1.28 (0.03)		-1.37 (0.03)	-1.37 (0.03)	-1.18 (0.03)
HR	-1.19 (0.03)	-1.24 (0.03)	-1.28 (0.03)		-1.33 (0.03)	-1.35 (0.03)	-1.25 (0.03)
TL	-1.17 (0.03)	-1.28 (0.03)	-1.28 (0.03)		-1.31 (0.03)	-1.32 (0.03)	-1.22 (0.03)
TR	-1.12 (0.03)	-1.19 (0.03)	-1.26 (0.03)		-1.31 (0.03)	-1.37 (0.03)	-1.22 (0.03)

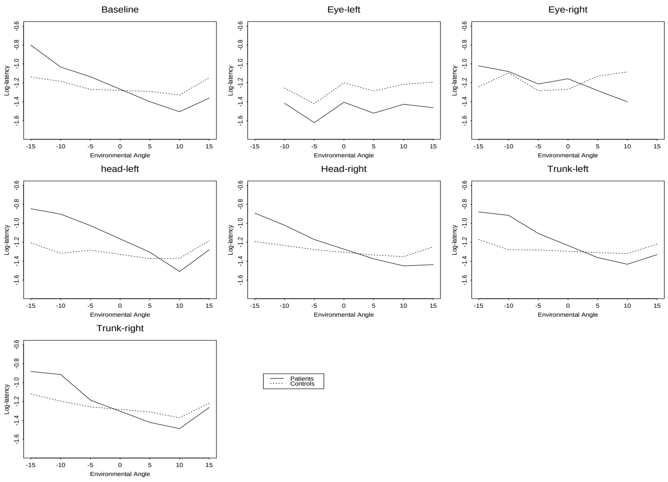

Figure 14: Observed means of log-reaction time for controls and patients.

B Appendix: Model selection for the control group

Here we present in detail the model selection for the control group. In the next table we can see the Log-likelihood and BIC value for polynomials of different order for patients and controls:

	Controls	
Model	**likelihood**	**BIC**
cond., Angle×cond. random: inter.	-1249.70	2621.38
cond., Angle×cond., Angle^2 random: inter.	-1214.78	2560.08
cond., Angle×cond., Angle^2,Angle^3 random: inter.	-1218.26	2575.59
	N=5157	I=10

Considering that a second order polynomial has the smallest value of the BIC for the control group too, we test if there is a significant random slope for the variable environmental angle using the likelihood ratio test:

Controls				
Model (random effects)	Df	Loglik	Lik.Ratio	P value
inter	17	-1214.8		
interc, Angle	19	-1210.3	8.9775	0.011234

Therefore we fit the following model for the control group:

$$y_{ikj} \quad = \quad \alpha + \alpha_i + \gamma_k + \beta X_{ikj} + \delta_i X_{ikj} + \beta_k X_{ikj} + \tau X_{ikj}^2 + \epsilon_{ikj}$$

The only difference with the model used for the patient group is the presence of a random slope $\delta_i \sim (0, \sigma_\delta^2)$, which allows each subject to have different slope.

C Appendix: Mean error proportion for the control group

Here we present the table of the mean error proportions ($\pm sd$) across subjects in the control group. The entries, $\overline{p}$, in the table are computed as follows:

$$\overline{p} = \sum_i \frac{n_i \hat{p}_i}{\sum_i n_i}$$

$$sd(\overline{p}) = \left(\sum_i \frac{n_i \hat{p}_i (1 - \hat{p}_i)}{(\sum_i n_i)^2} \right)^{1/2}$$

where $\hat{p}_i$ is the observed proportion of errors for subject i and n_i is the total number of trials for subject i.

	Controls						
	-15	-10	-5	0	5	10	15
B	0.01 ± 0.01	0.02 ± 0.02	0.05 ± 0.02		0.04 ± 0.02	0.01 ± 0.01	0.01 ± 0.01
EL		0.06 ± 0.02	0.12 ± 0.02	0.06 ± 0.02	0.01 ± 0.01	0.00	0.00
ER	0.00	0.00	0.02 ± 0.01	0.01 ± 0.01	0.04 ± 0.02	0.12 ± 0.03	
HL	0.01 ± 0.01	0.02 ± 0.01	0.04 ± 0.02		0.03 ± 0.01	0.01 ± 0.01	0.03 ± 0.01
HR	0.02 ± 0.01	0.00	0.06 ± 0.02		0.03 ± 0.01	0.00	0.00
TL	0.00	0.01 ± 0.01	0.01 ± 0.01		0.05 ± 0.02	0.00	0.01 ± 0.01
TR	0.00	0.00	0.01 ± 0.01		0.00	0.01 ± 0.01	0.00

D Appendix: Bugs code

Here we provide the code we used in BUGS for the analysis of the error trials using model (3) with the following priors for the model parameters:

$$\begin{aligned}
\alpha &\sim N(0, 10) \\
\gamma_k &\sim N(0, 10) \quad k = 2, ..7 \\
\tau_k &\sim N(\xi, \sigma_\tau^2) \\
\xi &\sim N(0, 10) \\
1/\sigma_\beta^2 &\sim \Gamma(1.44, .45) \\
1/\sigma_\tau^2 &\sim \Gamma(1.44, .45)
\end{aligned}$$

```
model patients;
const   N = 5, C = 7;
var     id[210],                 # nrows
        cond[210],
        err[210],               # errors
        diste[210],
        tot[210],               # total number of trials
        g[N],
        beta[N],
        gamma[C],                #cond effects
        p[N,C,6],                # prob in each cond. and angle
        tau[C],
        csi,
```

```
        sinvt, sinv,
        deviation[C-1];
data    id, cond, err, diste, tot in "datibugs";
inits in "patient.init";
{
        for (i in 1:N){
        g[i] ~ dnorm(0,sinv);
        beta[i] <- g[i]-mean(g[]);
                for (k in 1:C){
                        for(l in 1:6){
        logit(p[i,k,l]) <- beta[i]+gamma[k] + tau[k]*diste[l+(k-1)*6+(i-1)*42];
        err[l+(k-1)*6+(i-1)*42] ~ dbin(p[i,k,l],tot[l+(k-1)*6+(i-1)*42]);
                }}
        }
        for (i in 1:C){
                gamma[i]~ dnorm(0,0.1);
                tau[i] ~ dnorm(csi,sinvt);
        }
        csi ~ dnorm(0,.1);
        sinv ~ dgamma(1.44,.45);
        sinvt ~ dgamma(1.44,.45);
        for(i in 2:C){
        deviation[i-1] <- gamma[i]-gamma[1];
        }
}
```

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