Chapter 8

Temporal uncertainty explains peri-saccadic mislocalization; a Bayesian model

In preparation:
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Previous research has shown that people systematically misjudge the location of objects flashed near the time of fast eye movements (saccades). The mislocalization pattern is found to depend on the specific conditions, for instance whether the experiment is performed in the dark or with visual references. Here, we show that a simple Bayesian model describes the mislocalization patterns. We combine a temporal uncertainty about the time of the flash with a foveal bias to believe that the flash occurred near where one is looking. By changing the parameters of the foveal bias and the temporal uncertainty, we can reproduce the localization patterns that are found under a wide variety of conditions. The model also reproduces the different localization patterns that are found in the literature for different saccade amplitudes.
**Introduction**

Signals originating from a single event, such as the auditory, visual and tactile signals that arise from clapping your hands, take different times to reach the brain. These signals arrive with different delays in different brain areas where they are processed separately before being combined into a single perceived event. The brain is fairly good at dealing with the different delays when combining such signals, but there are conditions in which it makes systematic mistakes. One example is that visual objects that are flashed near the time of a saccade are often systematically mislocalized (Bischof & Kramer, 1968; Honda, 1990; Lappe et al., 2000; Maij et al., 2009; Matin & Pearce, 1965; Morrone et al., 1997; O'Regan, 1984; Ross et al., 1997). In order to correctly localize flashes that are presented around the time of a saccade, the signal arising from the image of the flash on the retina has to be combined with a signal related to the orientation of the eye at the time of the flash with a high temporal accuracy.

Despite the large amount of research on mislocalizing flashes near the time of saccades we still do not fully understand why these localization errors occur. The phenomenon was discovered in experiments performed in the dark. The errors that were found could be summarized as a shift in the perceived locations of flashes that was related to the time of the flashes relative to the saccade (Honda, 1990, 1991; Matin et al., 1970; Matin & Pearce, 1965; Schlag & Schlag-Rey, 2002). The retinal location of the flash made little difference, for an example see figure 1A. However, when experiments were later performed in the presence of visual references a spatial compression of the apparent locations of the flashes toward the saccade target was found (Awater, Burr, Goldberg, Lappe, & Morrone, 2001; Lappe et al., 2000; Maij et al., 2009; Morrone et al., 1997; Ross et al., 1997), for examples see figure 1B. The presence of visual references is certainly not the only factor that influences peri-saccadic mislocalization. For instance, stimulus luminance (Georg et al., 2008), stimulus contrast (Michels & Lappe, 2004), saccade amplitude (Lavergne et al., 2010), saccade speed (Östendorf et al., 2007), and independent additional temporal information about the time of the flash (Maij et al., 2009) all influence the precise pattern that also differs to some extent between individuals. All these findings make it hard to understand the origin of the mislocalization.

A transient shift of the perceived locations of the flashes in the direction of the saccade near the time of the saccade (as shown in figure 1A) could be explained by temporal low-pass filtering of the retinal (Pola, 2004) or the extra-retinal (Dassonville et al., 1992) signal, or by temporal uncertainty about the time of the flash relative to the saccade (Maij et al., 2009). However, the compression towards the saccade target (as shown in figure 1B) cannot be explained by temporal factors alone.

The peri-saccadic compression has been attributed to a remapping of receptive fields (Ross et al., 2001) or to shifts in spatial attention towards the saccade target (Hamker, 2005; Hamker et al., 2008), but such proposals do not explain why different patterns are found in different experimental settings. It has been proposed that a briefly presented flash is most likely perceived near the location towards which one’s eyes are oriented at the time of the flash (Brenner
et al., 2008; Brenner et al., 2006). This theory reasons that people are more likely to perceive things if their eyes are directed towards them, so if they saw them they were probably near where they were looking. Recently, we have shown that a combination of temporal uncertainty and a tendency to believe that flashes occurred where one was looking can reproduce the apparent positions of the flash in one particular study (Maij et al., 2011b).

**Figure 1.** Localization for each time of the flash relative to saccade onset in two studies with different experimental settings: Honda (Honda, 1991) conducted his study in complete darkness (A) whereas Maij et al. (Maij et al., 2011a) provided visual references (B). The studies also used slightly different flash locations and saccade amplitudes. Each color represents a flash location (dashed horizontal lines). Dots represent the indicated positions on single trials. The colored curves through the data points are smoothed Gaussian averages of the data. The black line is a minimum jerk movement simulating the eye position (Flash & Hogan, 1985). The pattern of errors near the time of the saccade is quite different in the two studies.

In this paper, we show that a Bayesian model based on normally distributed temporal uncertainty about the time of the flash (with standard deviation $\sigma_t$) and a bias towards where one is looking (modeled as a normally distributed foveal prior with standard deviation $\sigma_s$) can explain observed localization patterns. By changing the parameters of the model depending on the specific experimental conditions, this model reproduces the different localization patterns found under different conditions. We present a graphical description of the model to introduce the results. A mathematical description is presented in the methods section.

**Results**

**Model**

The normally distributed temporal uncertainty about the time of the flash relative to the saccade (orange area in figure 2A) is combined with the saccadic eye movement (black curve in figure 2A; saccade modeled as a minimum jerk movement (Flash & Hogan, 1985)) to obtain a likelihood for the orientation of the eye at the time of the flash (red area on the left of figure 2A). This likelihood
is shifted by an amount that equals the retinal position of the flash to provide a likelihood for the spatial location of the flash (transparent red curve in figure 2B). The resulting likelihood for possible flash locations is then multiplied by a normally distributed foveal prior (blue distribution) centered on the position towards which gaze is directed 70 ms after the flash (figure 2B). The mean of the distribution (purple distribution; figure 2C) that arises from this multiplication gives the prediction for the (mean) localization.

Figure 2A. Combining a normally distributed temporal uncertainty about the time of the flash ($\sigma_t = 30$ ms; illustrated in orange for a flash 15 ms after saccade onset) with the saccade itself (modeled as a minimum jerk movement of 20° in 77 ms; black curve), gives a likelihood distribution of eye orientation at the time of the flash (red distribution, with corresponding axis at the top of the graph). B. If the uncertainty about the retinal position of the flash is negligible, the likelihood distribution for the position of the flash in space will simply be a shifted version of the likelihood distribution for the eye orientation (red transparent curve for target at 10°). This likelihood distribution is combined with a normally distributed foveal prior (blue distribution; $\sigma_s = 5°$) centered where an efferent eye signal that precedes the actual eye movement by $d = 70$ ms indicates that the eye is looking. C. Multiplication of the likelihood and the foveal prior results in the posterior (purple distribution). The mean of the posterior is taken as the perceived position for that flash.

Model predictions were determined for two flash locations (figure 3). Changing the saccade amplitude, the temporal uncertainty or the foveal prior all changed the mislocalization pattern considerably. In figure 3A we see a predicted localization pattern for a 20° saccade, a foveal prior with a standard deviation of 5°, a temporal uncertainty with a standard deviation of 30 ms and a time difference between the corollary discharge and the actual eye movement of 70 ms (so that the eyes are considered to have moved before they actually did so). Note the compression towards the saccade target. For a smaller temporal uncertainty (5 ms), the errors are smaller (figure 3B). For a smaller bias towards where one is looking (foveal prior with a standard deviation of 40°), the compression disappears so that only a transient shift of the predicted location of the flashes remains (figure 3C). For a smaller saccade amplitude (5°) the errors are also smaller and the compression of the errors toward the saccade target becomes negligible (figure 3D). Note that this pattern resembles the transient shift as in figure 1A. When we set the value of the delay of the corollary...
discharge (d) to 0 ms the mislocalization pattern at the 50% flash location does not look similar to any mislocalization pattern found in the literature (figure 3E).

The difference between experiments in measured localization errors (shown in figure 1 for single subjects in the studies of Honda (1991), and Maij and colleagues (Maij et al., 2011a)) can be reproduced by changing the temporal uncertainty and foveal bias. We neglected spatial uncertainty in our model, but this will definitely play a role in some experiments. For our model, a high spatial uncertainty would have the consequence that the effect of the prior would be larger. We can approximate this effect in the model by reducing the width of the prior.

Figure 3A shows the spatial compression that is also apparent in figure 1B, which resembles results for experiments performed in the light (Lappe et al., 2000; Maij et al., 2011a; Ross et al., 1997). When experiments are conducted in the dark, the flash’s contrast is high and there are fewer distractions, which we propose will lead to a reduction of uncertainty (modeled as a wide prior). As a result, there will hardly be compression (figure 3C), in agreement with observations (figure 1A).

**Figure 3.** Predicted apparent positions of flashes presented at 50% (blue) and 150% (red) of the saccade length. The widths of the temporal uncertainty ($\sigma_t$) and the spatial prior ($\sigma_s$), the saccade amplitude (A) and the delay (d) are given in each panel. Panels B-E each differ from panel A in one value.
If we summarize the changes to the mislocalization curves shown in figure 3 by a single value, we can plot how this value changes with each of the parameters. In figure 4 we do so for the peak compression and shift (see caption for definitions). Increasing the width of the foveal prior (decreasing the bias) decreases the amount of compression. Increasing the width of the temporal uncertainty increases the compression. Increasing the saccade amplitude increases the compression. Increasing the delay of the corollary discharge does not change the compression at all (figure 4A). The value for the shift increases with the temporal uncertainty, but does not change as much as the compression when the other parameters are changed (figure 4B).

**Figure 4.** Dependence of mislocalization on four parameters (standard deviation of temporal uncertainty, standard deviation of foveal prior, saccade amplitude and delay). Compression (A) is defined as one minus the value obtained when the smallest distance between the localization curves is divided by the distance between the targets. Shift (B) is defined as the peak in the mean of the two localization curves divided by the saccade amplitude.

Compression and shift are generally defined as linear operations, not only in our definition, but also in the literature (Lappe et al., 2000). When presenting the flashes near the saccade target, this definition seems to be valid. However, shift and compression are found to be non-linear when flashes are presented at higher eccentricities (Richard et al., 2009). Our model predicts similar non-linear relations to those that were found by Richard and colleagues for flashes presented at high eccentricities (Richard et al., 2009; figure 5).
Figure 5. Non-linearity of compression. A. Predicted apparent positions for many possible flash locations (model parameters as in figure 3a). Each curve represents one flash location. Gray area represents saccade duration. B. The predicted apparent position at each flash location for a single time of the flash. Each panel represents a different time of the flash.

Discussion and conclusion
Our model shows that temporal uncertainty about the time of the flash and a prior to see things where one is looking can explain the localization patterns that are found in the literature. By changing the width of the Gaussian distribution representing either the foveal prior or the temporal uncertainty we can change the localization pattern considerably. The pattern is also different for different saccade amplitudes.

The fact that all three factors clearly influence compression probably explains the many discrepancies between previous studies. It has been shown that compression increases with increasing saccade amplitudes (Lavergne et al., 2010) (corresponding to the model prediction in figure 3D). But, for instance Brenner and colleagues did not find any compression for 5° saccades (Brenner et al., 2005), whereas Lavergne et al. (Lavergne et al., 2010) did find compression for that saccade amplitude. The difference between the studies is probably that Brenner et al. (Brenner et al., 2005) used a higher stimulus contrast and luminance. Increasing contrast and luminance has been shown to decrease compression (Georg et al., 2008; Michels & Lappe, 2004). Our model simulates this with the assumption that increasing stimulus luminance and contrast decreases the temporal uncertainty about the time of the flash.

The model replicated another finding that was found in the literature; a nonlinearity of the compression for higher eccentricities (Richard et al., 2009; figure 5). This is because the peak of the localization curves depends on the flash location (Maij et al., 2011a). Previous studies have assumed that compression and shift are linearly related to the position of the flash. For instance, compression and shift were defined as the standard deviation and the
mean of the mislocalization curves at each time to be able to compare the curves across subjects and conditions (Lappe et al., 2000). The fact that we found clear nonlinearities for the compression suggests that these are not valid measures to compare the mislocalization curves across subjects and conditions.

One factor that needs further justification is the 70 ms time difference that we chose as a delay for the foveal bias. The foveal prior is modeled as a Gaussian centered on the position that the eye will have 70 ms later. We assume that the bias is guided by a corollary discharge (CD). The value of 70 ms was taken from a review by Sommer and Wurtz (Sommer & Wurtz, 2008). However, it is not critical to know the exact value for our model as we found that peak compression and shift are hardly influenced by changing these values (figure 4), despite the clear change in the precise pattern of mislocalization for flashes at 50% of the saccade amplitude for very small delays (below 20 ms; figure 3E).

Another issue that needs to be mentioned is that we took the mean of the posterior and not the mode (maximum a posteriori; MAP). Some previous studies that use Bayesian models to explain their data have used the mean of the posterior (e.g. Roach, Heron, & McGraw, 2006; Saunders & Knill, 2001), others have used the MAP (e.g. Ernst, 2007; Kording & Wolpert, 2004), and still others have used both (Pouget, Dayan, & Zemel, 2000; Stocker & Simoncelli, 2006; Weiss, Simoncelli, & Adelson, 2002). For normal distributions it does not make a difference which one uses, but our distributions are clearly not normal (figure 2). If we take the mean of the posterior we find a pattern of results that is similar to the localization patterns reported in the literature. If we take the MAP the pattern does not resemble the localization patterns reported in the literature. The difference between the mode and the mean can be seen in figure 2C, the mode of the posterior is located at 10 degrees whereas the mean of the posterior is located just below 20 degrees. This means that if our model is correct, our brain must rely on the mean of the posterior.

To conclude, we have shown that a Bayesian model with temporal uncertainty about the time of the flash and a bias to believe that the flash was where one was looking as the only ingredients can explain the full range of localization patterns that are found in the literature for various saccade amplitudes.

**Methods**

**Model**

The model describes localization errors in the direction of saccades, around the time of saccades. Positions are expressed as visual angles \( x \). With no uncertainty about the time and location of the flash, the spatial location of the flash is a function of the retinal flash location and the eye position at the time of the flash:

\[
x_f = r_F + x_e(t_f)
\]

where \( x_e(t) \) is the actual eye position as a function of time, \( r_F \) is the retinal
location of the flash, $x_F$ is the actual flash location and $t_F$ is the time of the flash.

In reality, there is uncertainty in the sensed retinal location of the flash and in the sensed eye position at the sensed time of the flash. We assume that this uncertain information is combined with a prior to arrive at a final estimate. If we assume that the uncertainty in the saccade trajectory and in the retinal position of the flash are negligible, but that the time of the flash relative to the saccade is uncertain, we get:

$$p(\hat{x}_F = x) \propto p(x_{F,p} = x)p(r_F + x_e(\hat{t}_F) = x)$$  \hspace{1cm} (2)

where $p(x_{F,p} = x)$ is the prior, $p(r_F + x_e(\hat{t}_F) = x)$ is the likelihood, and $p(\hat{x}_F = x)$ is the posterior. The hat symbol above a parameter represents the estimate of that parameter.

The likelihood represents the spatial uncertainty that is caused by the temporal uncertainty about the time of the flash. The likelihood can therefore be written as:

$$p(r_F + x_e(\hat{t}_F) = x) = p(x_e(\hat{t}_F) = x - r_F) = p(\hat{t}_F = t) \left| \frac{\partial t(x_e)}{\partial x_e} (x_e - r_F) \right|$$  \hspace{1cm} (3)

where $\frac{\partial t(x_e)}{\partial x_e} (x_e - r_F)$ is the Jacobian of the transformation from $t(x_e)$ to $x_e$, that is, the inverse of $x_e(t)$.

This leads to the following posterior:

$$p(\hat{x}_F = x) \propto p(x_{F,p} = x)p(\hat{t}_F = t) \left| \frac{\partial t(x_e)}{\partial x_e} (x_e - r_F) \right|$$  \hspace{1cm} (4)

The expected value of the perceived flash location then becomes:

$$E(\hat{x}_F) = \int xp(\hat{x}_{F,p}) dx \frac{\partial t(x_e)}{\partial x_e} (x_e - r_F)$$

$$E(\hat{x}_F) = \int p(x_{F,p} = x)p(\hat{t}_F = t) \left| \frac{\partial t(x_e)}{\partial x_e} (x_e - r_F) \right| dx$$  \hspace{1cm} (5)

We further assume that the temporal uncertainty is a Gaussian centered on $t_F$ with a variance $\sigma_t^2$:

$$p(\hat{t}_F = t) = N(\hat{t}_F, \sigma_t^2)$$  \hspace{1cm} (6)

and that the prior is a Gaussian centered on the eye position achieved $d$ seconds later than the current position, with variance $\sigma_{r,p}^2$:

$$p(x_{F,p} = x) = N(x_e(t + d), \sigma_{r,p}^2)$$  \hspace{1cm} (7)
Finally, taking all factors together, we get:

\[
p(\hat{x}_F = x) \propto p(x_{F,x} = x)p(\hat{t}_F = t) \left| \frac{\partial f(x_i)}{\partial x}\right| (x_i - r_F)
\]

\[
N(x_i(t+d),\sigma^2)N(\hat{t}_F,\sigma^2) \left| \frac{\partial f(x_i)}{\partial x}\right| (x_i - r_F)
\]

We used a minimum jerk profile to describe the trajectories of saccadic eye movements (Flash & Hogan, 1985). Very similar results were found using other trajectories. The saccade duration (in ms) is given as a function of the amplitude (in degrees).

\[
Duration = 2.7 \cdot Amplitude + 23 \text{ ms}
\]

This formula is based on the experimental results of Collewijn and colleagues (Collewijn et al., 1988).