

Simulating the Fröhlich Effect of Motion Misperception as a Result of Top-Down Attentional Modulation in the Visual System

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Abstract

The term “Fröhlich effect” refers to the phenomenon that the initial position of a fast moving stimulus appears to be shifted in the motion direction. Based on the Asynchronous Updating Model (e.g., Müsseler & Neumann, 1992; Scharlau & Neumann, 2003) we simulated this perceptual illusion via a neural model. The model was capable of simulating the same main effects as those that were found in empirical data.

Introduction

More than 80 years ago, the German physiologist Friedrich Fröhlich discovered a localization error that occurs with fast moving stimuli: The stimulus did not seem to appear at its actual starting location but at a later position on the motion trajectory (Fröhlich, 1921, 1929). Most researchers explain the Fröhlich effect in terms of visuospatial attention (e.g., Müsseler & Aschersleben, 1998; Müsseler & Neumann, 1992; Müsseler, Stork, & Kerzel, 2002; Neumann & Müsseler, 1990). Neumann's Asynchronous Updating Model is based on only a few plain assumptions. It states that the stimulus onset triggers an attention shift towards its location. During the shift the stimulus moves, and because the stimulus can only be consciously perceived when the shift is completed, a later position is erroneously perceived as the first position.

In this paper we present a neural model that is aimed at simulating the Fröhlich effect by adopting the idea of a time-consuming attentional mechanism necessary for a conscious percept. We will then compare simulation results to basic empirical results on the Fröhlich effect for the stimulus parameters velocity, motion direction, and stimulus eccentricity

Description of the Artificial Neural Network

The model is based on only a few core assumptions: We started from the now well-known fact that feedforward as well as feedback connections exist in visual processing, and that feedback connections seem to be involved in higher cognitive processes like attention, consciousness, and cross modal integration of stimulus features (e.g., Di Lollo, Enns, & Rensink, 2000; Driver & Spence, 2000; Lamme & Roelfsema, 2000; Luck, 1998). We also assumed that the attention shift corresponds to a feedback loop from higher

visual areas back to V1, and that these reentrant processes are essential for the conscious percept. This is supported by studies that have shown feedback to V1 to be indeed essential for a conscious perception of certain stimulus features (Martinez et al., 1999; Pascual-Leone & Walsh, 2001). The Fröhlich effect results because the feedback loop is initially triggered by the actual onset position but meets later stimulus representations during the feedback process.

We restricted the model to horizontal motion because one-dimensional motion is sufficient for simulating the Fröhlich effect. Additionally, this keeps the model simple and makes its visualization easy. Just like the visual system, the model is hierarchical. It consists of five layers, the first of which explicitly represents the input (more precisely, it corresponds to one row of pixels on a computer screen). The second layer represents the primary visual cortex (V1), and the layers 3, 4, and 5 correspond to higher visual areas accordingly. Each neuron inside the model receives input from its receptive field (RF), which is a spatially contiguous set of neurons in the layer immediately below.

Obviously, the connections between the first and second layers do not represent direct links between neurons, but the mapping of the visual input - via optical projection and the early visual pathway - onto neurons in V1. The connectivity pattern between these two layers therefore differs from the other layers in order to reflect an important property of V1 - the cortical magnification factor. The size of receptive fields of V1 neurons increases drastically with increasing retinal eccentricity of its input. For determining the connections between the input layer and the second layer we took this magnification into consideration. The RF sizes were determined by using the formula provided by Rosa, Casagrande, Preuss, and Kaas (1997):

$$\text{RFsize (degrees)} = 0.57 \cdot \text{eccentricity}^{0.69}$$

The number of neurons in layer 2 and their RF sizes were computed by applying the formula for a central fixation point and a subject-screen distance of 40 cm (both were standard parameters in our Fröhlich experiments). For all RFs, including those in layer 1, the overlap with their neighbors was set to 40 percent. The number of neurons in higher layers was computed by approximately dividing the

number of neurons in the lower layer in half and by keeping the RF overlap of 40 percent. These constraints led to a network configuration of 1478 pixels in the first layer, 111 neurons in the second layer, 55 neurons in the third layer, 27 neurons in the fourth layer, and 13 neurons in the fifth layer.

The model simulates time, i.e., the time for the stimulus' movement and for transmitting information from one layer to the next. The motion is simulated by setting pixels in the input layer to 1 while setting the remaining pixels to 0 for specific time intervals. The standard stimulus used in most of our experiments (Carbone, 2001) and in the simulations was 14 pixels wide (0.67°) and was shifted by its entire width with every retrace of the screen (16.67 ms; 60 Hz).

The feedforward transmission delays were set on the basis of a meta-analysis on visual response latencies in the macaque cerebral cortex done by Lamme and Roelfsema (2000). According to the authors the "fast feedforward sweep of activity is completed within approximately 100 ms" (Lamme & Roelfsema, 2000, p. 575). They additionally established a mean response latency of 72 ms for V1. To yield a total transmission delay of 100 ms, we set the first delay (from the input layer to V1) to 72 ms and the other three delays to 9.33 ms. After each delay, the net input to neurons in the next-higher layer is computed by adding up the weighted outputs from that neuron's RF in the lower layer and dividing the sum by the number of these outputs:

$$net_i(t) = \frac{1}{|RF(i)|} \cdot \sum_{j \in RF(i)} w_{ij} o_j(t) ,$$

where $net_i(t)$ is the net input to neuron i at time t , $RF(i)$ is the set of neurons in the RF of neuron i , w_{ij} is the synaptic weight for input from neuron j to neuron i , and $o_j(t)$ is the output of neuron j at time t . Then the output of the higher layer is computed by applying a sigmoid activation function:

$$o_i(t) = \frac{1}{1 + e^{-(net_i(t) + o_i(t-1)/2) - \theta)/\tau}} ,$$

After the next transmission delay, the input of the next layer is computed by multiplying the output by the weights, and so on, until the information reaches the top layer TL. When the input has finally reached TL, a competitive process within TL determines a set of neurons $W_{TL}(t)$, which are the "winner" neurons with the highest output:

$$W_{TL}(t) = \left\{ i \in TL \mid o_i(t) \geq \alpha \cdot \frac{1}{|TL|} \cdot \sum_{j \in TL} o_j(t) \right\} ,$$

where α is a constant that determines the proportion of winners. In the present model, for all such competitions we set $\alpha = 0.5$.

This is where the feedback loop starts. For establishing the delays for the feedback delays we again consulted the meta-analysis done by Lamme and Roelfsema (2000). They found a latency of at least 200 ms for response enhancement in V1 for a curve-tracing task and attributed this long delay to recurrent processing. Since this complete delay comprised the feedforward as well as the feedback loop and the feedforward loop inside the model takes 100ms, we set the complete feedback delay to 100 ms and the delays for each of the three feedback steps to 33.33 ms (there are only three feedback steps in our model because the feedback terminates in V1). After the first feedback-delay of 33.33 ms, the winner neurons belonging to the receptive fields of the feedback neurons in the next higher layer are identified ($\alpha = 0.5$). This constitutes the end of the first step of the feedback loop. After the next delay the net searches for the most highly activated neurons inside the receptive fields of these neurons, and so on, until the feedback finally reaches the second layer.

As the final step, the model determines the perceived stimulus position that corresponds to the activation in V1. To achieve this, the activity pattern – more specifically its center of gravity – inside the highly activated neurons at the second level is compared to reference activity patterns. For a layer with neurons 1, ..., N , and o_i^{\min} being the minimal output of neuron i , the center of gravity of its activation is located at position $c(t)$ as computed by the following equation:

$$c(t) = \frac{\sum_{i=1}^N i \cdot (o_i(t) - o_i^{\min})}{\sum_{i=1}^N (o_i(t) - o_i^{\min})}$$

These reference center of gravity values were computed offline before the simulation. We "presented" the stimulus to the net at each starting position, computed the center of gravity and thereby mapped stimulus positions to locations in V1. The current center of gravity is compared to these reference values and the most similar one is taken as the network's "perceived" starting location.

These processes generate the Fröhlich effect because the activity pattern inside the net changes during the feedforward-feedback loop due to the fast stimulus motion. More precisely, the activation that corresponds to the actual starting location is transferred from the lowest up to the highest layer. Thus the first stimulus location actually triggers the feedback loop. But already during this feedforward processing, the activation patterns in the lower layers have changed in response to the shifting stimulus location. This updating continues during the feedback loop, and when the net determines the most highly activated neurons inside the current RFs, the center of gravity has shifted into the direction of the motion. This leads to a distortion of the feedback loop at each feedback step. The final distortion at the V1 level determines the amount of the

Fröhlich effect – the difference between the actual and the perceived starting location.

The network's architecture and the feedforward and feedback processes can be visualized during the simulation. The amount of activity inside the net is visualized by inking

the neurons and connections with red color and feedback is visualized by inking them with blue color. Figure 1 shows the final net state when the feedforward and the feedback processing has been completed. Since the net is too large for a complete depiction, only the central area is shown.

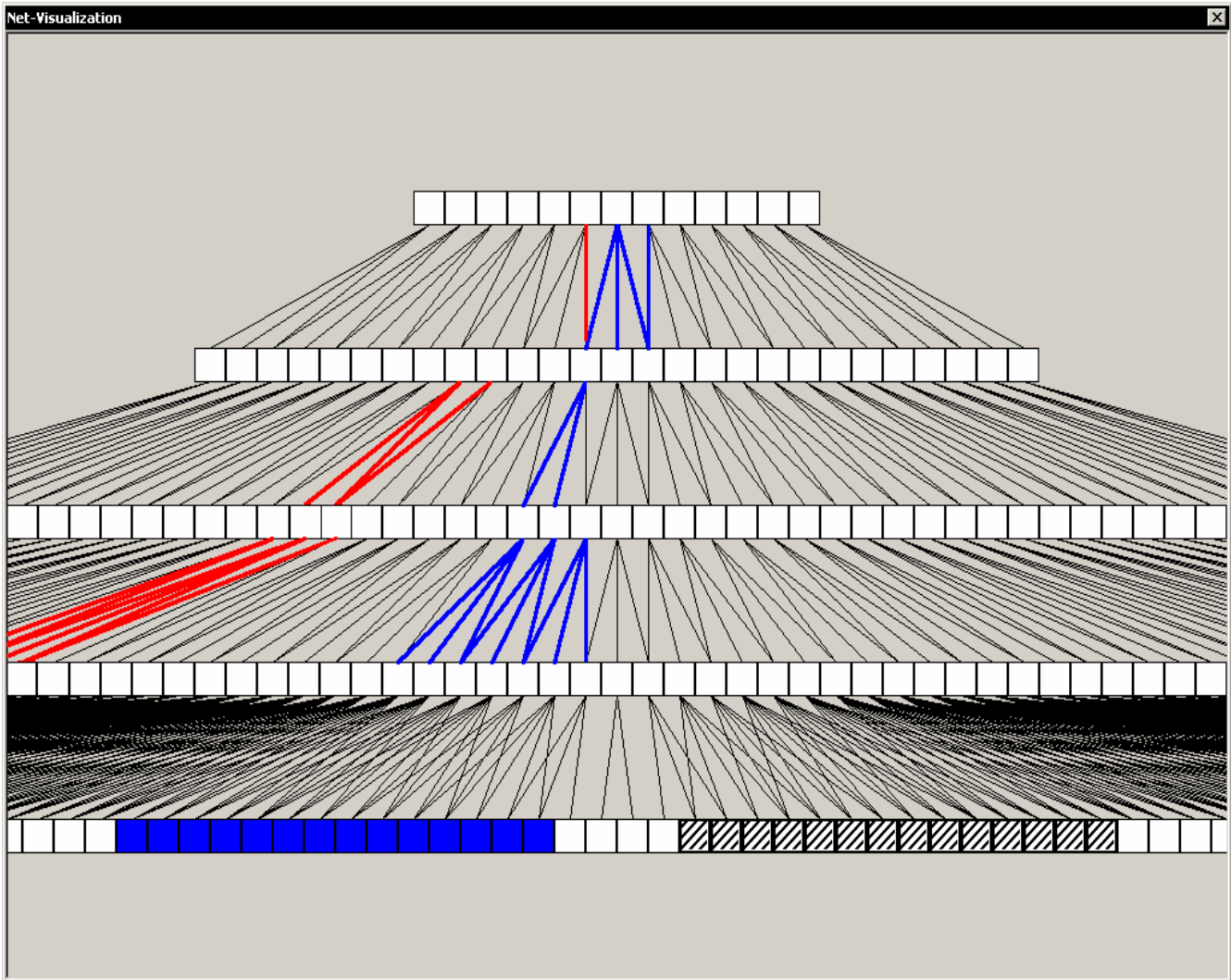


Figure 1. The network state inside the central area of the neural model after the feedback loop has been completed and the “perceived” starting location has been determined (blue squares). Activity is represented by red color and feedback by blue color. To simplify a comparison between the perceived and actual starting locations, the pixels of the actual starting location are filled with diagonal stripes.

Comparing Empirical and Simulation Data

To sum up, we tried to model the emergence of the Fröhlich effect based on the Asynchronous Updating Model through feedforward and feedback processes inside a neural model. Neumann's Asynchronous Updating Model states that the Fröhlich effect emerges because the stimulus onset triggers an attention shift towards its location and that the stimulus moves during the shift and can only be consciously perceived at the end of the attention shift. In the neural model, the stimulus onset triggering the feedback loop represents the triggering of

the attention shift by the stimulus. The ongoing motion changes the activity pattern inside the net and thus the feedback loop meets activity patterns belonging to later stimulus locations. This leads to a distortion of the feedback activation pattern in the direction of motion.

In the following part of the paper, we will compare empirical to simulation results for the stimulus parameters – velocity, motion direction, and eccentricity. We were mainly interested in whether the model would reproduce the main effects found in the empirical data. However, because the model in its current state does not produce

any variance, we could not statistically test for these main effects or test the empirical against the simulated data.

The effect of stimulus velocity was investigated by Müsseler and Aschersleben (1998). The authors used velocities of either 14° or 44° per second and found the Fröhlich effect to increase with velocity. The attentional model explains the velocity effect in a straightforward way: A fast stimulus covers a longer distance during the attention shift, which prolongs the attention shift and thus leads to a larger Fröhlich effect.

For the simulation of the velocity effect, we adapted the virtual retrace rates to Müsseler and Aschersleben's stimulus velocities: Instead of presenting the stimulus for 16.67 ms at each location, each stimulus position was shown for either 46.10 ms (low velocity) or 12.17 ms (high velocity). The corresponding virtual retrace rates were 21.69 and 82.19 Hz. The virtual retrace rates do not correspond to those used by Müsseler and Aschersleben (1998) because the subject-screen distance, the stimulus size and the way to generate the motion of the stimulus was different in the simulation and the experiments. Figure 2 depicts the empirical and the simulation results.

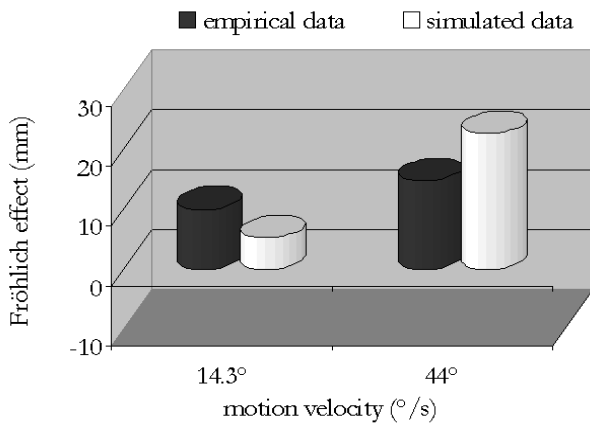


Figure 2. Empirical and simulated data for the stimulus parameter motion velocity.

As can be seen from this figure, the empirical as well as the simulated data show an increase in the Fröhlich effect with growing velocity. Thus, the model indeed reproduced the main effect of velocity, but this increase seems to be more pronounced for the simulated data.

The effect of the stimulus parameter motion direction was investigated by Carbone (2001). A black square was used as the stimulus and either moved away from the fixation point (foveofugal), towards it (foveopetal), or was flashed at the “starting location” for one retrace (16.7 ms), i.e., as long as the moving stimuli were shown at each stimulus location. The main effect for motion direction was significant. A post-hoc analysis revealed that the Fröhlich effect was more pronounced for the foveofugal than for the foveopetal motion, and that there was no mislocalization for the stationary stimulus.

The explanation of the attentional model for the effect of motion direction is based on the assumption that attention is centered at the fixation point at the beginning of each trial. When the stimulus appears, attention is shifted towards the onset location. On its way attention may either have to “catch up” with the stimulus or the stimulus moves toward the focus of attention. Thus, a stimulus that moves away from the fixation point “costs” the attention shift some additional distance whereas motion towards it can “save” the attention shift some distance.

Carbone (2001) also discussed another possible explanation for the effect of motion direction in accordance with the attentional explanation: Evidence found by Mateeff and Hohnsbein (1988) and Mateeff et al. (1991) supports the assumption that the visual system might be more sensitive to foveofugal than to foveopetal motion. For the moving square this would lead to an earlier start of the attention shift for foveopetal motion.

In the model, the different motion directions were simulated by shifting the active pixels (pixels with an output of 1) either further outward for the foveofugal motion or further inward for the foveopetal motion with each virtual retrace. The stationary stimulus was simulated by setting the pixels at the corresponding positions to one for a single retrace (16.7ms) only. The empirical and the simulated data are shown in Figure 3.

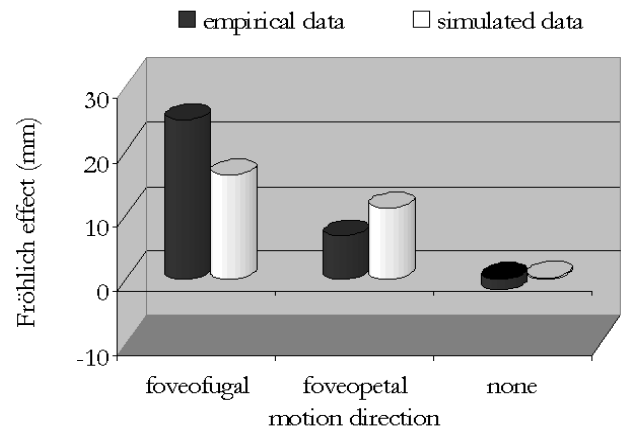


Figure 3. Empirical and simulated data for the stimulus parameter motion direction.

A glance at this figure indicates that the model does not generate a mislocalization for the stationary stimulus. This shows that the misperception is indeed produced by later stimulus positions during the feedforward and feedback processes inside the neural model. The figure also indicates a main effect for motion direction: For the simulated data, just like for the empirical ones, the Fröhlich effect was stronger for the foveofugal motion than for the foveopetal motion. However, in the simulation the difference between the two conditions is smaller. As for stimulus velocity the simulated data match the empirical data qualitatively but not numerically.

Moreover, the influence of stimulus eccentricity on the Fröhlich effect was investigated by Carbone (2001). Starting from the fixation point, the starting location varied between 0 and 58.8 mm (0 - 8.36°). The results showed a linear increase of the Fröhlich effect along with eccentricity.

The attentional account is capable of explaining this increase by assuming that the attention shift takes longer for a larger distance. Another explanation that is also in accordance with the Asynchronous updating model is that the start of the attention shift might be delayed because it is more difficult to program the target of the attention shift (Carbone, 2001). For the simulation, the same eccentricities as in the original experiments were used by setting the corresponding pixels to 1. The empirical and simulated data are shown in Figure 4.

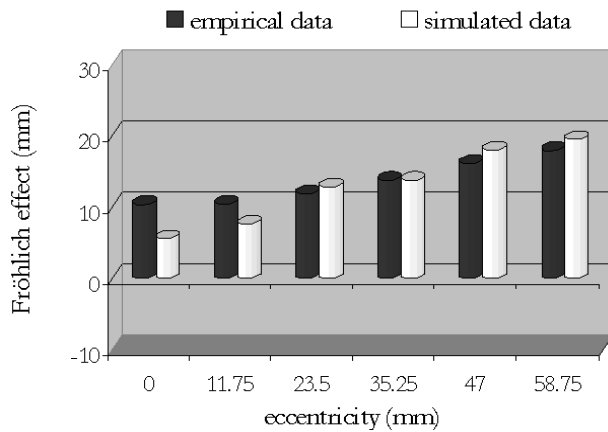


Figure 4. Empirical and simulated data for stimulus eccentricity.

The simulated data resemble the empirical ones quite closely. Like the empirical data, the simulated data increase with eccentricity.

Discussion

In this paper, we presented a neural model that simulates the emergence of the Fröhlich effect through feedforward as well as feedback processes based on Neumann's Asynchronous Updating Model. The hierarchical model comprises five levels, with the first one being the input level and the other levels being visual processing levels of increasing complexity. The cortical magnification factor was considered in modeling the RF sizes between the first and the second layer. The virtual moving stimulus was generated by setting the corresponding pixels at the first level to 1. The transmission delays for the feedforward processes were adopted from Lamme and Roelfsema (2000). The attention shift that – according to the Asynchronous Updating Model – is necessary for the conscious perception is modeled via a feedback loop from the highest layer back to V1. As were the feedforward transmission delays, the feedback delays were also

adopted from Lamme and Roelfsema (2000). The Fröhlich effect – the distortion of the perceived onset location – emerges because the activity inside the net changes during the processing of the first stimulus location. The feedback loop meets these later stimulus representations and is distorted in the direction of stimulus motion. When the feedback finally reaches V1, the amount of this distortion determines the amount of the Fröhlich effect.

When the original attentional model was developed by Neumann approximately 25 years ago (Neumann, 1978, 1982), little was known about the physiology of high-level processes like attention or consciousness and about feedback processes. Accordingly, Neumann did not speculate about the physiological mechanisms underlying the attention shift and the conscious perception. Nevertheless, the model is not only compatible with feedback mechanisms, but including feedback processes may even be physiologically more plausible than a sheer feedforward model, because it is in accordance with new physiological evidence (e.g. Di Lollo, Enns, & Rensink, 2000; Lamme & Roelfsema, 2000; Martinez et al., 1999) and it creates the Fröhlich effect in a quite natural manner.

After describing the model, we tried to simulate basic properties of the Fröhlich effect. We showed that a misperception only occurred with moving and not with stationary stimuli. Additionally, the main effects for motion direction, stimulus eccentricity and stimulus velocity could be simulated. Nevertheless, the amount of the simulated misperception did not correspond to the empirical Fröhlich effect. In our view, the established main effects are more important than the numerical resemblance because the size of the Fröhlich effect may differ strongly between experiments, probably due to the particular sample of subjects, but the direction of the main effects rarely does. Additionally, we could have tuned the model to resemble the absolute effect sizes more closely by adjusting various model parameters. But we considered the model to be more convincing if we only adapted basic physiological parameters (like the RF sizes or the transmission delays) from the literature.

Several steps are conceivable in evaluating the model further. First, other properties of the Fröhlich effect should be simulated. For example, Müsseler and Aschersleben (1998) have found that a valid cue – a cue that is shown at the starting location in advance of the actual moving stimulus – reduces the Fröhlich effect, but an invalid cue does not enlarge it. More importantly, our model should be applied to other phenomena that the Asynchronous Updating Model is supposed to explain, such as metacontrast (Neumann, 1982). Additionally, we could derive hypotheses about the effects of certain stimulus parameters from model simulations and investigate them in experiments. And finally, the feedback model should be tested against different computational models, especially pure feedforward models.

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