

Detecting multimodality in saccadic reaction time distributions in gap and overlap tasks

Stefan Gezeck¹, Jens Timmer²

¹ Brain Research Unit, Institute of Biophysics, University of Freiburg, Freiburg, Germany

² Center for Data Analysis and Modelling, University of Freiburg, Freiburg, Germany

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Abstract. In many cases the distribution of saccadic reaction times (SRT) deviates considerably from a unimodal distribution and may often exhibit several peaks. We present a statistical approach to determining the number and form of the individual peaks. The overall density of the reaction times $f_i(t)$, $i = 1 \dots M$ obtained in M different experiments with the same subject is described as the sum of K basis functions $x_k(t)$, $k = 1 \dots K$ with different weights and an error term. A change in the experimental conditions is assumed to cause a change in the weights, not in the basis functions. We minimize the square of the difference (measured data minus approximation), divided by the error of the data. Incrementing K step by step we determine the necessary number of basis functions. This method is applied to data of six subjects tested in different saccade tasks. We detect five different modes: two in the range 80–140 ms (express modes), two in the range 145–190 ms (fast-regular mode) and one at about 230 ms (slow-regular mode). These modes are located at about the same positions for different subjects. The method presented here not only proves statistically the existence of several modes in SRT distributions but also allows the distributions to be described by a few characteristic numbers that go beyond the mean values and standard deviations.

visible when the target appears in the overlap paradigm, it is switched off before target onset in the gap paradigm. The time between fixation point offset and target onset is the gap duration. The usual method is to measure saccadic reaction times (SRT) in the overlap and gap conditions and to test whether the differences in the mean values are significant at a given level.

Saslow (1967) computed the mean values of SRT for 16 values of asynchrony, at 50-ms intervals, from an extreme overlap of 350 ms to an extreme gap of 400 ms. The result was a decrement in the mean SRT from 250 ms in the overlap to 130 ms in the gap 300 ms condition (gap effect). When the gap duration was incremented to 400 ms the mean of the SRT increased to 150 ms.

When Fischer and Ramsperger (1984) repeated the experiment they found that the distribution of SRTs from gap trials was bimodal or even trimodal. Saccades contributing to the first peak are called express saccades; the others are called regular saccades. Fischer and Ramsperger also considered mean values but considered the implications of multimodal SRT distributions for processes preceding voluntary visually guided rapid eye movements.

The absence of a statistical method for detecting the number and position of the modes has led to different opinions concerning multimodality. Reuter-Lorenz (1995) didn't analyse the contributions of different peaks because of the difficulties in identifying the peaks in data, and proclaim to use reliable and robust statistical methods based on mean values and standard deviations.

Many authors have reported whether or not they could detect multimodal SRT distributions by simple inspection. Examples of multimodal SRT distributions have been published for both monkeys and human subjects (Fischer and Boch 1983; Fischer and Ramsperger 1984; Jüttner and Wolf 1992; Munoz and Wurtz 1992; Sommer and Schiller 1992; Nothdurft and Parlitz 1993; Currie et al. 1993; Priori et al. 1993; Rohrer and Sparks 1993; Matsue et al. 1994; Schiller and Lee 1994; Tam and Ono 1994). Nozawa et al. (1994) reported

1 Introduction

One approach to studying the temporal and spatial control of saccades has relied on the gap/overlap paradigm (Saslow 1967). Subjects are required to look at a fixation point in the middle of the screen and to make a saccade to the stimulus when it appears at an eccentric location. While the fixation point remains

Correspondence to: S. Gezeck,
Bekstrasse 15, D-75180 Pforzheim, Germany

that 23% of their subjects produced clearly separate modes and 'many others did not have clearly defined modes but could still have come from a mixture of two distributions'. Other authors found multimodal distributions in some subjects but not others (Reuter-Lorenz 1991). Still others reported problems in finding bimodal distributions (Wenban-Smith and Findlay 1991; Sereno and Holzman 1993; Kingstone and Klein 1993).

Reuter-Lorenz et al. (1991) attributed the gap effect to a facilitation of premotor programming in the superior colliculus. A general shortcoming of the facilitation concept, proposed also by Reulen (1984a), is that it cannot explain the occurrence of more than one mode in the latency distribution; neither can it account for the increase in SRT when increasing the gap duration from 200 ms to 400 ms.

Fischer and Ramsperger (1984) were the first to report multimodal SRT distributions. Some authors adopted the idea of multimodality. Rogal and Fischer (1986) proposed a model for SRT that can exhibit different peaks, based on the idea that the SRT includes the time required for the afferent and efferent processes (for example delays in pathway) and central processes such as computation of the movement metrics. In this model it is assumed that the preparation of saccades is composed of sequential processes.

The three-loop model proposed by Fischer (1987) is based on the idea that differences between the peak positions refer to the time required for a brain process that is included only in the reaction times of the later peak. Fischer proposed that saccades are generated by three main pathways (loops) connecting the retina of the eye with the efferent eye movement generating system. Each loop is associated with a certain brain process that must be accomplished during saccade preparation, thus contributing to the reaction time. Saccades generated through the shortest loop are express saccades (SRT = 100–135 ms), forming the first peak. If two or three processes have to be completed after target onset, fast-regular saccades (140–180 ms) or slow-regular saccades (above 200 ms) are obtained, again forming separate peaks. Fischer et al. (1995) presented a computer simulation of the three-loop model. This reproduces the gap effect in a very similar way to the experimental data, by means of a simple neural network. The three-loop model has been confirmed by experiments in naive adults, teenagers, children, and trained adults (Fischer et al. 1993).

Cavegn (1996) asked his subjects to make a saccade to a target appearing randomly to the left or the right and used location cues to direct visual attention and start saccade programming. When the cue indicated the target location, the generation of express saccades was facilitated; otherwise express saccades were abolished and mainly fast-regular saccades observed. The results are explained by the fixation-gating model, according to which the state of a separate fixation system and not attention disengagement decides which type of saccade (express or regular) is generated.

Carpenter and Williams (1995) observed the express mode in the overlap paradigm that was first detected by Fischer et al. (1993). The strength of the express mode is modulated by the probability of the direction of the stimulus.

A quantitative model that predicts temporary and spatial aspects of saccades was proposed by Kopeck (1995). It is based on concepts of saccadic preparation conducted by fixation point offset, fixation point onset and general warning events (Ross and Ross 1980, 1981; Reulen 1984a,b; Reuter-Lorenz et al. 1991). This model could not produce multimodal distributions and express saccades.

All the models considered above rely on neurobiological findings and assumptions. Another approach is to model data. To our knowledge, this approach has never been reported for saccadic eye movements in literature. Yantis et al. (1991) developed a maximum-likelihood test of multimodality that results in the number of basis functions, their distributions and their weights. Unfortunately, it can only be used if separate samples from each of the underlying basis distributions are available, an assumption not fulfilled in saccadic eye movement experiments.

The different studies on SRTs have been interpreted in different ways depending on whether multimodality was found or not. It is therefore of great interest to use an objective method to test the possibility of different modes forming the SRT distributions. In this study we present a statistical method for detecting the number of modes in SRT distributions and their shape (basis functions, BFs). Each BF is described by its contributions to all bins. We assume that each subject has individual BFs and each reaction time obtained in different experiments is a random number of one of these BFs. Then the empirical distributions are superpositions of these BFs. In our experiments we varied only the time of fixation offset, all other experimental parameters being constant. We assume that the distribution of each BF remained unchanged in the different experiments. Each subject has two individual sets of BFs: one for saccades to the left and one for saccades to the right.

While the BFs remain unchanged, the weights of the BFs change from one experimental condition to another. We propose a model for the number of saccades in the bins that is linear in BFs and linear in weights of the BFs. The superposition of the BFs fits the data better if the number of BFs is increased. How can one decide about the true number of BFs? We accept the lowest number of BFs that allows a satisfactory description of the data. The number of BFs, the shape of all BFs and the contribution of each BF to all empirical samples (their weights) are a result of the analysis.

We analysed data of different gap and overlap paradigms of six trained subjects and found three or four BFs in all subjects. The peaks are classified into two classes of express peaks (range 80–140 ms) and two classes of fast-regular modes (range 145–190 ms). The slow-regular mode 'S' with SRT above 200 ms appears in one subject.

2 Experimental methods

2.1 Subjects and data base

Six normal subjects (age range 28–53 years) contributed to the data base of this study. They had previously performed the gap task (gap duration 200 ms) until stable distributions were obtained. They are considered trained subjects in the sense of Fischer et al. (1984).

2.2 Data collection

All reaction time data were collected using the same methods described in detail in Weber and Fischer (1995). The Iris Scalar system was used for recording the position of the left eye. Reaction times were determined off line using a velocity criterion for detecting saccades. The latency was defined by the time the velocity reached 15% of its maximum in each detected saccade. Latency values below 80 ms were considered anticipatory by means of the occurrence of direction errors (Wenban-Smith and Findlay 1991) and were excluded from this analysis.

2.3 Visual display

All visual stimuli were generated on a RGB monitor using a high-resolution graphic interface (micrograph 510). Target onset time was synchronized to the screen (frame rate 83 Hz) and the position of the target at the screen. All saccades were made to targets presented 4° to the left or right in random order. The size of the white target was 0.2° × 0.2°; the red fixation point was 0.1° × 0.1° in size. Both had a luminance of 50 cd/m², while the green background was 20° × 15° in size with a luminance of 10 cd/m².

2.4 Saccade tasks

The subjects performed the gap task with eight different gap durations between 0 ms (step paradigm) and 700 ms and two overlap tasks: the overlap task with attentive fixation and the 'normal' overlap task with no instruction with respect to fixation. The fixation period prior to target presentation was 1.2 s. The targets remained visible for 800 ms. The intertrial interval was 1 s. Subjects were instructed to fixate the fixation point and to look at the target when it appeared. They were not encouraged to respond 'as fast as possible'. During one experimental session 200 saccades were measured in both directions (left/right). Most measurements were repeated once, resulting in 400 saccades for each task.

3 Experimental results

Here we describe very briefly the experimental distributions that are to be analysed. We point out the different modes whenever they can be seen clearly.

The SRT distributions of saccades to the left are presented on the left side of each figure; the SRT distributions of saccades to the right are presented correspondingly on the right side of each figure. Figures 1–6 show the data obtained from the six subjects. Many subjects are asymmetric, which means that they produce different results when the stimulus appears on the left side compared with the results on the right side (Weber and Fischer 1995). Therefore the saccades on the left were analysed separately from the saccades on the right.

The SRT distributions are estimated using a gaussian kernel with a bandwidth of 3 ms. From bottom to top the time of fixation offset decreases relative to the onset of the stimulus.

For subject B.F. (Fig. 1) the SRT distribution for the overlap with attentive fixation is presented in the first line; in the next line the SRT distributions for the 'normal' overlap task are presented. Visual inspection of the resulting SRT distributions for the two overlap tasks reveals a large mode at about 150 ms in all distributions and a mode at about 200 ms, which is decreased in the 'normal' overlap. In all gap tasks there are no saccades in the range of the mode at about 200 ms, but the mode about 150 ms is present in all distributions, its contribution to the whole distributions varying between 10% (gap 100 ms and 200 ms for saccades to the right) and 100% (gap 0 ms for saccades to the left). A mode about 100 ms appears in the gap 100 ms task and dominates the distributions of all gap durations between 200 ms

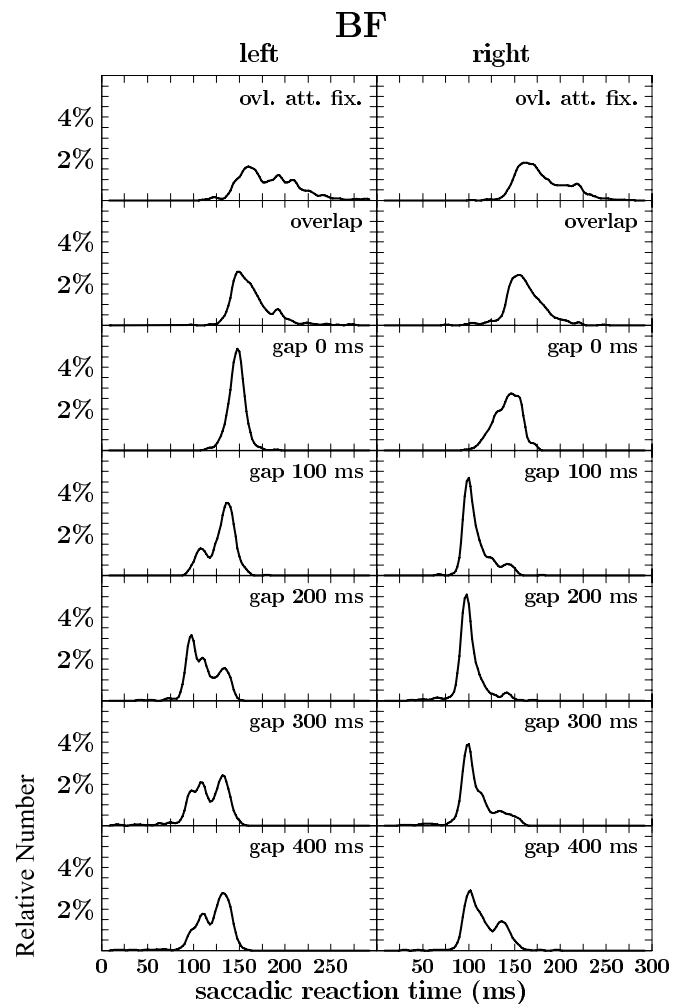


Fig. 1. Gap data of B.F. Saccadic reaction time (SRT) distributions of B.F. in the overlap task with attentive fixation (*first row*), the 'normal' overlap and five different gap durations from 0 ms (*third row*) to 400 ms are presented. SRT distributions of saccades to the left and to the right are analysed separately and presented in the corresponding columns

and 400 ms. For saccades to the left this first mode may consist of two twin peaks at 95 ms and 105 ms, because this mode has two maxima at these positions in the distribution for gap 200 ms, 300 ms and 400 ms. For gap 200 ms the first maximum is larger than the second; for gap 300 ms and 400 ms the second is larger than the first. The occurrence of these peaks depends on the bandwidth of the gaussian smoothing function; the peaks disappear when the gaussian is enlarged. But the occurrence of both modes at the same position in several distributions supports the hypothesis that there are different basis functions.

Subject H.W. (Fig. 2) produces shorter reaction times when looking to the right compared with saccades to the left. In the overlap tasks with attentive fixation and the 'normal' overlap there are two clearly separate modes at 150 ms and 200 ms to the left, while the distributions to the right are unclear. When a gap is introduced, a mode at about 100 ms appears at the right and increases with increasing gap duration. When increasing the gap

duration from 200 ms to 400 ms the first mode becomes smaller again in advance of the second mode. Saccades to the left exhibit a small mode at 100 ms only for gap durations of 200 ms and 300 ms.

Subject C.A. (Fig. 3) shows three peaks to the left which turn into one for gap durations of 100 ms and above. Only in the overlap with attentive fixation do reaction times over 200 ms occur.

Subject M.B. (Fig. 4) produces a distinct mode at about 200 ms to the left. The mode at about 150 ms appears in all tasks except for gap 200 ms. The first mode at about 100 ms is present for gap durations between 100 ms and 400 ms.

Subject D.C. (Fig. 5) shows large differences in SRT distributions to the right and left direction. At the left the mode about 100 ms is present in all tasks, even in the overlap (left saccades). Similar to subject B.F. (Fig. 1) visual inspection allows the assumption that the first peak is a twin peak. The mode at about 150 ms is rather small for the gap tasks 100 ms, 200 ms and 300 ms to

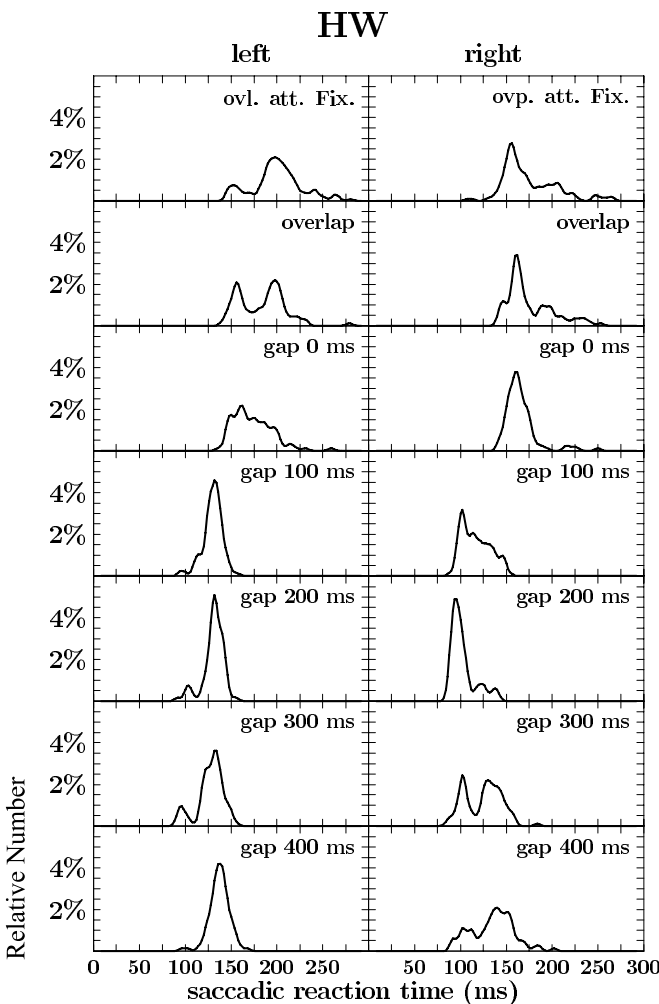


Fig. 2. Gap data of H.W. Same format as Fig. 1. In both overlap tasks there are two clearly separate modes at about 150 ms and 200 ms. In the gap task an express peak at about 100 ms occurs in both directions

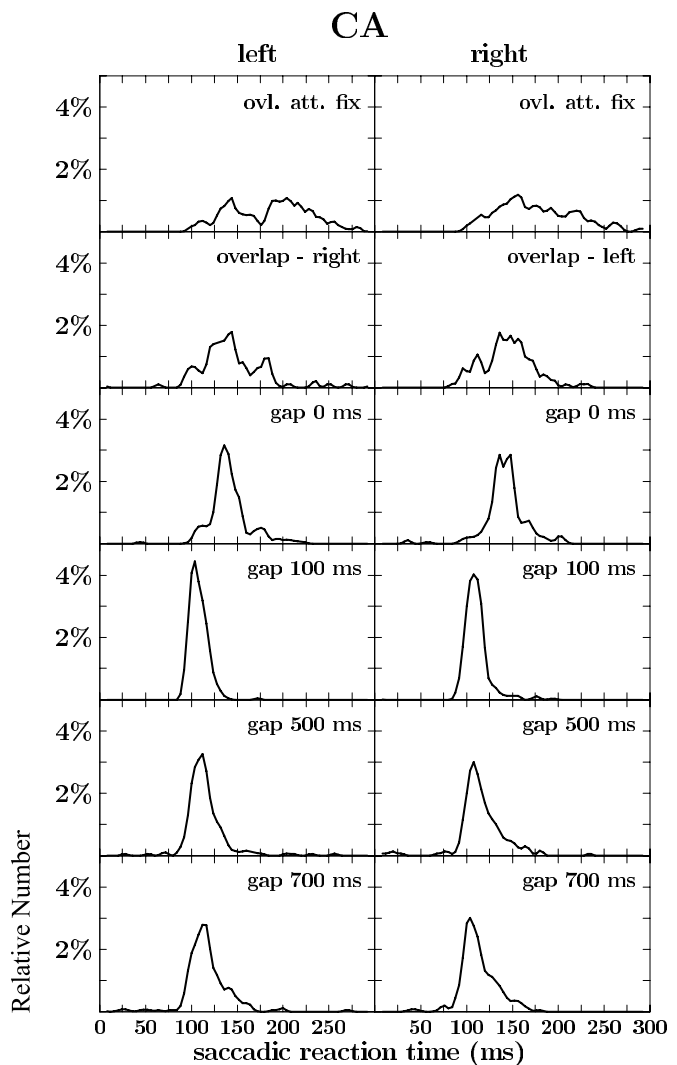


Fig. 3. Gap data of C.A. Same format as Fig. 1. This subject produced a mode at about 100 ms in both overlap tasks and in the gap 0 ms task. This mode grew when a gap was introduced

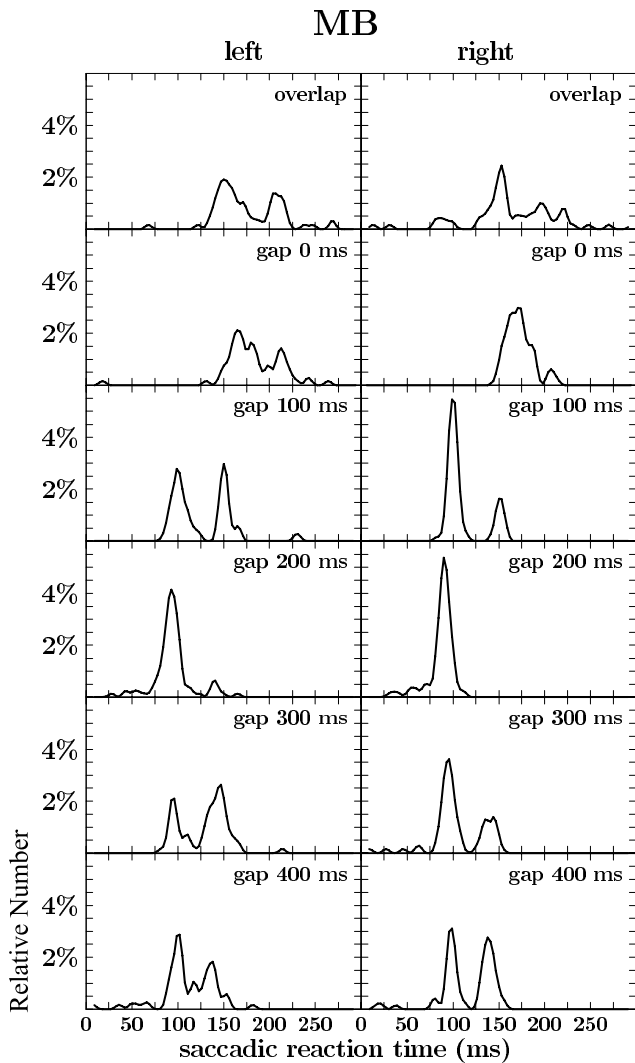


Fig. 4. Gap data of M.B. Same format as Fig. 1. This subject produced clearly separated modes at 100 ms (all gap tasks), at 150 ms (both overlap and all gap tasks, with the exception of gap 200 ms) and at 200 ms (both overlap tasks)

the left. The third mode at about 200 ms appears in the overlap to the right and is rather small in the overlap to the left.

Subject O.K. (Fig. 6) produces multimodality in almost all conditions. While the first mode at about 100 ms appears even in the overlap, the mode at about 200 ms remains present for gap durations 100 ms, 200 ms and 300 ms at the right.

In this section we have considered the data of six different subjects. Visual inspection of the data supports the idea that all SRT distributions of the same subject when looking in the same direction consist of a small number of identical modes. The basic idea is that only the contribution of the modes changes from one experiment to another, and that the shape of each mode remains unchanged. Of course, this question cannot be decided by visual inspection since the visual impression depends, for example, on the width of the smoothing kernel. Thus, we introduce a statistical test to judge

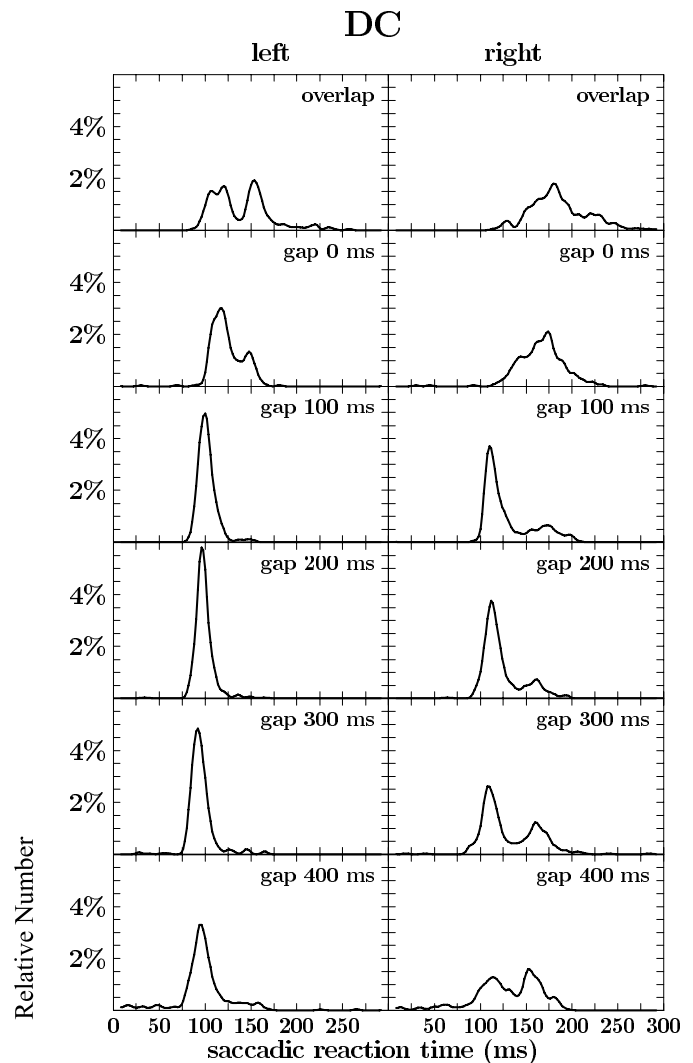


Fig. 5. Gap data of D.C. Same format as Fig. 1. This subject showed large differences in SRT distributions to the left and right direction. At the left the mode about 100 ms is present in all tasks, even in the overlap

whether the SRT distribution can be modelled in this way, the number K of modes in all SRT distributions and the shape of these modes.

4 Statistical methods

We assume that a subject is tested in M different experimental conditions and the SRTs in the same direction are collected in N bins $y_{ij}, i = 1 \dots M, j = 1 \dots N$. The first index i is the number of the experiment, the second index j is the number of the bin, and y_{ij} is the number of saccades collected in that bin.

Each data point y_{ij} is considered as the superposition of an unknown number K of modes. The distribution of each mode is called the basis function (BF). We use a non-parametric form for the BFs. Therefore K BF consist of the same number of bins N as the data y_{ij} , resulting in one parameter for each bin of each of the K

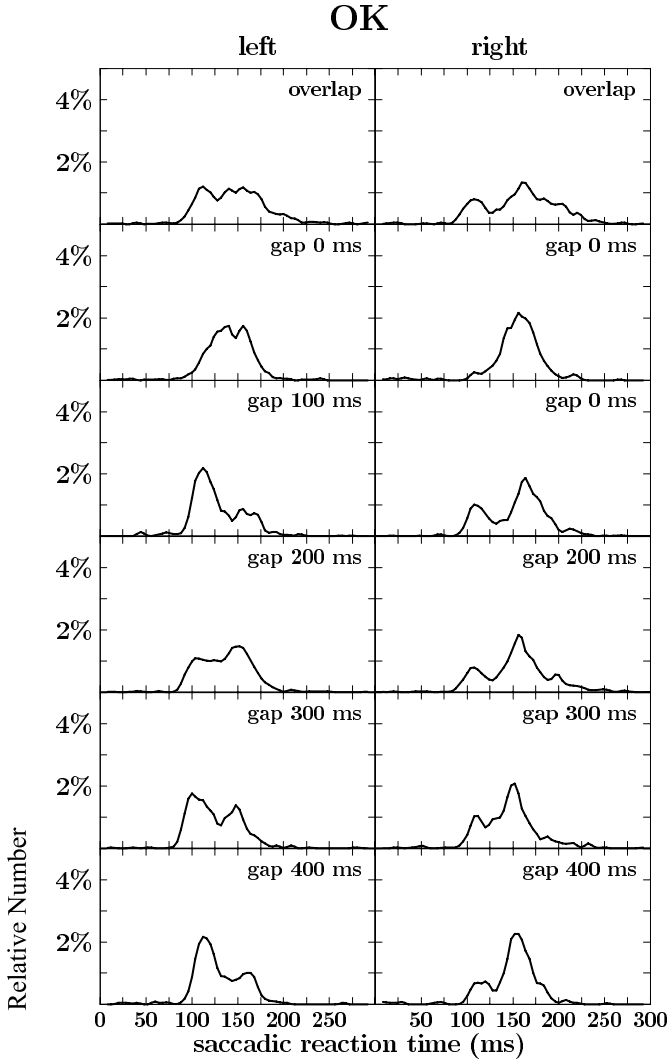


Fig. 6. Gap data of O.K. Same format as Fig. 1. This subject produced multimodality in almost all conditions

BF. The contribution of the bin j to the k th BF is called x_{kj} , $k = 1 \dots K, j = 1 \dots N$. The weight of the k th BF in the i th SRT distribution is named a_{ik} , $i = 1 \dots M, k = 1 \dots K$. The number of saccades in a bin y_{ij} is expressed by the sum of the contributions of each BF and an individual error ϵ_{ij} :

$$y_{ij} = \sum_{k=1}^K a_{ik}x_{kj} + \epsilon_{ij} \quad (1)$$

The same model equation is treated by factor analysis. [For a detailed description of factor analysis see Harman (1967); a shorter description and more examples are given in Malinowski (1991).] Here and in factor analysis neither the weights a_{ik} nor the BFs x_{kj} are known, whereas in a standard regression framework x_{kj} is known. The classical factor analysis model is designed to reproduce maximally the observed correlations. Here a minimization is performed, implying that all parameters a_{ik} and x_{kj} are fitted in order to minimize the error E :

$$E = \sum_{i=1}^M \sum_{j=1}^N \frac{(y_{ij} - \sum_{k=1}^K a_{ik}x_{kj})^2}{\sigma_{ij}^2} \quad (2)$$

where the standard deviation of the number of saccades in each bin y_{ij} is σ_{ij} . The distributions of all BFs and their weights in the samples are obtained by the minimization of E . By minimizing E we get the least-squares estimator for all parameters. We select the conjugated gradient method (Press et al. 1986) in order to minimize E . This algorithm does not guarantee that the global minimum is reached. We investigated the existence of local minima in the present optimization problem by simulation studies. Therefore, we started the iterative minimization algorithm from different initial values. Apart from a trivial permutation of the BFs and the corresponding coefficients, the results were unique. This confirms the common experience that local minima are rare in high-dimensional optimization problems.

Before fitting the parameters it is necessary to set the number K of BFs. An obvious procedure is to set the number of BFs to $K = 1$, fit all parameters and test the model. If the model is rejected by the test, K is increased by 1, all parameters are fitted again and the model is tested again. We repeat this procedure until the model can not be rejected. Using this method the smallest number of BFs and parameters is found to give a satisfactory result.

In order to build the distribution of the test statistic E it is necessary to investigate the distribution of y_{ij} . The number of saccades in a bin y_{ij} is multinomially distributed. In order to compute its standard deviation σ_{ij} , we define the estimator of the number of saccades \hat{U}_i in the i th SRT distribution:

$$\hat{U}_i = \sum_{j=1}^N \sum_{k=1}^K a_{ik}x_{kj} \quad (3)$$

The probability \hat{p}_{ij} that one reaction time of the i th data set falls into bin number j can be estimated by

$$\hat{p}_{ij} = \frac{\sum_{k=1}^K a_{ik}x_{kj}}{\hat{U}_i} \quad (4)$$

Then the standard deviation σ_{ij} of the number of saccades y_{ij} is given by

$$\sigma_{ij} = \sqrt{\hat{U}_i \hat{p}_{ij} (1 - \hat{p}_{ij})} \quad (5)$$

If the number of saccades y_{ij} exceeds 5, the multinomially distributed number of saccades y_{ij} can be approximated well by a gaussian distribution. For a gaussian distribution of the data the maximum likelihood parameter estimation reduces to a conventional least-squares estimation. Furthermore, model testing can be performed in the frame of well-known statistics. To achieve five saccades in all bins of all data sets, neighbouring bins of the same data set were put together until the number of saccades in a bin exceeded five. Furthermore, bins were considered by this method only

if they included more than five saccades in at least two data sets. We need a sufficient number of saccades in two data sets and not in only one data set because otherwise the corresponding BF may be identical in that distribution in a range resulting in an optimal fit.

5 Test of the number of basis functions

If the model is true, the error E is χ^2 -distributed with a number of degrees of freedom according to the difference in the number of data points and the number of effective parameters. The solution may be rotated in a k -dimensional space, the effective number of parameters being the difference between the total number of parameters and $k(k-1)/2$. The number of data points is the sum of the number of bins of all samples and the total number of parameters is $(N+M)K$, because there are N parameters for each of the K BFs and K parameters for the weights of the BF for each of the M samples. After fitting the parameters a_{ik} and x_{kj} the values of the parameters must fulfil the following conditions:

$$a_{ik} \geq 0 \quad \forall i = 1 \dots M, k = 1 \dots K \quad (6)$$

$$x_{kj} \geq 0 \quad \forall k = 1 \dots K, j = 1 \dots N \quad (7)$$

$$\sum_{j=1}^N x_{kj} = 1 \quad \forall k = 1 \dots K \quad (8)$$

These three equations have the following meaning: All weights (6) and the contribution of all bins to all BFs (7) are positive numbers. All BFs are standardized to 1.0 (8). Each solution not satisfying these conditions is discarded. This raises a problem concerning the application of the χ^2 -test, because some parameters may lie on a boundary. A second problem is that the model is not linear, because of the product term of the parameters a_{ik} and x_{kj} .

We performed a simulation study to check whether the distribution of the test statistic E corresponds to the theoretical χ^2 -distribution. As BF we choose three gaussian f_1, f_2, f_3 functions with standard deviation 10 ms and means 120 ms, 150 ms and 180 ms. For each of the $i = 1 \dots M$ simulated samples we define the weights $a_{i,1}, a_{i,2}$ and $a_{i,3}$ of the three BFs as realizations of a uniformly distributed random variable and standardize the weights $\sum_{k=1}^3 a_{ik} = 1$. Then we draw random numbers $r_{i,1} \dots r_{i,A}$ of the superposition $f_s(t) = \sum_{k=1}^3 f_k(t)$. We minimize the test statistic E as described above (2) and consider the value of the test statistic E . All steps have been repeated 100 times and the empirical cumulative distribution of the test statistic E is compared with the χ^2 distribution with the correct number of degrees of freedom as described above. In Fig. 7 the results of both functions are presented. The number of simulated samples has been varied between $M = 10$ and $M = 20$ and the number of random numbers has been varied between $A = 100, 200, 500, 1000$.

In Fig. 7 the empirical distributions are represented by the thick lines and the theoretical distributions by the

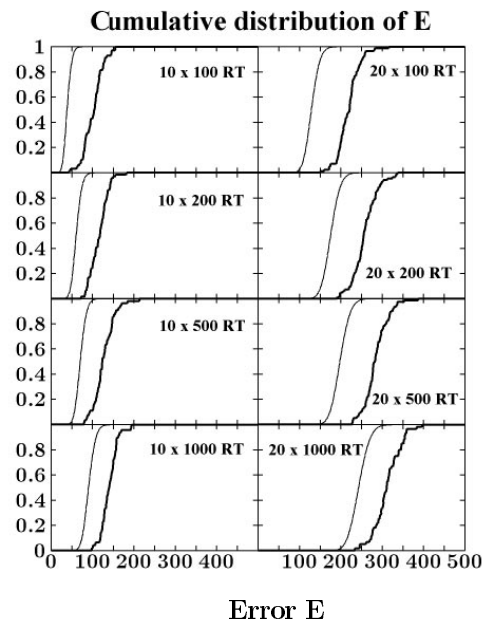


Fig. 7. Cumulative distribution of the error E . Ten (left) or 20 (right) data sets containing 100 (top), 200, 500 or 1000 (bottom) random numbers are generated. The *thick line* represents the simulated cumulative distribution of the error E and the *thin line* represents the corresponding cumulative χ^2 distribution. In all cases the simulated distribution is on the right of the χ^2 distribution.

thin lines. In all eight cases the empirical distribution of the test statistic E yields larger values than the theoretical distributions for the reasons listed above. This difference between the empirical and the theoretical functions may cause errors when deciding whether a number of BFs must be rejected: It may happen that a model will be rejected by mistake.

Because of these problems the χ^2 test cannot be used to test the model. Fortunately modern computers provide another possibility for testing a model: we simulate the distribution of E . In order to simulate the distribution of the test statistic E the number of saccades y_{ij} (1) has been computed. Now we know the distributions y_i of all tested conditions (each distribution y_i is given by N bins: $y_{ij}, j = 1 \dots N$). From all distributions y_i random samples are drawn. Each sample consists of the same number of random numbers as has been measured in the experiment. The simulated data have been binned in the same way as the empirical data; they were called y_{ij}^{sim} . Then the error

$$E^{\text{sim}} = \sum_{i=1}^M \sum_{j=1}^N \frac{(y_{ij} - y_{ij}^{\text{sim}})^2}{\sigma_{ij}^2} \quad (9)$$

was computed. We repeated the resampling and computing of E^{sim} 99 times. The distribution of the test statistic E is estimated by the 99 values of E^{sim} . The model is rejected at the significance level of 1% if the empirical error E^{emp} is larger than the 99 values of the simulated values E^{sim} (Hope 1968).

Next we want to know whether the BFs are reproduced correctly by this method. In the first line of Fig. 8

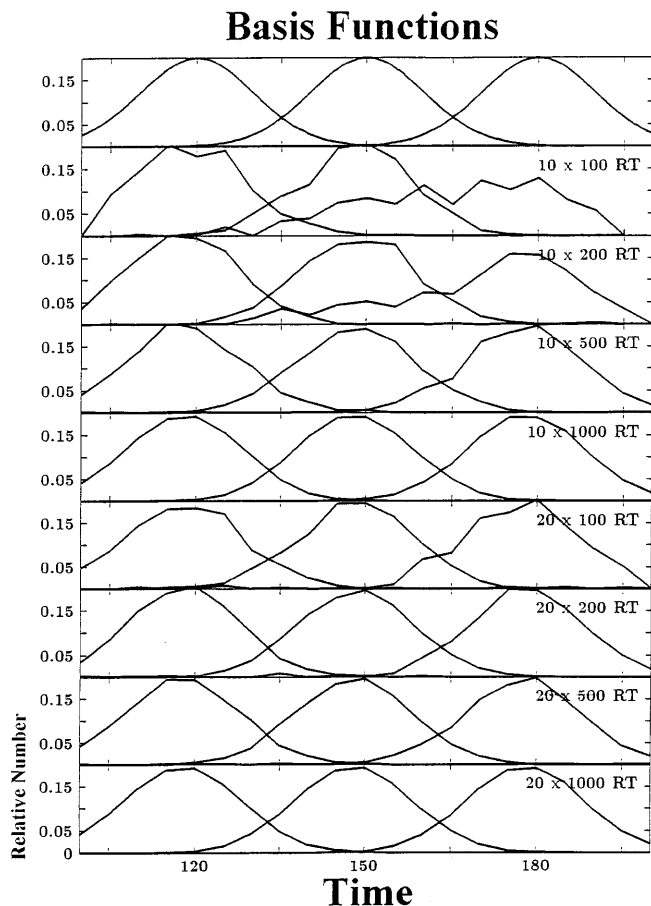


Fig. 8. Ten or 20 data sets containing between 100 and 1000 reaction times are generated. Each data set is a mixture of the distribution shown at the *top*. All basis functions reproduced by the fitting procedure presented in this article are shown. The third basis function is not reproduced correctly when using 10 data sets each containing 100 reaction times (*second row*) and when using 10 data sets each containing 200 reaction times (*third row*). Using more data sets (*fourth row* or *fifth row*) leads to better results. A good fit results when using 20 data sets each containing 100 reaction times (*sixth row*). Incrementing the number of reaction times naturally leads to better results in all data sets

the distributions of the three BF's have been plotted. As described above we use gaussian distributions with means 120 ms, 150 ms and 180 ms and a standard deviation of 10 ms. Below this the fitted BF's are plotted for $M = 10, 20$ and $A = 100, 200, 500, 5000$. The BF's are reproduced adequately if we use $M = 20$, even if the number of reaction times was $A = 100$. We conclude that this method is suitable for our data.

A simulation study not presented here was performed to check what happens, if the samples are not a superposition of a small number of BF's. We simulate $M = 20$ samples of a superposition of three gaussian distributions but change the mean of each gaussian distribution for each data set. As the mean position we choose realizations of uniformly distributed random numbers in the interval $T = [100 \text{ ms} \dots 250 \text{ ms}]$. The result is that the number of BF's $K = 1, 2 \dots 6$ are rejected. When incrementing the number of BF's to $K = 7$ the overall number of parameters reaches the number of data points

and can fit all samples exactly. Such a model does not impose any restrictions on the data and is therefore useless.

6 Application to SRT distributions

The statistical method proposed in the previous section decomposes a SRT distribution of the same subject containing saccades to the same direction into different modes. Therefore it is necessary that all SRT distributions consist of the same modes and that only the weights of these modes vary between different experiments. If this assumption is not fulfilled, the simulation study concerning data sets with different given BF's reveals that the minimal number of BF's, K , is incremented until the number of parameters is greater than the number of bins. If a small number K of BF's give a satisfactory fit to the empirical data, it seems very likely that the assumption is fulfilled. Otherwise one may assume that the position and shape of the BF's change from one tested condition to another.

The next point concerns the support of the BF's. The empirical distributions are decomposed into several modes by the statistical method described above. Because this method modelled only the bins that included more than five saccades in at least two data sets, only those basis functions were detected that occur in at least two data sets with a sufficient weight.

It is necessary to spend some time selecting the binwidth. The binwidth must be much smaller than the difference between all neighbouring BF's, because otherwise the saccades of two modes will be put into the same bin and the method can not detect both BF's. Because neighbouring bins of the same data set are put together until the number of saccades in that bin exceeds five, there exists a lower boundary for the binwidth. We choose the binwidth 5 ms.

7 Results

We tested different experimental conditions twice, resulting in $M = 20$ SRT distributions. The statistical method described above was applied to data of six different subjects. For five subjects the saccades are analysed separately in the left and right directions; only for subject O.K. were the distributions of saccades pooled in both directions because in the SRT distributions the peaks were at exactly the same position. In Fig. 9 the decrease in the error E with incrementing number of parameters is shown. In some cases the number of BF's was determined to $K = 3$; in the other four cases K was 4. In the upper part of Fig. 9 all cases with $K = 3$ are plotted; in the lower part the case with $K = 4$. Note the small decrease in the error E if a new BF ($K + 1$) is introduced.

All BF's of all subjects and both directions of saccades are plotted in Fig. 10. The plots are sorted from top to bottom by the position of the maximum of the first peak. The three BF's of subject M.B. for saccades to the left are

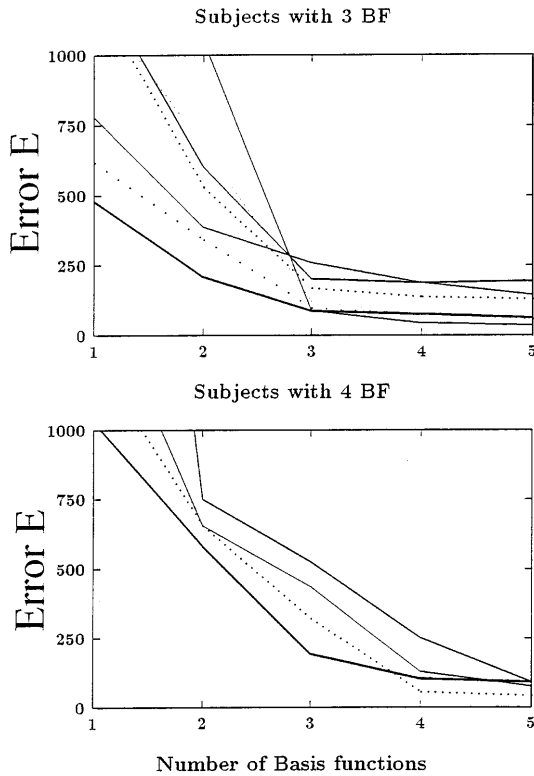


Fig. 9. Error E for a number of basis functions between one and five. This figure shows for all subjects/saccade directions the development of the error E when fitting different numbers of basis functions. *Above*: all subjects/saccade directions that allow a satisfactory fit with three basis functions; *below*: four basis functions. Note the 'elbow' at three basis functions (*above*) or four basis functions (*below*). Further incrementing the number of basis functions leads to only a small improvement in the error E

shown in the first line. There is a first mode between 80 ms and 105 ms, a second mode between 130 ms and 170 ms, and a third broad mode between 160 ms and 220 ms. Note that a BF may be bimodal; an example is subject B.F. left, whose second mode between 100 and 130 ms has a small maximum at 110 ms and a large one at 130 ms. But most BFs are unimodal.

The SRT distributions of subject C.A. left exhibit three peaks: the first between 85 and 120 ms, a second between 95 and 130 ms, and a third between 120 and 150 ms. Note that the first and the third modes of C.A. left are located at almost the same positions as the first and the second mode of M.B. left, whose SRT distributions do not exhibit a mode corresponding to the second mode of C.A. left.

Therefore, and because the first and the second modes of C.A. left overlap, the question arises whether the first and the second modes of C.A. left are twin peaks, i.e. are descended from the same class of peaks. Considering all subjects we find seven who have both peaks (C.A. left and right, D.C. left, B.F. right and left, H.W. left and right). The other four have only one mode between 80 and 140 ms (M.B. left and right, O.K., D.C. right). For example, we investigate the data of B.F. left (Fig. 1) by visual inspection. This data set supports the view of twin peaks: in the gap 200 ms task there are two maxima at

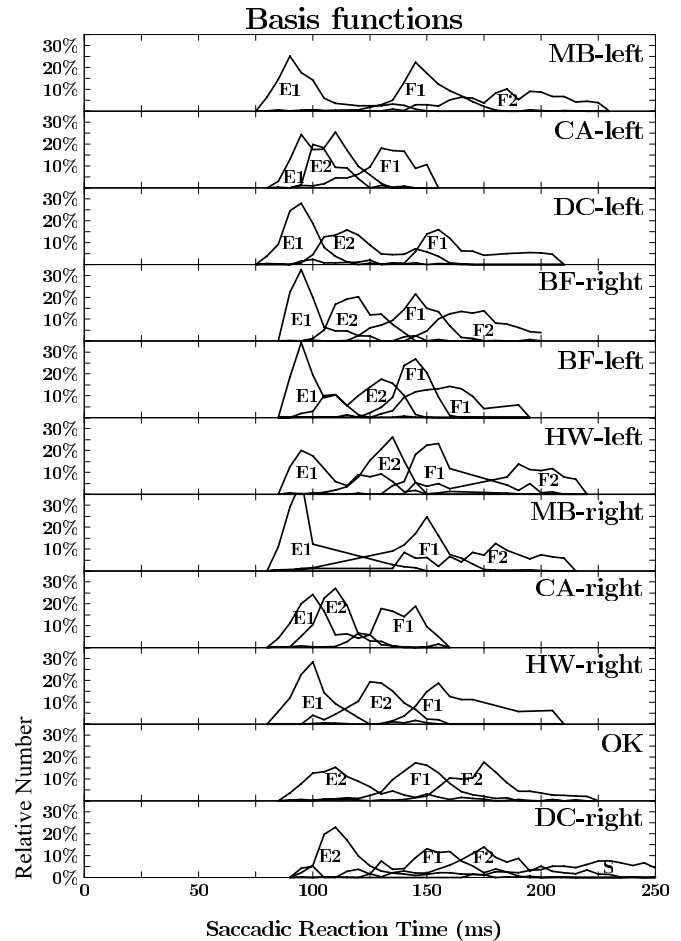


Fig. 10. All basis functions of all subjects and both saccade directions. The plots are sorted from *top* to *bottom* by the position of the maximum of the first peak. See text and Fig. 11 for peak designation

95 and 110 ms, the first higher than the second. In the gap 300 ms and 400 ms task there are maxima at the same positions, but the contribution to the two modes has changed, the maximum at 110 ms being higher than the maximum at 95 ms. In the distributions of C.A. the superposition of the first and second peaks is unimodal; therefore the distributions do not have two maxima in the range between 90 and 120 ms, and only the shape of the first peak varies. The distribution of C.A. left has larger values at 95 ms compared with 110 ms in the gap 100 ms task and lower values in the gap 500 ms and gap 700 ms tasks.

To classify all modes we consider the position of the maximum of all 37 modes found in 11 analyses. Their distribution is shown in Fig. 11. The maximum positions form five regions (E1, E2, F1, F2 and S), separated by regions without a maximum. We name the first two peaks 'E1' and 'E2' because they occur in the same subjects forming twin peaks. If all peaks of both classes 'E1' and 'E2' were put into one class 'E', many subjects would have two peaks of the same class! To avoid this we subdivide the 'E' and 'F' classes. Only in subject B.F. right are there two modes classified 'F1', and the later one may be classified as 'F2' if the classification is

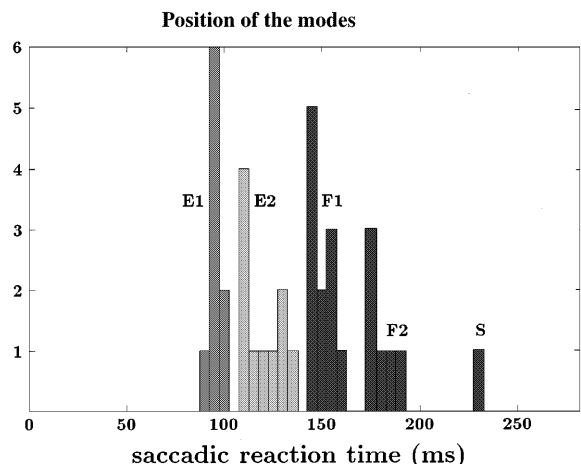


Fig. 11. The position of the maximum of all 37 modes found in 11 analyses. The maximum positions form five regions designated E1, E2, F1, F2 and S. These are separated by regions without a maximum. We call the first two peaks ‘E1’ and ‘E2’ because they both occur in the same subjects forming twin peaks

based on the mean instead of the maximum of the modes.

The modes are named ‘E1’ and ‘E2’ because both modes are express modes ranging from 80 ms to 140 ms. The ‘F1’ and ‘F2’ modes are fast-regular modes ranging from 145 ms to 190 ms. The slow-regular mode ‘S’ appears very seldom in gap and overlap experiments with trained subjects. Naive subjects (i.e. subjects without training) very often produce slow-regular saccades in overlap experiments and sometimes in gap experiments (Fischer et al. 1993; Gezeck et al. 1997).

To build the distribution of the number of modes we assign each SRT distribution the number of modes with weight larger than 10% as number of modes. The result was that 25% of all distributions are unimodal, 58% are bimodal and 17% exhibit three or more modes.

Using this classification the SRT distributions are described by the weights of all peaks. In the next section

this method is applied to give a new description of the gap effect.

8 Gap effect

The mean of the weights of the modes is shown in Fig. 12. The mean is computed among all subjects and both stimulus directions for each gap duration. In the overlap with attentive attention and the ‘normal’ overlap most saccades contribute to the F1 and F2 mode (both about 40), and only a small number of E1 or E2 saccades occur. The contribution of the F1 and F2 mode varies between subjects from 0 to 100% and the contribution of the E1 and E2 mode is below 20% in all cases.

The mean of the contribution of the F1 mode increases to 70% in the gap 0 ms task. When a gap is introduced, all subjects show an increase in the E1 peak. The mean of its contribution is 35% in the gap 100 ms task and 55% in the gap 200 ms task. When the gap duration is increased to 400 ms all subjects show a decrease in the contribution of the E1 peak, and the mean decreases to 35%. The contribution of the F1 mode, which dominates the gap 0 ms distributions, is decreased when the gap duration is increased to 200 ms in all subjects. A further increase in gap duration to 400 ms leads to an increment of the contribution of the F1 peak in all subjects (mean 10% in gap 200 ms condition and mean 25% in the gap 400 ms condition).

Contrary to the E1 and F1 modes the E2 and F2 modes develop differently for different subjects. The subjects with a small number of E1 saccades in the gap 200 ms task have a high number of E2 saccades; this number is greater than in the gap 100 ms task and in the gap 300 ms task. In contrast the subjects with a high number of E1 saccades in the gap 200 ms task have only a few E2 saccades in the gap 200 ms task and more in the other gap durations. For all gap durations there is at least one subject whose contribution of the E2 peak is below 10% and at least one subject whose contribution

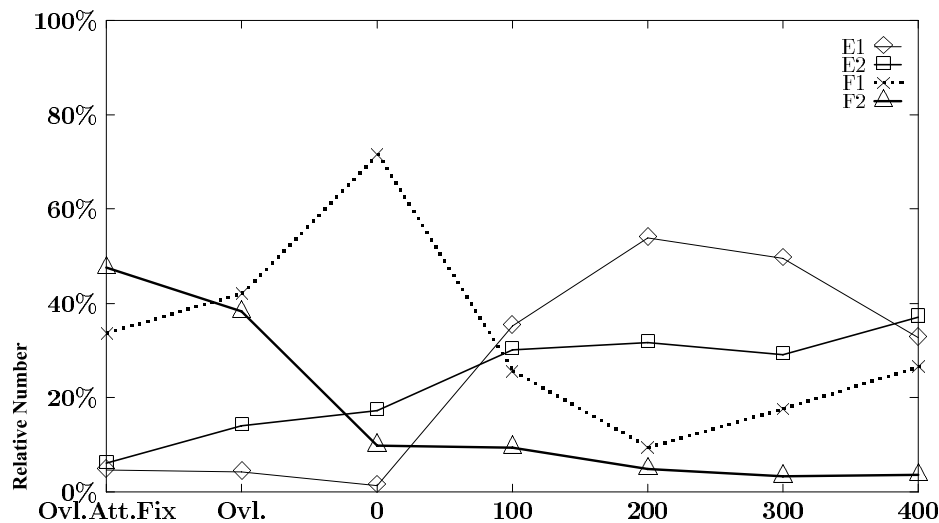


Fig. 12. The mean of the weights of the modes. The mean is computed among all subjects and stimulus directions for each gap duration. In the overlap with attentive fixation and the ‘normal’ overlap most saccades contributed to the F1 and F2 modes (both about 40%), and in gap tasks the E1 and E2 modes dominated the distributions

of the E2 peak is above 60%. The mean of the contribution of the E2 mode is about 30% for all gap durations. Similar to the E2 mode the F2 mode develops non-uniformly for different subjects. The mean of its contribution is below 10% for all gap durations.

9 Discussion

The present study has shown that SRT distributions consist of different modes. At least three modes are necessary to describe in a satisfactory way the data of at least six different test conditions. These modes are grouped into five classes. Two of these are classes of express peaks that have their maximum between 85 ms and 105 ms and between 110 ms and 135 ms, respectively. Two classes are classes of fast-regular peaks that have their maximum between 140 ms and 165 ms and between 170 ms and 190 ms, respectively. One subject contributes a mode named slow-regular mode at about 230 ms.

The main conclusion is that distributions can be described as being composed of basis functions with fixed maximum position. We clearly identified different peaks in the SRT distributions. These can be classified by their maximum position into express, fast-regular and slow-regular peaks. All subjects have two peaks in the same range. In some cases these are independent peaks that are incrementing and decrementing at the same position (twin peaks; examples in Figs. 1 and 5). Another hypothesis is that one mode is shifting its mean to lower values when incrementing gap duration (Saslow 1967). Indeed we recognize a small shift of some peaks, for example in Fig. 1 in the first three panels. But the shift changes the SRT distribution rather little compared with the change due to an increasing peak: All SRT distributions presented in this article (including the distributions of Fig. 1) can be described as being composed of a small number of basis functions with fixed maximum position. Small shifts effect a small increment in the error function, E , that does not lead to a large increase in the required number of basis functions.

One may believe that twin peaks occurs this way: A mode that is shifting in a small range can be described by two basis functions centred at the edges of this range. The weights of both basis functions control the position of the shifting mode. But we observe many distributions that have two maxima in different experimental conditions at the same position (Fig. 1, left, gap 200–400 ms and Fig. 5, left, overlap-gap 100 ms). These maxima stay at the same position when the weights of the peaks change! This fact is not compatible with the idea of one shifting mode. There are some modes that exhibit only one local maximum and that change the position of the maximum between different gap conditions (for example Fig. 1, left, panel 1–3). These distributions can be described by twin peaks and by one shifting mode. We support the hypothesis of twin peaks, because *all* experimental distributions are compatible with this idea, contrary to the idea of one shifting mode.

The results support the three-loop model (Fischer 1987; Fischer et al. 1995). Twin peaks can be introduced

into the three-loop model by adding a small loop in one module that contributes to express and fast- and slow-regular saccades – a condition only fulfilled by the attention module ATT. A small amount of time is added to the SRT of all trials that use the small extra loop added in module ATT. This small enlargement can produce two kinds of express saccades, two kinds of fast-regular saccades and two kinds of slow-regular saccades. In summary it explains all the new results. There is no need for a five-loop model because the peaks can be classified into the three ranges express, fast- and slow-regular saccades. Other saccadic models by Kopecz (1995) and Reulen (1984a) need an expansion to explain multimodal distributions and twin peaks.

The statistical method presented here makes it possible to analyse 10 or more SRT distributions of the same subject/saccade direction. The question arises how to analyse single multimodal distributions of a subject. Fischer et al. (1993) suggested fitting a superposition of three gaussians to the data. Another approach is to split the data into regions: for example, Fischer et al. (1997) considered all saccades in the range 80–134 ms as express saccades. Biscaldi et al. (1997) used the same range as the express range and called saccades with latencies between 135 ms and 179 ms fast-regular saccades, saccades with latencies between 180 and 399 ms slow-regular saccades and saccades with latencies between 400 and 699 ms late saccades (Biscaldi et al. 1997). The latter method has the advantage of avoiding problems when fitting three gaussians to small data sets (below 200 saccades per direction). Furthermore no assumptions about the shape of the modes are necessary.

Another approach is used by Gezeck et al. (1997). They use the excess-mass test (Müller & Sawitzki 1991) to detect peaks in 963 data sets. The idea of the excess-mass test is that a mode is present where an excess of probability mass is concentrated. The result is that the peak positions can be classified into express (90–120 ms), fast-regular (135–170 ms) and slow-regular (200–220 ms). Because twin peaks very often overlap and exhibit only one local maximum they are rarely detected by the excess-mass method. Using the results of Gezeck et al. (1997) it seems very likely that all saccades with latencies in the range of 80–134 ms should be considered express saccades, and those in the range 135–179 ms as fast-regular saccades (Biscaldi et al. 1997). Saccades with longer latencies are considered as slow-regular saccades (180–349 ms) and as late saccades (350–699 ms).

Only if all modes are clearly separated in at least one task can the test of Yantis et al. (1991) be applied to analyse several SRT distributions. But our analysis reveals that few subjects fulfil this criterion (for an example see subject M.B., Fig. 4); in most subjects SRT distributions consist of overlapping modes.

Multimodal SRT distributions support the hypothesis that the saccade system consist of different systems working serially. The time consumption for each process is added to the reaction time. Then each mode can add 20–50 ms, an order of magnitude that can be accounted for with the help of neural summation time. If a process is completed before target onset only in some trials, the

time consumption of this process is added to the SRT of the other trials and the SRT distribution becomes bimodal. Therefore the analysis suggests that the saccade system works serially. It may not be concluded whether some processes are working in parallel.

The facilitation model of Reulen (1984a) can explain the gap effect as far as the decrease in the mean value of the reaction time is concerned, but it cannot produce multimodal distributions. Carpenter and Williams (1995) make assumptions about the shape of a mode of a SRT distribution. The analysis of their data, all obtained from overlap trials, shows that the model predictions are not fulfilled: instead of a single straight line the data form two sections with an 'elbow' at about 140 ms. They conclude that at least two modes can be identified in the data and that the second mode begins at about 140 ms. This is in fair agreement with the present analysis because the transition between the express and the fast-regular mode occurs between 130 and 140 ms. According to Ruhnau and Haase synchronized oscillations in the visual cortex produce multimodal distributions (Ruhnau and Haase 1993; Kirschfeld et al. 1996).

The early version of the three-loop model assumes serial processing of three central stages but needs the additional assumption of a probabilistic variable that determines the chances of the optomotor system being in one or the other state at the time of target presentation (Rogal and Fischer 1986). More recently, a two-stage serial model has been presented that produces bimodal distributions and also takes into account the sensory factors such as stimulus intensity and visual-auditory integration in saccade generation (Nozawa et al. 1994). The fixation-gating model of Cavegn (1996) can produce multimodal SRT distributions. According to the fixation-gating model the state of a separate fixation system and not attention disengagement decides what type of saccade (express or regular) is generated. When the processes were implemented as assemblies of interacting neurons the probabilistic aspects of the them being in one or the other stage are provided "automatically" in the form of the stochastic nature of impulse trains in the sensory channels representing the effect of stimulus onset and fixation point offset (Fischer et al. 1995).

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References

- Biscaldi M, Gezeck S, Stuhr V (1998) Poor saccadic control correlates with dyslexia. *J Neurophysiol*, in press
- Carpenter R, Williams M (1995) Neural computation of log likelihood in control of saccadic eye movements. *Nature* 377:59–62
- Cavegn D (1996) Bilateral interactions in saccade programming. *Exp Brain Res* 109: 312–332
- Currie J, Joyce S, Maruff P, Ramsden B, McArthur-Jackson C, Malone V (1993) Selective impairment of express saccade generation in patients with schizophrenia. *Exp Brain Res* 97:343–348
- Fischer B (1987) The preparation of visually guided saccades. *Rev Physiol Biochem Pharmacol* 106:1–35
- Fischer B, Boch R (1983) Saccadic eye movements after extremely short reaction times in the monkey. *Brain Res* 260:21–26
- Fischer B, Ramsperger E (1984) Human express saccades: extremely short reaction times of goal directed eye movements. *Exp Brain Res* 57:191–195
- Fischer B, Boch R, Ramsperger E (1984) Express-saccades of the monkey: effect of daily practice on probability of occurrence and reaction time. *Exp Brain Res* 55:232–242
- Fischer B, Weber H, Biscaldi M, Aiple F, Otto P, Stuhr V (1993) Separate populations of visually guided saccades in humans: reaction times and amplitudes. *Exp Brain Res* 92:528–541
- Fischer B, Gezeck S, Huber W (1995) The three-loop model: a neural network for the generation of saccadic reaction times. *Biol Cybern* 72:185–196
- Fischer B, Biscaldi M, Gezeck S (1997) On the development of voluntary and reflexive components in saccade generation. *Brain Res* 754:285–297
- Gezeck S, Fischer B, Timmer J (1997) Saccadic reaction times: statistical analysis of multimodal distributions. *Vision Res* 37:2119–2131
- Harman H (1967) *Modern factor analysis*. University of Chicago Press, Chicago
- Hope A (1968) A simplified Monte Carlo significance test procedure. *J R Stat Soc B* 30:582–598
- Jüttner M, Wolf M (1992) Occurrence of human express saccades depends on stimulus uncertainty and stimulus sequence. *Exp Brain Res* 89:678–681
- Kingstone A, Klein R (1993) What are human express saccades? *Percept Psychophys* 54:260–273
- Kirschfeld F, Feiler R, Wolf-Oberhollenzer F (1996) Cortical oscillations and the origin of express saccades. *Proc R Soc Lond* 263:459–468
- Kopecz K (1995) Saccadic reaction times in gap/overlap paradigms: a model based on integration of international and visual information on neural, dynamic fields. *Vision Res* 35:2911–2925
- Malinowski E (1991) *Factor analysis in chemistry*. Wiley, New York
- Matsue Y, Osakabe K, Saito H, Goto Y, Ueno T, Matsuoka H (1994) Smooth pursuit eye movements and express saccades in schizophrenic patients. *Schizophrenia Res* 12:121–130
- Müller D, Sawitzki G (1991) Excess mass estimates and tests for multimodality. *J Am Stat Assoc* 86:738–746
- Munoz D, Wurtz R (1992) Role of the rostral superior colliculus in active visual fixation and execution of express saccades. *J Neurophysiol* 67:1000–1002
- Nothdurft H, Parlitz D (1993) Absence of express saccades to texture or motion defined targets. *Vision Res* 33:1367–1383
- Nozawa G, Reuter-Lorenz P, Hughes H (1994) Parallel and serial processes in the human oculomotor system: bimodal integration and express saccades. *Biol Cybern* 72:19–34
- Press W, Flannery B, Teukolsky S, Vetterling W (1986) *Numerical recipes*. Cambridge University Press, Cambridge
- Priori A, Dertolasi L, Rothwell J, Day B, Marsden C (1993) Some saccadic eye movements can be delayed by transcranial magnetic stimulation of the cerebral cortex in man. *Brain* 116:355–367
- Reulen J (1984a) Latency of visually evoked saccadic eye-movements. 1. Saccadic latency and the facilitation model. *Biol Cybern* 50:251–262
- Reulen J (1984b) Latency of visually evoked saccadic eye-movements. 2. Temporal properties of the facilitation mechanism. *Biol Cybern* 50: 263–271
- Reuter-Lorenz P, Hughes H, Fendrich R (1991) The reduction of saccadic latency by prior offset of the fixation point: an analysis of the gap effect. *Percept Psychophys* 49:167–175
- Reuter-Lorenz P, Oonk H, Barnes L, Hughes H (1995) Effects of warning signals and fixation point offsets on the latencies of pro- versus anti-saccades: implications for an interpretation of the gap effect. *Exp Brain Res* 103:287–293

- Rogal L, Fischer B (1986) Eye-hand coordination: a model for computing reaction times in a visual reach task. *Biol Cybern* 55:263–273
- Rohrer W, Sparks D (1993) Express saccades: the effects of spatial and temporal uncertainty. *Vision Res* 33:2447–2460
- Ross L, Ross S (1980) Saccade latency and warning signals: stimulus onset, offset and change as warning events. *Percept Psychophys* 27:251–257
- Ross S, Ross L (1981) Saccade latency and warning signals: effects of auditory and visual stimulus onset and offset. *Percept Psychophys* 29:429–437
- Ruhnau E, Haase V (1993) Parallel distributed processing and integration by oscillations. *Behav Brain Sci* 16:587–588
- Saslow M (1967) Effects of components of displacement-step stimuli upon latency for saccadic eye movement. *J Opt Soc Am* 57:1022–1029
- Schiller P, Lee K (1994) The effects of lateral geniculate nucleus, area V4, and middle temporal (MT) lesions on visually guided eye movements. *Vision Neurosci* 11:229–241
- Sereno A, Holzman P (1993) Express saccades and smooth pursuit eye movement function in schizophrenic, affective disorder, and normal subjects. *J Cogn Neurosci* 5:303–316
- Sommer M, Schiller P (1992) Express saccades elicited during natural fixations of visual search. *Soc Neurosci Abstr* 18: 1398
- Tam W, Ono H (1994) Fixation disengagement and eye-movement latency. *Percept Psychophys* 56:251–260
- Weber H, Fischer B (1995) Gap duration and location of attention focus modulate the occurrence of left/right asymmetries in the saccadic reaction times of human subjects. *Vision Res* 35:987–998
- Wenban-Smith M, Findlay J (1991) Express saccades: is there a separate population in humans? *Exp Brain Res* 87:218–222
- Yantis S, Meyer D, Smith J (1991) Analyses of multinomial mixture distributions: new tests for stochastic models of cognition and action. *Psychol Bull* 110:350–374