

Running head: A NEURAL MODEL SIMULATING THE FRÖHLICH EFFECT

Motion Misperception Caused by Feedback Connections:

A Neural Model Simulating the Fröhlich Effect

Elena Carbone¹ & Marc Pomplun²

¹Department of Psychology, Bielefeld University

²Department of Computer Science, University of Massachusetts at Boston

Mailing Address:

Elena Carbone

Department of Psychology, Bielefeld University

P. O. Box 100131, D-33501 Bielefeld, Germany

email elena.carbone@uni-bielefeld.de

Abstract

When asked to indicate the starting position of a fast moving stimulus, observers do not indicate the actual starting position but a later position on the motion trajectory. This perceptual illusion is known as the "Fröhlich effect". We present a neural model aimed at simulating this phenomenon based on feedforward and feedback connections. The basic simulation mechanisms seem compatible with the attentional and the motion extrapolation account. A comparison between simulated and empirical results showed that the model is capable of generating the same main effects as those found in the empirical data.

Motion Misperception Caused by Feedback Connections: A Neural Model Simulating the Fröhlich Effect

Introduction

The so-called Fröhlich effect refers to a localization error that occurs when observers are asked to indicate the first position of a fast moving stimulus. Compared to the actual starting location, the perceived starting location is shifted in the direction of motion. This perceptual illusion was named after Friedrich Fröhlich. The German physiologist discovered the phenomenon more than 80 years ago (Fröhlich, 1921, 1929) and attributed it to the time it takes to elicit the sensation that corresponds to a physical stimulus ("Empfindungszeit"). Nowadays, this phenomenon is mostly explained in terms of visuospatial attention (e.g., Müsseler & Aschersleben, 1998; Müsseler & Neumann, 1992; Müsseler, Stork, & Kerzel, 2002; Neumann & Müsseler, 1990). Neumann's attentional model – which has lately been termed "Asynchronous Updating Model" (Scharlau & Neumann, 2003) – states that the stimulus onset triggers an attention shift towards its location. During the shift, the stimulus changes its location, and because the conscious perception depends on the stimulus being attended, a later position is consciously perceived as being the first position (for a more detailed description of Neumann's attentional model, see Scharlau, this issue). Recently, a different account – namely motion extrapolation – has been applied to the Fröhlich effect (Carbone & Ansorge, submitted). This account, which was suggested by Nijhawan (1994, 1997, 2002), assumes that the visual system extrapolates the current position of a moving stimulus in order to compensate for the perceptual delay. Without such compensation, this delay would – according to Nijhawan – lead to the perception of outdated stimulus positions because the stimulus would have moved to a new location during the delay. Originally, motion extrapolation was applied to the flash-lag effect – that is, the phenomenon that a flashed stimulus seems to lag behind a moving stimulus although both stimuli are actually presented at adjacent locations. According to this account, the flash-lag effect emerges

because the moving stimulus is extrapolated to a later position based on the processing of certain motion features, whereas the flash cannot be extrapolated and thus is perceived at its actual location. This account might be suitable for explaining the Fröhlich effect, assuming that the extrapolation process based on the first stimulus locations is faster than the perceptual latency for the first stimulus location. The Fröhlich effect would emerge because information about the first stimulus positions would be used to extrapolate the current stimulus location. The first extrapolated stimulus position would then be mistaken for the actual starting location.

The main aim of our simulations was to investigate if a simple neural model is capable of simulating the basic properties of the Fröhlich effect. Although we intended to model an attentional network, mechanisms implemented by the model – mainly a feedback loop that meets later stages of visual processing – are relatively abstract, and can be considered as modeling motion extrapolation as well. In essence, feedback in the model might be regarded as a time-consuming process of focusing attention on the stimulus or as a means to extrapolate the motion signal. After the description of the model we will compare simulation results with results of experiments on the Fröhlich effect.

The neural model

In a nutshell, the neural model is based on three assumptions. The first one is the now well-known fact that feedforward as well as feedback connections exist in brain areas responsible for visual processing, and that feedback connections are involved in higher cognitive processes like attention, consciousness, and crossmodal-integration of stimulus features (e.g., Di Lollo, Enns, & Rensink, 2000; Driver & Spence, 2000; Lamme & Roelfsema, 2000; Luck, 1998). Secondly, we assume that a feedback loop from higher cortical areas back to V1 plays an important role in the formation of the conscious percept. This is in line with studies that have shown such reentrant processes into V1 to be indeed essential for a conscious perception of visual stimulus features (Martinez et al., 1999;

Pascual-Leone & Walsh, 2001). And finally, we believe that the Fröhlich effect results from the feedback loop of processing being initially triggered by the actual onset position of the moving stimulus but terminating on a shifted stimulus position representation when processes finally reenter at the V1 level.

Since one-dimensional motion is sufficient for simulating the Fröhlich effect, we restricted the model to the horizontal direction. This has the additional advantages of keeping the model simple and making the visualization rather easy. Like the visual system, the model is hierarchical. It consists of five layers, with the first layer representing 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 levels 3, 4, and 5 correspond to higher cortical areas accordingly. Each neuron inside the model is connected to other neurons in the neighboring layers below and above it (except for the outer layers).

Cortical magnification in V1 – that is, increasing receptive field (RF) sizes of V1 neurons with increasing eccentricity – was modeled by applying the formula provided by Rosa, Casagrande, Preuss, & Kaas (1997)¹ for a central fixation point with a subject-screen distance of 40 centimeters (both of which were standard parameters in our Fröhlich experiments). The overlap between neighboring RFs was about 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. All connection weights were set to 0.8.

These constraints led to our standard model for simulating the Fröhlich effect. It consisted of 1,478 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. This is the smallest possible model comprising a complete row of pixels on a standard computer screen with a resolution of 1024×768 pixels (without allowing activity to reach a dead end when transmitted from one layer to the next).

Transfer of information inside the net

In simulating the Fröhlich effect, the model simulates time, i.e., the time it takes 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 a specific time interval. The standard stimulus used in most of our experiments (Carbone, 2001) and in most of 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). Feedforward transmission delays were estimated based on a meta-analysis of visual response latencies in the macaque cerebral cortex (Lamme & Roelfsema, 2000): A mean response latency of 72 ms was used for V1, and three delays of 9.33 ms were successively added per layer so as to yield a total transmission delay of 100 ms (Lamme & Roelfsema, 2000, p. 575). After each delay, activation of neurons in the next-higher layer is computed by adding up the weighted outputs of the lower layer and dividing the sum by the number of outputs of the lower layer. Then half of the former activation value is added to this input value, and the output of the higher layer is computed by applying a sigmoid activation function to the sum². Including the former activation value allows for a continuing effect of former stimulus locations. After the next appropriate transmission delay, the input of the following layer is computed by multiplying the output by the weights, and so on, until the information reaches the final layer. When the input has finally reached the highest layer, the most highly activated neurons – more specifically, neurons with an output above the average – are identified. These neurons indicate the start of the feedback phase. Like the delays for the feedforward processes, the delays for the feedback-transmission are based on work by Lamme and Roelfsema (2000) in this case measured as a response enhancement in V1 with a curve-tracing task. Because this delay of 200 ms comprises both the feedforward as well as the feedback loop, 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 output values of the neurons belonging to the receptive fields of the feedback neurons in the next higher layer are inspected and those with an above-average output are identified. This is where the first step of the feedback loop ends. 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. In the final computational step, it needs to be determined to which perceived stimulus position the activation in layer 2 (V1) corresponds. To achieve this, the activity pattern – more specifically its center of gravity³ – inside the highly activated neurons at the second level is compared to reference activity patterns. These reference center of gravity values were determined offline before the simulation, by "presenting" the stimulus to the net at each possible position and computing the center of gravity, and, thereby, mapping stimulus positions to locations in layer 1 (V1). Each stimulus location and the corresponding center of gravity value were stored in a data file. The reference center of gravity value that best matches the current center of gravity value is selected and the corresponding stimulus location is the net's "perceived" starting location.

How do these processes account for the distortion of the perceived first stimulus location? For a fast moving stimulus, the activity pattern inside the net changes while activity is transferred to higher levels and also during the feedback phase. This is the case because the stimulus location changes more rapidly than the time it takes for a complete feedforward and feedback loop. In more detail, the information that corresponds to the actual starting location is transferred from one layer to the next until it reaches the highest layer. Thus, the first stimulus location actually triggers the feedback loop. But already during this feedforward sweep, lower layers have updated their activation in response to the shifting stimulus location. This updating continues during the feedback phase. 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 and the feedback loop is distorted in the same direction. This distortion occurs at

each step of the feedback phase, and 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 net's architecture and the feedforward and feedback processes can be visualized during the computational process. 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 various net states during the feedforward and feedback phases. Since the net is too large for a complete depiction, only its central area is shown.

Insert Figure 1 about here

Comparing empirical and simulation results

To summarize, we tried to model the emergence of the Fröhlich effect through feedforward as well as feedback processes inside a neural model. In principle, the attentional as well as the motion extrapolation account seem compatible with the proposed mechanisms: The Asynchronous Updating Model states that the stimulus onset triggers an attention shift towards its location and that the Fröhlich effect arises because the stimulus moves during the shift and can only be consciously perceived after attention has been shifted to its position. In the neural model, the triggering of the attention shift would be mimicked by the stimulus onset triggering the feedback loop and the feedback loop would correspond to the attention shift. Since the stimulus moves during the shift, the activity pattern inside the net changes, and when the feedback loop finally terminates at the V1 level, the pattern belonging to a later stimulus location determines the conscious percept of the seemingly first stimulus position. The motion extrapolation account states that the first stimulus locations are used to extrapolate the current position of the stimulus. Inside the neural model, the feedback loop might be regarded as the extrapolation mechanism. The distortion of the percept into the motion direction might then be regarded as the correction of the perceived stimulus towards

the current stimulus location. However, the extrapolation can never compensate for the whole perceptual delay and, thus, never leads to the perception of the current stimulus location. The reason is that the feedback is directed only towards second layer (V1) neurons which are already delayed relative to the retinal input.

In the following part of the paper, we will describe empirical results of Fröhlich experiments for the stimulus parameters velocity, motion direction, and eccentricity, and compare them to simulation results. The most important question is whether our simple model is capable of simulating the main effects found in the empirical data. However, it is not possible to statistically test for these main effects or to test the empirical against the simulated data, because the model does not produce any variance.

To start with, Müsseler and Aschersleben (1998) investigated the effect of stimulus velocity on the Fröhlich effect. The stimulus velocity was either 14.4° or 55° per second. They found that the Fröhlich effect increased with velocity. This is explained by the attentional model in a straightforward way: Compared to a slower stimulus, a faster stimulus covers a longer distance during the attention shift, which leads to a larger Fröhlich effect. Similarly, the motion extrapolation account would explain this result by assuming that since the extrapolation process estimates the current stimulus location from earlier locations, stimulus parameters like motion velocity would be considered for the extrapolation.

Inside the net, we simulated the effect of velocity by adapting the virtual retrace rates in order to match Müsseler and Aschersleben's velocities: Instead of "shifting" the stimulus with every 16.67 ms, each stimulus position was shown for either 45.77 ms (low velocity) or 8.23 ms (high velocity)⁴. Figure 2 depicts the empirical results and the simulation results.

Insert Figure 2 about here

The figure shows that the model is capable of simulating the main effect of velocity. However, the absolute values of empirical and simulated data differ from one another. The empirical as well as the simulated data show an increase of the Fröhlich effect with growing velocity but this increase seems to be more pronounced for the simulated data.

Among other stimulus parameters, Carbone (2001) studied the effect of motion direction on the Fröhlich effect. A black square either moved away from the fixation point (foveofugal), towards it (foveopetal), or not at all. The stationary stimulus did not move, but was flashed at the "starting location" for one retrace (16.7 ms) - that is, as long as the moving stimuli were shown at each stimulus location. This manipulation of motion direction yielded a significant main effect. A post-hoc analysis showed that there was no mislocalization of the stationary stimulus, and that the Fröhlich Effect was more pronounced for the foveofugal than for the foveopetal motion. This difference between the foveofugal and foveopetal motion is explained by the attentional model as follows: Before the stimulus is shown, attention is centered at the fixation point. Then the stimulus appears and attention is moved towards its location. A stimulus that moves away from the fixation point may "cost" the attention shift some additional distance, whereas motion towards it can "save" the attention shift some distance. In other words, attention either has to "catch up" with the stimulus or the stimulus moves toward the focus of attention. Another possible explanation for the effect of motion direction in accordance with the attentional explanation was discussed by Carbone (2001): Evidence found by Mateeff and Hohnsbein (1988) and Mateeff et al. (1991) suggests that the visual system might be more sensitive to foveofugal than to foveopetal motion. In case of the moving square this may lead to an earlier start of the attention shift. The motion extrapolation account per se would not have predicted such an effect for motion direction.

Inside the model, the different motion directions were simulated by "presenting" the stimulus either to the left or to the right of the virtual fixation point and 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 results of the experiment and the simulations are shown in Figure 3.

Insert Figure 3 about here

A glance at Figure 3 indicates no mislocalization for the stationary stimulus in the simulated data. 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 stronger Fröhlich effect for the foveofugal motion compared to the foveopetal motion just as for the empirical data. But the difference between the two conditions is smaller. As for stimulus velocity, the simulated data match the empirical data qualitatively but not numerically.

Carbone (2001) also investigated the influence of stimulus eccentricity on the Fröhlich effect. The starting location varied between 0 and 58.8 mm (0-8.36°) from the fixation point. The results showed a linear increase of the Fröhlich effect along with eccentricity. The attentional account explains this increase by assuming that the attention shift takes longer for a larger distance or that the start of the attention shift is delayed because it is more difficult to program the target of the attention shift (Carbone, 2001). The extrapolation account would not predict such an effect of stimulus eccentricity, although Baldo, Kihara, Namba and Klein (2002) found the flash-lag effect to increase along with an increasing eccentricity of the flash.

For the simulation, the virtual stimulus started at the same eccentricities as the ones used in the experiment by setting the corresponding pixels to 1. The empirical and simulated data are shown in Figure 4.

Insert Figure 4 about here

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. 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. In modeling the RF sizes between the first and the second layer we took into consideration the cortical magnification factor. The moving stimulus is generated by setting the corresponding pixels at the first level to one. For the feedforward processes, the neurons at the higher layers are updated according to transmission delays observed by Lamme and Roelfsema (2000). The most essential component for simulating the Fröhlich effect is the 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 distortion of the perceived onset location – the Fröhlich effect – is created by activity changes inside the net due to later stimulus positions. The feedback loop meets these later location 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.

As we have already emphasized, the basic mechanisms inside the net are compatible with the attentional and the motion extrapolation explanation of the Fröhlich effect. Although neither Neumann nor Nijhawan discussed the possibility of a feedback mechanism as a possible physiological basis, both models do not only seem to be compatible with a feedback mechanism, but such reentrant processing seems to be physiologically even more plausible than a pure feedforward model. More specifically, there is growing evidence that indeed feedback connections back to V1 are essential for conscious visual perception. Martinez et al.

(1999), for example, found attentional modulations in V1, using functional magnetic resonance imaging (fMRI), and hypothesized a reentrant feedback from higher visual areas. Pascual-Leone and Walsh (2001) used transcranial magnetic stimulation to interfere with the feedback signal at various points in time after stimulus motion onset and concluded that feedback to V1 is critical for the awareness of visual motion. Di Lollo, Enns and Rensink (2000) make the even stronger claim, that all major visual areas have reentrant connections with V1. However, it should be noted that recently Baldo and Caticha (2004) have presented a pure feedforward neural network that was capable of simulating the flash-lag effect and the essence of the Fröhlich effect as well.

After the description of the model, we tried to show that basic properties of the Fröhlich effect can be simulated with the model. A misperception only occurred with moving and not with stationary stimuli, and the direction of the main effects for motion direction, stimulus eccentricity, and stimulus velocity were simulated by the neural model. Nevertheless, the absolute Fröhlich values of the empirical and the simulated data differed from one another. In our opinion, 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 thought the model to be more convincing if we would only use estimates based on observed physiological parameters such as the RF sizes and the transmission delays.

Besides the fact that having successfully simulated the basic properties of the Fröhlich effect were successfully modeled, it is important to discuss how the main effects are generated by the neural net, and whether the fact that the attentional model predicted the main effects found in the empirical and the simulation results means that it is more plausible than the extrapolation account? The attentional account explains the more pronounced Fröhlich

effect for foveofugal motion with the assumption that an attention shift to a stimulus that moves away from the fixation point would take longer or is triggered later than a shift to a stimulus that moves towards the fixation point. Similarly, the attentional model proposes that the increasing Fröhlich effect with growing eccentricity is caused by longer durations of attention shifts or a delayed start of the shift with larger distances.

Inside the model, the transmission delays for the feedback loop – and therefore the start and the duration of a hypothetical attention shift – are the same, irrespective of motion direction and stimulus eccentricity. Actually, the model so far contains no purely attentional mechanisms and therefore does not favor the attentional account. We supposed that the net's motion direction and eccentricity effects were caused by the cortical magnification. This was supported by an additional simulation without the cortical magnification factor. With all RFs having the size of three neurons, the effect of motion direction disappeared (6.5 for foveofugal and 6.9 mm for foveopetal motion) and the misperception did not depend on eccentricity (from low to high eccentricity 5.9, 6.2, 6.6, 8.7, 6.4, and 6.4 mm). Thus, the simulations indicate that the sole physiological structure might be responsible for effects that so far have been attributed to higher processes.

In evaluating the model further and in determining whether the feedback loop corresponds to attention or to motion extrapolation, several steps are possible. The first of these steps will be to test the model for other properties of the Fröhlich effect. For example, Müsseler and Aschersleben (1998) have found that a valid cue – a cue that is shown at the starting location prior to the actual moving stimulus – reduces the Fröhlich effect, but that an invalid cue does not enlarge the effect. An even more important step will be to apply the model to other phenomena, for example, metacontrast masking which was attributed to attentional processes (Neumann, 1982). With respect to the motion extrapolation account, it is interesting to note that the original account does not explain why the flash-lag effect is absent when the stimulus reverses its direction at the instant the flash appears (Carbone, 2002;

Purushothaman, Patel, Bedell, & Ogmen, 1998). A flash-lag effect would be expected under these conditions by the standard motion extrapolation account (cf. Nijhawan, 1994), because the visual system does not know in advance that the stimulus is going to change its direction, and, thus, should extrapolate further into the original motion direction. Contrary to these hypothetical effects, the feedback loop inside our neural net would not create such an overshoot, because the feedback signal can be altered only in the direction of positions at which the moving stimulus really happened to be. Apart from using simulations to investigate hypotheses based on previous evidence, we should also derive new hypotheses from model-simulations and investigate them in new experiments. Finally, the feedback model should be tested against different computational models, especially pure feedforward models.

References

- Baldo, M. V. C., & Caticha, N. (2004). Computational neurobiology of visual illusions: The flash-lag and Fröhlich effects emerge from simple neural networks. *Perception*, *33*, S32.
- Baldo, M. V. C., Kihara, A. H., Namba, J., & Klein, S. A. (2002). Evidence for an attentional component of the perceptual misalignment between moving and flashing stimuli. *Perception*, *31*, 17-30.
- Carbone, E. (2001). *Die Rolle von Aufmerksamkeitsprozessen bei der Fehlwahrnehmung dynamischer Reize* [The role of attentional processes in the misperception of dynamic stimuli] oder so ähnlich?. Unpublished dissertation, Bielefeld University, Germany.
- Carbone, E., & Ansorge, A. (submitted). Investigating the Fröhlich Effect for Size. *Vision Research*.
- Di Lollo, V., Enns, J. T., & Rensink, R. A. (2000). Competition for consciousness among visual events: The psychophysics of reentrant visual processes. *Journal of Experimental Psychology: General*, *129*, 481-507.
- Driver, J., & Spence, C. (2000). Multisensory perception: Beyond modularity and convergence. *Current Biology*, *10*, 731-735.
- Fröhlich, F. W. (1921). Untersuchungen über periodische Nachbilder [Studies on periodic afterimages]. *Zeitschrift für Sinnesphysiologie*, *52*, 60-88.
- Fröhlich, F. W. (1929). *Die Empfindungszeit* [The sensation time]. Jena: Fischer.
- Lamme, V. A. F., & Roelfsema, P. R. (2000) The distinct modes of vision offered by feedforward and recurrent processing. *Trends in Neurosciences*, *23*, 571-579.
- Luck, S. J. (1998). Neurophysiology of selective attention. In H. Pashler (Ed.), *Attention* (pp. 257-295). Hove: Psychology Press.
- Martinez, A., Anllo-Vento, L., Sereno, M. I., Frank, L. R., Buxton, R. B., Dubowitz, D. J., Wong, E. C., Hinrichs, H., Heinze, H. J., & Hillyard, S. A. (1999). Involvement of striate and extrastriate visual cortical areas in spatial attention. *Nature Neuroscience*, *2*,

364-369

- Mateeff, S., & Hohnsbein, J. (1988). Perceptual latencies are shorter for motion towards the fovea than for motion away. *Vision Research*, 28, 711-719.
- Mateeff, S., Yakimoff, N., Hohnsbein, J., Ehrenstein, W. H., Bohdanecky, Z., & Radil, T. (1991). Selective directional sensitivity in visual motion perception. *Vision Research*, 31, 131-138.
- Müsseler, J., & Aschersleben, G. (1998). Localizing the first position of a moving stimulus: The Fröhlich effect and an attention-shifting explanation. *Perception & Psychophysics*, 60, 683-695.
- Müsseler, J., & Neumann, O. (1992). Apparent distance reduction with moving stimuli (Tandem Effect): Evidence for an attention-shifting model. *Psychological Research*, 54, 246-266.
- Müsseler, J., Stork, S., & Kerzel, D. (2002). Comparing mislocalizations with moving stimuli: The Fröhlich effect, the flash-lag effect and representational momentum. *Visual Cognition*, 9, 120-138
- Neumann, O. (1978). Visuelle Aufmerksamkeit und der Mechanismus des Metakontrastes [Visual attention and the mechanism of metacontrast]. *Report No. 6/1978, Department of Psychology at the Ruhr-University Bochum, Cognitive Psychology Unit.*
- Neumann, O. (1982). Experimente zum Fehler-Raab-Effekt und das 'Wetterwart'-Modell der visuellen Maskierung [Experiments on the Fehler-Raab effect and the 'Weather-Station' model of visual masking]. *Report No. 24/1982, Department of Psychology at the Ruhr-University Bochum, Cognitive Psychology Unit.*
- Neumann, O., & Müsseler, J. (1990). Visuelles Fokussieren: Das Wetterwart-Modell und einige seiner Anwendungen [Visual focussing: The Weather-Station model and some of its applications]. In C. Meinecke & L. Kehrner (Eds.), *Bielefelder Beiträge zur Kognitionspsychologie* (pp. 77-108). Göttingen: Hogrefe.
- Nijhawan, R. (1994). Motion extrapolation in catching. *Nature*, 370, 256-257.

- Nijhawan, R. (1997). Visual decomposition of colour through motion extrapolation. *Nature*, 386, 66-69.
- Nijhawan, R. (2002) Neural delays, visual motion and the flash-lag effect. *Trends in Cognitive Sciences*, 6, 387-393.
- Pascual-Leone, A., & Walsh, V. (2001). Fast backprojections from the motion to the primary visual area necessary for visual awareness. *Science*, 292, 510-512.
- Purushothaman, G., Patel, S. S., Bedell, H. E., & Ogmen, H. (1998). Moving ahead through differential visual latency. *Nature*, 396, 424.
- Rosa, M. G. P., Casagrande, V. A., Preuss, T., & Kaas, J. H. (1997). Visual field representation in striate and prestriate cortices of a prosimian Primate (galago garnetti). *Journal of Neurophysiology*, 77, 3193-3217.
- Skapura, D. M. (1996). *Building neural networks*. New York: Association for Computing Machinery (ACM) Press.
- Scharlau, I., & Neumann, O. (2003). Perceptual latency priming by masked and unmasked stimuli: Evidence for an attentional explanation. *Psychological Research*, 67, 184-197.

Author Note

This work was supported by a fellowship within the postdoc program of the German Academic Exchange Service (DAAD) to Elena Carbone and Grant AN 393/1-1 by Deutsche Forschungsgemeinschaft to Ulrich Ansorge, Holk Cruse, and Odmar Neumann.

We thank Ulrich Ansorge, Mark Elliott, Ingrid Scharlau, and one anonymous reviewer for their comments on an earlier draft. Correspondence should be addressed to Elena Carbone, Abteilung für Psychologie, Universität Bielefeld, Postfach 100131, D-33501 Bielefeld, Germany, e-mail elena.carbone@uni-bielefeld.de

Figure Captions

Figure 1. Various net states inside the central area of the neural model during the feedforward and feedback processing of a moving stimulus. Activity is represented by red color and the feedback by blue color. From left to right and from top to bottom, part (a) of the figure shows the onset of the stimulus, which is simulated by setting the pixels inside the input layer to one. Part (b) depicts the state when the feedforward activity has reached the highest layer. In part (c), the feedback-loop is completed. Part (d) shows the net's "perceived" starting location (blue squares). To simplify a comparison between the perceived and the actual starting location, we visualized the actual starting location by inking the pixels with green color.

Figure 2. Empirical and simulated data for stimulus velocity.

Figure 3. Empirical and simulated data for motion direction.

Figure 4. Empirical and simulated data for stimulus eccentricity.

Footnotes

¹ RFsize (degrees) = $0.57 \cdot \text{eccentricity}^{0.69}$ (after Rosa et al., 1997)

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

where $net_i(t)$ is the weighted sum of inputs and $o_i(t)$ is the output of neuron i at time t (after Skapura, 1996, but the former output is added to the input value).

³ For a layer with neurons $1, \dots, N$, 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:

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

⁴ This led to virtual retrace rates of 21.85 Hz and 121.55 Hz. The virtual retrace rates do not match those of Müsseler and Aschersleben (1998) because the subject-screen distance, the stimulus size, and the way to generate the motion of the stimulus differed between the simulation and the actual experiments.







