RESEARCH ARTICLE

Perceptual learning with perceptions

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Abstract   In this work we present an approach to understand neuronal mechanisms underlying perceptual learning. Experimental results achieved with stimulus patterns of coherently moving dots are considered to build a simple neuronal model. The design of the model is made transparent and underlying behavioral assumptions made explicit. The key aspect of the suggested neuronal model is the learning algorithm used: We evaluated an implementation of Hebbian learning and are thus able to provide a straight-forward model capable to explain the neuronal dynamics underlying perceptual learning. Moreover, the simulation results suggest a very simple explanation for the aspect of "sub-threshold" learning (Watanabe et al. in Nature 413:844–884, 2001) as well as the relearning of motion discrimination after damage to primary visual cortex as recently reported (Huxlin et al. in J Neurosci 29:3981–3991, 2009) and at least indicate that perceptual learning might only occur when accompanied by conscious percepts.

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Introduction

A range of studies confirm that the ability to detect and discriminate a small amount of coherent motion amongst randomly moving dots increases with training (e.g. Ball and Sekuler 1987; Vaina et al. 1998), and that this ability might even increase without an actual perception (Watanabe et al. 2001). Furthermore, neuroimaging studies demonstrated that changes in cortical activations might accompany perceptual learning in general (e.g. Yotsumoto et al. 2008) and that attention modulates neuronal activities for different levels of motion coherence (Furlan and Schwarzbach 2009; Tsushima et al. 2006). Recently Huxlin et al. (2009) even demonstrated that motion discrimination might be relearned after damage to the primary visual cortex. In this work we aim to investigate potential neuronal mechanisms underlying perceptual learning using a biophysically detailed neurodynamical model which proved to be useful in a range of tasks (see e.g. Deco et al. 2004; Stemme et al. 2005, 2007; Szabo et al. 2006; Stemme and Deco 2008). To understand perceptual learning we focussed on the neurodynamical simulation of the ground breaking results presented by Watanabe et al. (2001) who used subliminal stimuli for the (task irrelevant) training of participants. After training participants showed an increase in detection performance for these subliminal trained stimuli only, however, if they were presented *above* the perceptual threshold. These results represent a challenge for neurodynamical simulations because it is necessary to find a set of parameters which is able to trigger a learning effect but not a performance increase for a fixed external stimulus level.

An important aspect of the neurodynamical model is thus the learning algorithm. In the simulations we rely on a Hebb-based learning method which does not require any

kind of artificial reinforcement learning. "Reinforcement learning" usually incorporates mechanisms which explicitly manipulate selected neuronal connections dependent on the correctness of a *behavioral* response. However, on a neuronal level the behavioral correctness of a response is unknown,[1] and hence biological plausible learning mechanisms are to rely rather on *neuronal* aspects as e.g. spiking rates, spike timing, etc. within an Hebbian paradigm. In the following sections we outline the design of a neuronal model, capable to simulate the results obtained by Watanabe et al. (2001) under this given constraints. Major parameters and underlying behavioral assumptions are explicated thus keeping the model design transparent. Overall a straight forward mechanism for perceptual learning is presented which allows as well to address later—partly contradictory—results with respect to perceptual learning (e.g. Seitz et al. 2005; Tsushima et al. 2008).

Neurodynamical model

General setup

A biologically inspired neuronal model is used for the simulations (see as well Stemme et al. 2007). It is based on a framework first introduced by Brunel and Wang (2001) and represents a selected cortical area comprising excitatory pyramidal cells and inhibitory interneurons. The neurons are coupled via the three most common synaptic connection types found so far—excitatory AMPA and NMDA connections and inhibitory GABA connections. The calculation of the signals transmitted over the different kind of glutamergic connections acknowledges that signals transmitted via AMPA receptors are comparatively fast whereas NMDA connections are slower and require the release of a Magnesium-gated channel. Hence central neuronal properties are described within this model (see supplementary material). The synaptic connections are weighted thus representing the structure in the neuronal model (see Fig. 1).

A range of studies confirm direction selectivity of the human cortical area MT+ (e.g. Zihl et al. 1983; Vaina et al. 1998; Tsushima et al. 2006; Huxlin et al. 2009; Furlan and Schwarzbach 2009) and hence we assume that groups of neurons within this area might respond to stimuli moving in a specified direction.[2] For the purpose of the

simulations we considered eight groups or pools of neurons which respond when a substantial amount of dots move coherently into their preferred direction. Every neuron within the model receives a certain amount of background input from neurons outside the network modeled to account for general cortical connectivity. For the approximation of the background input it is considered that neurons always show a certain level of activity, i.e. a spiking rate of approximately 3 Hz for pyramidal cells and 9 Hz for interneurons, also called "spontaneous rate". For the purpose of the simulation we considered every neuron to receive external excitatory input from 800 distant neurons, hence the background input for every neuron within the model turns out to be 2.4 kHz. During the simulation a "presentation" of a stimulus to the network is represented by an increase of the background input to a selected group of neurons compared to the remaining ones. The concrete distribution of this external input is influenced by a random number generator which determines the exact time point of the individual stimulation. During the simulations, different random seeds might thus be used to simulate different test persons.

Important parameters of the model are the value of the external stimulus height and the initial strength of neuronal connectivity which together determine stimulus sensitivity and the starting point of the model before learning.

Response rule

An important decision with respect to the model design is the response rule of the model. It is necessary to specify general rules which interpret the spiking rates in terms of model responses. Considering the directional selective neuronal pools we might for example assume that a response of the model is present when the spiking rates of one or more pools are higher than the rates of the other pools. The behavioral assumption underlying such a response rule is that a certain level of spiking activity might lead to a conscious percept. We chose to use a *relative* threshold for the spiking rate and not an absolute threshold as for example the famous waterfall illusion[3] indicates that relative levels of spiking rates might be important in the case of motion perception. Thus the response rule chosen for the simulations of perceptual learning is based on the *deviation* of the spiking rate of a single pool compared to the average spiking rate of all pools during the stimulus phase.

Hence, let x_i be the spiking rate of the direction selective pool i and n be the number of directional selective pools.

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[1] See as well the principle criticism on machine or reinforcement learning, Dreyfus (1992).

[2] A similar model was suggested by Furman and Wang (2008). However, the model itself is of course neutral with respect to the concrete cortical area, see Pilly et al. (2010) with respect to the hypothesis that rather area V1 might be important.

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[3] The "waterfall illusion" refers to the illusion of contra-directional motion of a static surface following the fixation of a motion signal. (See e.g. Goldstein 2001).
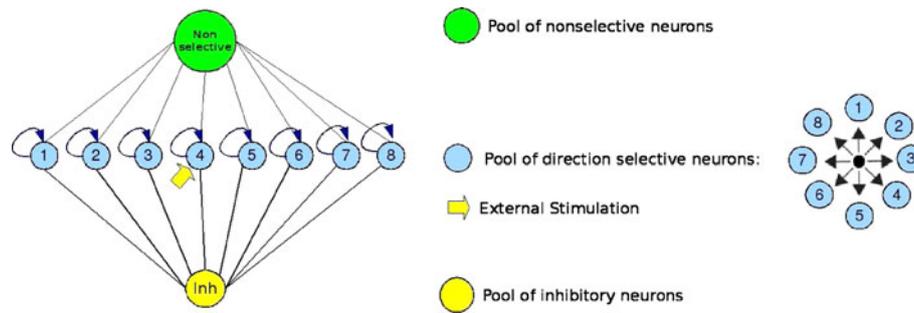
Fig. 1 Neuronal model comprising eight direction selective pools. The network of neurons is fully connected (for the detailed set of equations please refer to the supplementary material). For the simulations we used an examplary network consisting of 200 inhibitory interneurons, 20 neurons in every directional pool and further 640 non selective neurons. Thus the ratio of excitatory to inhibitory neurons equals 80%:20%, consistent with neurophysiological findings (Abeles 1991). Simulations started with a flat network, hence all connection weights were set to 1.0 initially. A stimulus is presented to the network of neurons by increasing the external stimulation the neurons receive from non-modelled cortical areas (as e.g. primary visual cortex)

Thus the average spiking rate across all pools turns out to be:

$$\bar{x} = \frac{\Sigma x_i}{n} \tag{1}$$

The response of the model in a simulated trial is considered to be i, if

$$x_i > \bar{x} + t_{\text{thresh}} \tag{2}$$

and undefined (i.e. no motion detected) otherwise.

Learning rule

We decided to base the learning rule solely on the basic principle formulated already in 1949 by Hebb (1949): If pre- and postsynaptic neurons are both active an increase in synaptic strength between these neurons might occur.

The idea of Hebbian learning was to a certain extent confirmed by studies inducing Long Term Potentiation (LTP, see e.g. Linden 1994) in hippocampal neurons. LTP and its counter part, Long Term Depression (LTD), are usually induced by specific experimental protocols stimulating selected synapses (usually in slices of rat cortex) and measuring corresponding changes in synaptic responses. These changes usually last from hours to days (Linden 1994) and might depend on NMDA receptor activation and/or on the level of postsynaptic Calcium (Linden 1994; Hansel et al. 1996). Thus the exact mechanism responsible for synaptic plasticity in terms of LTP and LTD are still unknown and subject of intense debate and theorizing.[4] Moreover, the present work aims to investigate neuronal mechanisms underlying *perceptual* learning which, first of all, is suspected to take place in the medial temporal lobe or related cortical areas in the visual pathway and at least

particularly not the hippocampus. Furthermore, the learning gain achieved in perceptual tasks appears to be persistent as demonstrated by retesting after several weeks (see e.g. Ball and Sekuler 1987; Yotsumoto et al. 2008). Whereas hippocampal structures might be responsible for other and more temporal aspects of memory storage[5] and thus might require different(iated) methods, perceptual learning appears to be more similar to the learning of bicycle-driving: Once learned it is not unlearned even if you do not use a bike for years or learn to drive a car. Thus for the modeling of perceptual learning we focussed on the strengthening of synaptic connections rather their abolishment, hence on a very general Hebbian learning rule based on the estimated probability that pre- and postsynaptic spikes occurred simultaneously and we assumed that this probability increases with the spiking rate of the corresponding neurons. The basic assumption underlying this learning rule is actually a very common one: The more a certain pathway is used the broader it becomes. However, compared to the development of a path from a "beat-track" to an "highway" it takes a much longer time the other way round ("overgrow" in case of non-use) which would explain the persistency observed with *perceptual* learning.

Hence, let again x_i be the spiking rate of the direction selective pool i within the time interval dt. Let $w_{ij}(t)$ be the strength (weight) of the synaptic connection between two directional pools i and j at a certain time point t, and n be the number of times the spiking rates of pools i and j exceeded a certain threshold T_{thresh} in the time interval $[t, t + 1)$. Let f be a fixed, to be determined factor. The connection strength between these two pools at the next time step, $w_{ij}(t + 1)$, is thus determined as:

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[4] See e.g Graupner and Brunel (2007) for a suggestion of a spike time dependent model of bistable synapses for LTP/LTD.

[5] As substantiated for example by the famous case study of H.M., see e.g. Corkin (2002).

$$w_{ij}(t+1) = w_{ij}(t) + (n*f) \qquad (3)$$

Perceptual learning

Experimental setup

Watanabe et al. (2001) used slightly varying experimental setups to investigate the capability of perceptual learning when only subliminal and task irrelevant stimuli are presented to the subjects. The basic experimental setup is outlined in Fig. 2.

The experiments consisted of different stages. In a first test stage participants judged whether coherent motion was present or not. The stimulus display consisted of random dot motion displays comprising 5 or 10% coherent motion in one of eight different directions. For every direction and coherence level 20 trials had to be completed. Following this test stage training of the participants started the next day. During the training (also referred to as "exposure stage") the participants viewed the same peripheral display but were to conduct a central letter discrimination task (not shown). However, the task irrelevant coherent motion display in the periphery comprised always 5% coherent motion of a specific, to be trained direction. During the training phase participants completed 960 trials per day for a period of 20 days. After the training participants performed a second test and judged motion coherence.

Behavioral results

The major experimental results of Watanabe et al. (2001) are sketched in Fig. 3. The most striking aspect of the experiments is that although participants obviously viewed peripheral stimuli showing only 5% coherent motion for almost 20,000 trials (960 trials per day on 20 successive

days) no improvement in the performance on *this* coherence level was achieved.

But the results of the second test after training clearly indicate that perceptual learning took place: The performance for the 10% motion signal increased significantly only for the trained direction.

We now need to determine how it is possible that a comparatively weak signal was able to trigger a learning effect without leading to an increase in performance for this level (5% coherent motion). Hence we need to find a suitable configuration of the envisaged neuronal model.

Model configuration

Before training, experimental participants emitted equally distributed correct rates across all tested directions for both coherence levels. Obviously, these results represent the capability of an untrained brain to detect coherent motion amongst randomly moving dots: All directions are recognized equally well. Hence, for an untrained brain we might assume the strength of the neuronal connections to be equal which represents a balanced sensitivity across different directions. Thus the strengths of all connections might be set to "1" (Table 1).

To determine possible values for the response threshold (t_{thresh}) and the amount of external stimulation (λ_{stim}) we conducted example simulations comprising 24 trials each. After each simulation we determined the amount of correct responses of the model. The results Watanabe et al. (2001) obtained in their first test, before learning took place, indicate that there are two levels of coherent motion: One which leads to a performance of almost 0% and the other leads to a detection rate of about 50–60%. Figure 4 shows that similar results are obtainable for all three response thresholds evaluated, when using different values for the
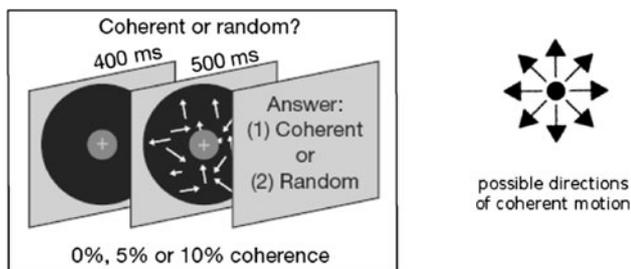

Fig. 2 Experimental Setup used by Watanabe et al. (2001). Subjects were required to fixate a central cross (1° visual angle) and to judge whether coherent motion was present in the periphery (10°) or not. Coherent motion was present with a coherence level of 0, 5 or 10% and equally distributed over eight different directions: 20 trials for each of the eight directions and in 160 trials 0% coherence was used. Reprinted from Watanabe et al. (2001, Fig. 3a) with permission
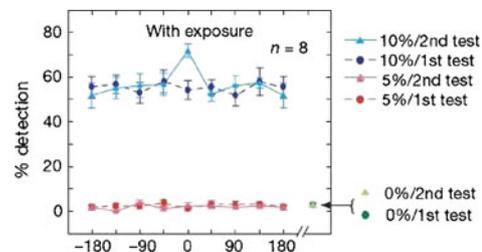

Fig. 3 Experimental results obtained by Watanabe et al. (2001). Outlined are the average results for eight subjects for a first (before training) and second test (after training). On the *x*-axis relative directions to the trained direction ("0") are marked. Notably the detection rate for the trained direction increases only for a stimulus coherence level of 10%. Reprinted from Watanabe et al. (2001, Fig. 3b) with permission

Table 1 Connection strengths (weights) of the model before training

Weight value	Dir 1	Dir 2	Dir 3	Dir 4	Dir 5	Dir 6	Dir 7	Dir 8	NonS	Inh
Dir 1	1	1	1	1	1	1	1	1	1	1
Dir 2	1	1	1	1	1	1	1	1	1	1
Dir 3	1	1	1	1	1	1	1	1	1	1
Dir 4	1	1	1	1	1	1	1	1	1	1
Dir 5	1	1	1	1	1	1	1	1	1	1
Dir 6	1	1	1	1	1	1	1	1	1	1
Dir 7	1	1	1	1	1	1	1	1	1	1
Dir 8	1	1	1	1	1	1	1	1	1	1
Nons	0.84	0.84	0.84	0.84	0.84	0.84	0.84	0.84	1	1
Inh	1	1	1	1	1	1	1	1	1	1

All weights were set to 1 except the weights from the non selective pool to the directional pool. These weights were used to match the constraint that the sum of all weighted input connections to a given pool equals 1 to avoid "overexcitation" of the neurons. Thus, the weight w_{nonsX} from the non-selective pool to a directional pool x was set to: $w_{\mathrm{nonsX}} = 1 - \sum_i f * w_{ix}$ where w_{ix} denotes the weight from the directional pool i to the directional pool x and f equals the respective fraction of neurons in pool i. With $f = 0.02$ as chosen for the model w_{nonsX} turns out to be 0.84
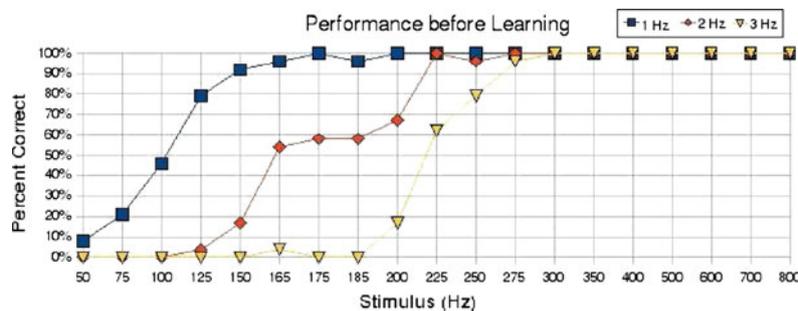

Fig. 4 Model performance before learning. The performance (percent correct) obtained during the simulations using a flat network of interconnected neurons (compare Table 1) for different values of the response threshold $t_{\mathrm{thresh}} - 1$, 2 and 3 Hz, and for different levels of external stimulation (λ_{stim}) are shown. For each threshold value 24 trials were simulated

external stimulation: When the response threshold is set to 2 Hz, for example, a value of 100 Hz for λ_{stim} leads to about 0% correct responses whereas a stimulus height of 175 Hz allowed to achieve about 50 correct model responses. It should be noted that these extra external stimulation rates of 100, respectively 175 Hz, are very low compared to the background noise of 2,400 Hz which every neuron within our model receives.

Translated into neuronal questions, the challenging finding of Watanabe et al. (2001) turns out to be that the lower value of the external stimulation remained on the low level of performance even after learning whereas the higher level of external stimulation lead to increased performance.

Hence we need to find a model configuration which would be able to hit this result. In this respect the connection strengths of the neurons *within* a certain directional pool is of special importance: The higher the weight, say W_{44} for example, representing the strength of the connection between neurons within the directional pool "Dir 4", the stronger the response of the neurons in this pool to an external stimulation. To evaluate this directional sensitivity

further simulations were conducted with different values for all weights W_{xx}. The results are presented in Fig. 5.

Considering again the performance values obtained when a response threshold of 2 Hz is used it is easy to see that for a value of 100 Hz for the external stimulation the performance is still at level of about 0% correct whereas the performance achieved with a stimulation value of 175 Hz increased. For the other response thresholds (1, 3 Hz) other values might be suitable. However, a response threshold of 1 Hz, implicating that the response of the model is determined based on a difference of just one spike in a second (on average), might be in general too low and for the 3-Hz-threshold higher values of external stimulation would be required to hit the initial, untrained results. Thus a response threshold, t_{thresh}, of 2 Hz appears to be a suitable choice at this point.

Now we need to find out how, in general, a network of interconnected neurons might reach a configuration state which lead to the described performance levels using plausible learning rules and only a rather low level of external stimulation. To get an idea we conducted
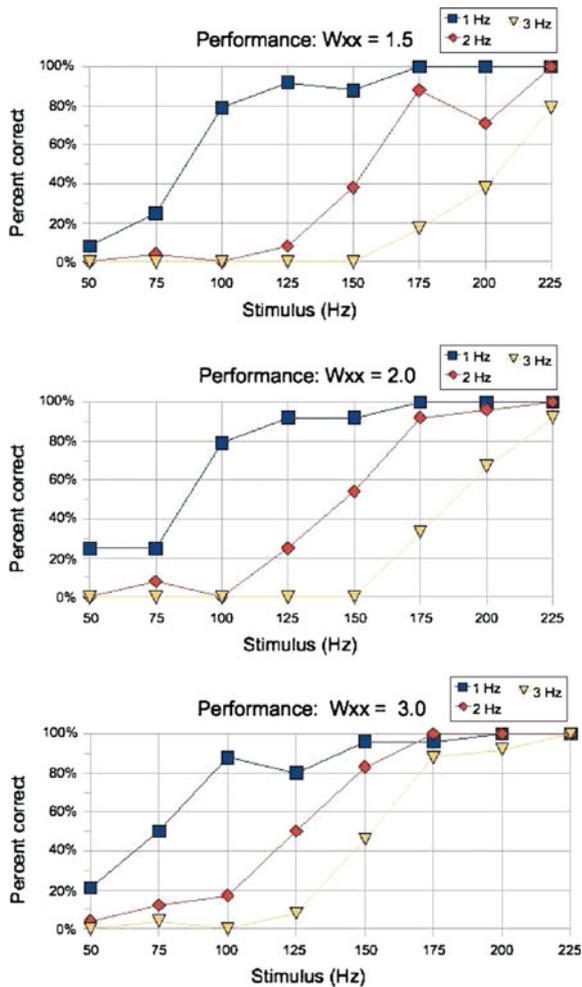
Fig. 5 Model performance dependent on weight set. The performance (percent correct) obtained during the simulations using different response thresholds (1, 2 and 3 Hz) and values for the weights (W_{xx}) determining the sensitivity of the directional pools: $W_{xx} = 1.5$ (*top*), $W_{xx} = 2.0$ (*middle*), $W_{xx} = 3.0$ (*bottom*)

simulations comprising 100 trials each and used different parameters for the learning rule. As already outlined above, we assumed that a strengthening of synaptic connections might take place when a certain activity level is crossed (T_{thresh}). In concrete we validated 10, 12, 14 and 16 Hz as such a threshold. Furthermore we investigated two different values for the external stimulation, 50 and 100 Hz.

In all simulated trials only one of the pools, "Dir 4" was stimulated. During the simulations we increased *every* weight within the model by a factor $f = 0.001$ whenever the spiking rates of the corresponding pools crossed the configured threshold (10, 12, 14 or 16 Hz respectively). Thereby it is possible to determine how often such an event took place. After the simulations we investigated the resulting weight distribution. The experimental results we aim to simulate implicate that weight, w_{44}, should be the

only weight affected by the learning rule or at least affected to the largest extent. The final weight distributions are presented in Fig. 6 and demonstrate that it is well possible to achieve a learning gain when using only a comparatively low level of external stimulation.

However, a value of 50 Hz (middle column, Fig. 6) appears to be too low as in this case not only the trained weight but other weights tend to get affected. For a value of 100 Hz (right column) we observe a substantial amount of crossing events for the trained weight respectively the concerned pools (in 80% of the trials for a threshold of 12 Hz) whereas for the other weights only in a minority of trials such an event took place. As already mentioned above the learning speed of the model is determined by the concrete value of the factor *f*, chosen here to be 0.001. Hence a constant adaption of this factor would explain the 20,000 trials necessary to achieve Watanabe's training effect.

Simulating behavioral results

For the simulation of the first test, i.e. before any learning took place, we conducted eight simulations using different random seeds (which determine the concrete distribution of the external input), comprising 160 trials each with a flat network of neurons (see Table 1) and a value of 100 Hz for the external stimulation (λ_{stim}), representing the 5% coherent motion condition. The presentation of a random dot pattern comprising 10% of coherently moving dots was simulated by using an extra external stimulation of 175 Hz for one of the directional pools. For the second test we used the same setup, with just one exception: The weight value w_{44}, representing the strength of the connection of the neurons within the directional pool "Dir 4", was set to 1.5. Hence the learning gain in terms of weight strength for this task comes out to an increase of 0.5. The resulting model performance in terms of correct responses is presented in Fig. 7, bottom left.

However, for the simulation of the different experimental tests we are to take into consideration that the behavioral results (repainted in Fig. 7, top left, for comparison) show the *detection rate* as achieved by the participants. Hence this diagram outlines the amount of correct responses *above* the chance level. In order to translate a detection rate into the real amount of correct responses provided by the participants we are thus to devide the values given by the detection rate by two and add 50%, the chance level for this test. A rough estimation of the resulting amount of percent correct responses for the experiments is sketched in Fig. 7, top right. The key question turns out to be now whether the simulations should consider the "detection rate" (Fig. 7, top left) or rather the behavioral performance measures in terms of
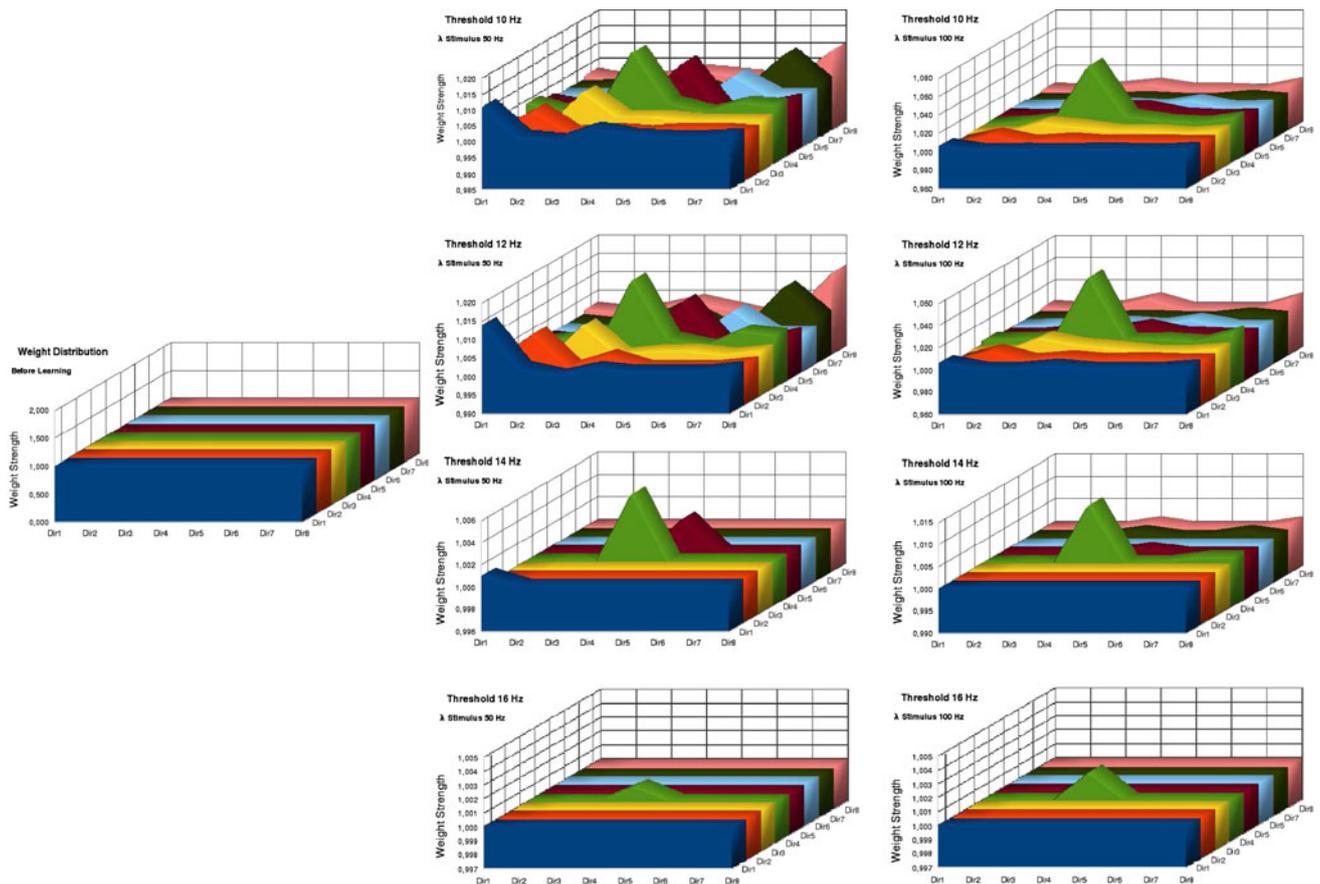
Fig. 6 Evaluation of learning rule parameters. The *diagrams* show the connection strengths between the different directional pools before learning (flat network, *left*) and after a training period of 1,000 trials when different levels for the learning threshold (T_{thresh} = 10, 12, 14 and 16 Hz) and the external stimulation of a single pool were used (λ_{stim} = 50 and 100 Hz). For every threshold crossing event of two connected pools the weight connecting them was increased by a factor $f = 0.0001$. For a threshold, T_{thresh}, of 10 Hz, for example, and a value of 50 Hz for the external stimulation, λ_{stim}, this happened many times for almost all pools although only one pool, "Dir 4", received the external stimulation. Contrary, when using a threshold value of 16 Hz this happened only one time in 1,000 trials and only the weight subject to training was concerned (w_{44})

correct responses (Fig. 7, top right). In this respect there are two possibilities:

(1) If we consider the real performance of the participants in terms of correct responses to be the suitable base for the simulations we would have to look for other suitable parameter for the model configuration and quite clearly the learning gain in terms of weight strength would decrease substantially. However, a comparatively small increase in weight strength opens at least the possibility to question the comparatively small effect (Fig. 7, top right) per se as a comparable amount of variance is well possible within the flat network of neurons (Fig. 7, bottom left, 1st test with 10% motion coherence)

(2) The neurodynamical model does so far neither cheat nor guess responses. Hence we might assume that model responses, determined by the response rule based on spiking rates (as described in the previous

section) form only one part of behavioral responses. Thus whenever the model did not deliver a clear response we might use a random component to determine the model answer and thus simulate a kind of "guessing" as well.

The resulting performance outcomes of the simulations when considering the second case are outlined in Fig. 7, bottom right. The results match astonishingly well the performance measures as estimated for the experiments of Watanabe et al. (2001). They were determined by simply considering an *additional* random guess with a probability of 50% for a correct response whenever the response of the model did not lead to a clear signal, hence when none of the spiking rates of the different pools crossed the relative threshold. The neurodynamical model thus provides the first testable prediction: If this explanation is valid an experimental setup where the participants are asked to report coherent motion only in cases when they are indeed sure
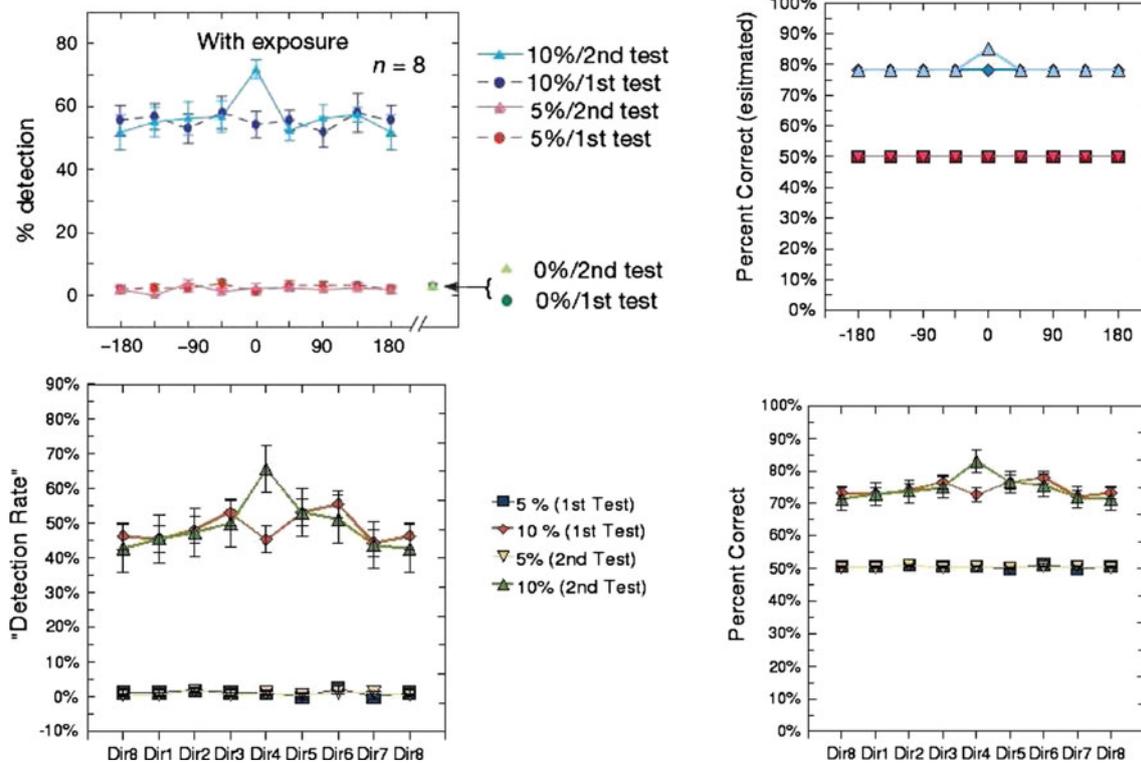
Fig. 7 Comparison of experimental and simulation results for sub-threshold learning. The *top* two diagrams show the behavioral results as described by Watanabe et al. (2001): Performance results in terms of the achieved detection rate (*top left*, reprinted with permission, see as well Fig. 3), i.e. the amount of correct responses above the chance level. A detection rate translates into the actual amount of correct responses by considering the chance level; an approximation is sketched in the diagram *top right* (please refer as well to the text). The *bottom* two diagrams show the respective performance measures as emitted by the neurodynamical model. *Bottom, left*: Average results obtained in eight different simulations of 160 trials using different random seeds. For the simulations of the first test all weights for the directional pools were set to 1.0 and a value of 100 Hz for λ_{stim} was used to simulate the presentation of a random pattern consisting of 5% coherent motion. A 10% coherent motion pattern was simulated by an external stimulation of 175 Hz for λ_{stim}. For the simulations of the second test, after learning took place, the weight strength ("w44") of the trained direction (Direction "4") was set to 1.5. Presented are the model responses as determined by the spike rates of the different pools, hence an equivalence of the "detection rate". These results translates into percent correct when adding a chance component (*bottom right* diagram). In this case the model response is "guessed" (i.e. correct with a 50% probability) whenever no response based on spiking rates is possible. Please refer as well to the text

about this observation should drive the performance results in terms of correct responses close to the detection rate.

Beyond these consideration with respect to "correct" performance measures we are able to compare learning speeds for different levels of external stimulation. Figure 8 shows the development of the weight subject to stimulation and training (w_{44} in our example) using the same constant factor $f = 0.01$. This factor allowed the reduction of necessary trials to simulate from 20,000 (as the results of Watanabe et al. 2001, indicate) to about 1,000 trials. The performance results obtained during the simulation of the experimental tests (Fig. 7) show that a weight value of about 1.5 is necessary for the observed improvement in experimental performance. The simulations demonstrated that about 1,000 trials with an external stimulation of 100 Hz (representing the 5% coherence level) are necessary to achieve this gain when a factor $f = 0.01$ is used. If we reduce this factor to be $f = 0.01/20 = 0.0005$ this would thus explain the 20,000 trials necessary to achieve the learning gain as observed by Watanabe et al. (2001).

For higher rates of external stimulation perceptual learning is much faster. Following the model we developed so far, this has two reasons: First of all the weight strength and thus stimulus sensitivity increases faster when a stronger stimulus is used and secondly, a lower sensitivity value is required when the stimulus is itself stronger. Thus in concrete: If the participants in Watanabes experiment would have been trained with stimuli comprising 10% of coherently moving dots the amount of necessary trials should reduce to about two to three thousand, provided that the 20,000 trials were in deed necessary to achieve the learning gain and provided that the motion signal is not inhibited by potential higher attentional mechanisms (see e.g. Seitz and Watanabe 2009).

Fig. 8 Learning speed for different levels of external stimulation. Comparison of relative learning speeds in terms of weight development for different levels of external stimulation. The other parameter (learning threshold, response threshold) are kept constant
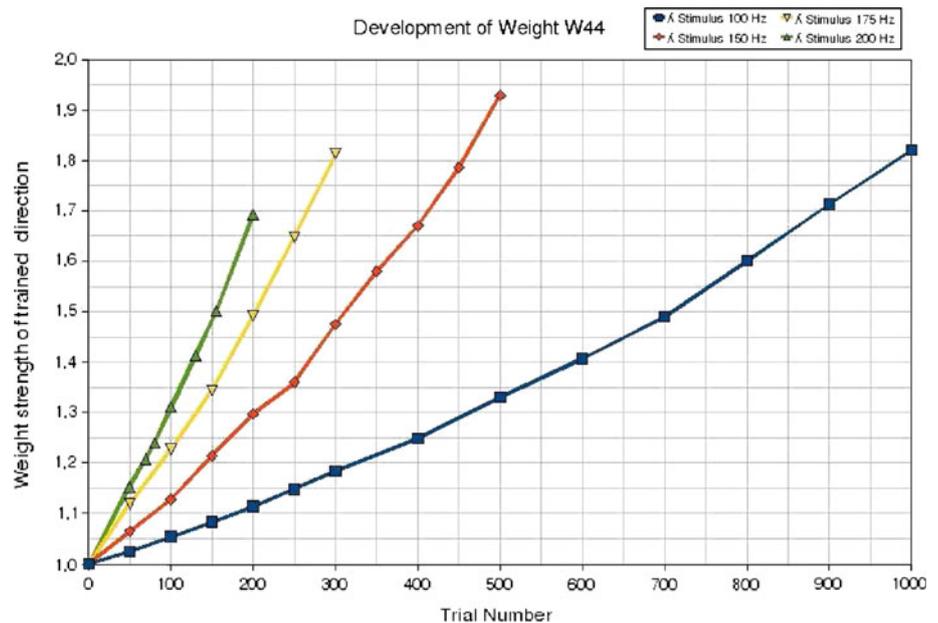
Explaining behavioral results

First of all we accomplished two points: We demonstrated that a neuronal network configuration (a) leads to the performance results obtained in the first test (as presented by Watanabe et al. 2001), and that a network configuration (b) might be able to explain the results obtained in the second test after training. Moreover, we outlined a rather simple learning rule which is able to take the network from state (a) to state (b) using a substantial amount of trials with a very low, potentially "subliminal" stimulus (5% coherently moving dots or 100 Hz of extra external stimulation).

However, as the considerations so far indicated: There are a range of parameter sets possible and it turns out to be more than probable that individual participants require individual parameters. As only average results are available in Watanabe et al. (2001) a single parameter set appeared to be sufficient to simulate the test results before and after the training.

An important prediction of our neuronal model is thereby that perceptual training using higher levels of coherence should improve the performance on lower coherence levels for the same direction. Hence the learning gain achieved for higher levels of coherence when using low levels of stimulus coherence in the training, as demonstrated by in Watanabe et al. (2001), translates as well the other way round: Training with higher levels of coherence (should) improve the performance with lower level of motion coherence, at least if they are actively trained and task relevant and only up to a level of 5% which appears to be a "natural" detection threshold not leading to conscious percepts, following Watanabe et al. (2001).

Which brings us back to the question of perceptions accompanying the different levels of motion coherence. Of course, the key question turns out to be: What happened here? And what is the relationship between perceptual learning and perceptions?

Examining the spiking rates occurring during our simulations in more detail (see Fig. 9) we see that in the training phase (i.e. only 5% of coherent motion or 100 Hz external stimulation) the spiking rate of a pool might increase substantially compared to the remaining ones. In the example (Fig. 9, left), neuronal pool "Dir 4" at 5,100 ms. Such events might occur as well for other pools and with our model configuration we actually looked for such events to trigger learning, i.e. an increase in weight strength. After training—Fig. 9, middle and right, both represent trials with correct responses—we see several of such events which we deemed actually responsible for the model responses.

Following the overall simulation results we obtained, both assumptions—with respect to the learning and response rule—appear to be plausible. Moreover, even if we consider other parameter ranges or potentially a complete different model as the "right" neuronal model, in any case we will end up with similar assumptions regarding the weight development: There must be a criterion to determine the increase in weight strength while still accounting for behavioral results. If we assume that either a certain spiking level or a difference in spiking levels might account for conscious percepts it is well possible that the individual events which actually triggered learning lead as well to probably very short but at least conscious percepts.

Within our neuronal simulation the major reason for the spontaneous increases in spiking rates are fluctuations in
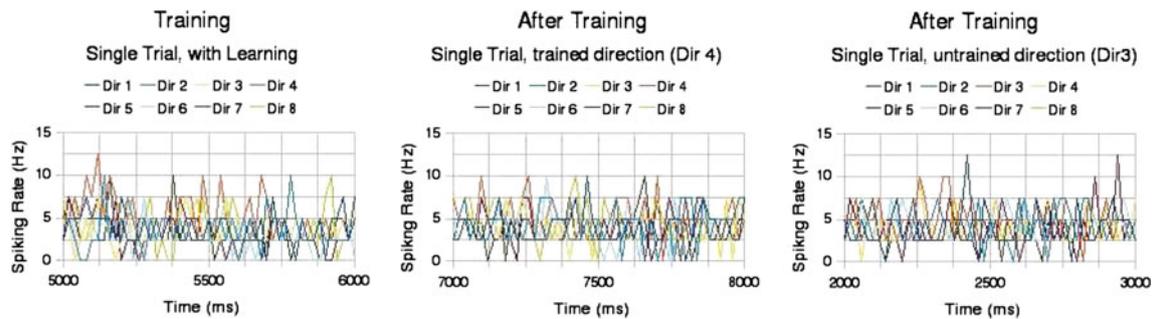
Fig. 9 Development of spiking rates in exemplary trials. Excerpt of spiking rates emitted within a trial under different conditions. *Left*: During a training trial with a learning "event" for w_{44}. *Middle*: After training using 175 Hz of external stimulation for the pool "Dir4". *Right*: After training using 175 Hz of external stimulation for the pool "Dir3"

the external stimulation input. These fluctuations are influenced by a random number generator and might modulate the spiking rates of the pools. In concrete this means that although we intended to stimulate a pool with 100 Hz, for example, fluctuations might lead to higher stimulations for very short intervals although on average the target rate is kept.

Translating these considerations into the question of (cortical) perceptual learning a very simple and at least possible explanation for the results of Watanabe et al. (2001) would be that the stimuli themselves carried very occasionally a stronger signal than 5% of coherent motion. This might accidentally happen when the production of the random dot patterns relies on computational "random" calls. In this case "random" calls might lead to additional dots moving in the target direction, leading to a stronger target motion signal than intended, or to a different, second 5% motion signal.[6] And only these stronger signals triggered learning. This would explain why almost 20,000 trials were necessary and why the participants were not able to detect the 5% signal in the test. Another explanation would require to assume a kind of "impreciseness" within the brain leading to small deviations in spiking rates probably due to intense strain during the training. But again the consequence is a temporal increase in spiking rates and thus even the latter case opens the possibility that perceptual learning only occurred in conjunction with conscious percepts.

However, independently of these considerations further research is available indicating that substantially shorter training times are possible (Seitz and Watanabe 2003) and even weak motion signals (3 or 5% of coherently moving dots) are detectable and might thus be accompanied by conscious percepts (Seitz et al. 2005; Tsushima et al. 2008).

In Seitz and Watanabe (2003) the authors modified the setup during the training or "exposure" phase, respectively, with respect to the central letter discrimination task in such a way that only the target letters were paired with a target motion signal of 5% coherently moving dots while the remaining six letters were paired with distractor directions of the same coherence level. However, the learning effect was reduced substantially: Whereas in Watanabe et al. (2001) the performance increase for the motion *discrimination* task turned out to be about 20% (and approximately 7% for the motion *detection* task, as depicted in Fig. 7) in Watanabe et al. (2001) the performance increase for the motion *disrcimination* task turns out to be only approximately 8% with very large error marks and hence it has to be expected that results for a detection task would accordingly be even lower thus questioning an effect for the here considered *detection* task per se. Nevertheless, a detailed analysis would require individual results which are unfortunately not available.

In Tsushima et al. (2008) participants conducted a similar task to the one described so far. However, the task load of the central letter discrimination task ("RSVP" task) was reduced substantially with every letter or digit now presented for 350 ms (compared to 33 ms for Watanabe et al. 2001) and accordingly a high RSVP task performance already before the exposure stage, contrary to the results presented by Watanabe et al. (2001). Moreover, the initial motion detection threshold turned out to be 15.3% (compared to 8.3% reported in Watanabe et al. 2001), hence the stimulus material appears to be incomparable. Nevertheless, with the modified setup Tsushima and colleagues found a *summed* increase in performance for again a motion *discrimination* task when the peripheral stimuli in the exposure stage comprised 5 or 15% of coherently moving dots but not with 3 or 50% coherently moving dots as peripheral stimuli.

Astonishingly, Tsushima and colleagues summed the performance increases obtained for tests with 3, 5 and 15% coherently moving dots which indicates that for all of these

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[6] For the problem of computational random number generation see for example Hellekalek (1998).

three levels of coherently moving dots an increase in performance has been detected and hence, that these stimuli were obviously "visible" and thus accompanied by conscious percepts, following the interpretation of Watanabe et al. (2001). Unfortunately individual results for the three motion coherence levels are not available, nor are data for the distractor directions (Personal communication). Thus an explicit simulation or even comparison with the earlier results (Watanabe et al. 2001) appears impossible and it remains to be clarified why motion signals below the motion detection threshold of 15.3 (before training) or 13.0% (after training) were able to trigger an increase in performance (Tsushima et al. 2008) which was obviously not the case for the study of Watanabe et al. (2001). Hence, besides all speculations on the question of "visibility" of the presented motion signals the results appear to contradict the earlier findings (Watanabe et al. 2001) where no performance increase for weak motion signals was detected and thus their invisibility was concluded.

If we follow this line of interpretation we are to conclude that the study of Tsushima et al. (2008) demonstrates the visibility of motion signals comprising only 3% of coherently moving dots. If, on the other hand, we follow the interpretation of Tsushima et al. (2008) it is unclear why in Watanabe et al. (2001) no performance increase for the 5% stimulus was detectable although all of these stimuli (5 and 15% of coherently moving dots) are now *together* to be considered as "parathreshold" (Tsushima et al. 2008) or "perithreshold" (Seitz and Watanabe 2009, p. 2506), respectively.

Quite similar, in a comparable though modified experimental setup Seitz et al. (2005) reported a performance of almost 25% correct responses, hence substantially above the chance level of 16.67%, for a motion *discrimination* task for stimuli comprising only 5% of coherently moving dots even *before* any training took place. After the peripheral and task-irrelevant training in a "No Attentional Blink" condition this performance even increased to a certain degree. Unfortunately, performance results for "distractor" motion directions are unavailable (Personal communication) which would at least be necessary to judge and simulate the effect in comparison to the findings of Watanabe et al. (2001). But the circumstance that performance above the chance level was observed for a 5% signal underlines at least again the question whether these motion signals are detectable, and hence visible, contrary to the results as presented by Watanabe et al. (2001).

A principal solution to address these divergent results with respect to the question of detection or visibility of—weak—motion signals might be to consider the time frame of the experiments and the exploding use of computer games in the past decade. Hence it is possible that intense use of computer games improved the perceptual abilities of

the participants with respect to perceptual learning as tested with the experimental paradigms presented in this work, which underlines again the necessity to consider perceptual abilities on a rather individual base.

However, so far the findings of Tsushima et al. (2008) and Seitz et al. (2005) appear to substantiate the hypothesis that perceptual learning occurs only accompanied with at least weak but nevertheless conscious percepts of coherent motion: Considering the very low motion detection threshold (8.3%) reported for Watanabe et al. (2001) and the large amount of trials necessary to achieve the learning gain, the hypothesis that learning only occurred when the spiking rate crossed a certain threshold, as indicated by the simulations described in this work, and thus might well have been accompanied by conscious percepts, appears to be substantiated by the results as presented by Tsushima et al. (2008) and Seitz et al. (2005) where very weak motion signals proved to be detectable by the participants.

The results recently reported by Huxlin et al. (2009) actually point in a similar direction. Huxlin et al. (2009) trained their experimental participants at various locations in their blind field in a forced-choice direction discrimination task using coherently moving dots in a staircase method, hence the range of motion directions was increased upon correct responses and decreased otherwise. In the time course of training the subjects conducted direction range threshold tests which revealed a great variability: Between 6,000 to 30,000 trials were necessary until the patients stabilized at a normal value for this task (about 290°). However, before training the patients were not able to accomplish the task at all—in their blind field—(initial direction range threshold: 0°). After the direction range threshold returned to normal values the patients achieved a normal level of performance in a range of other tasks, including a forced choice motion discrimination task. Huxlin and colleagues reported that "awareness of training stimuli grew stronger and more complex as training progressed, paralleling improvements in integration thresholds." (Huxlin et al. 2009, p. 3987). Hence initial weak but at least conscious stimulus percepts grew stronger in the time course of training.

A challenging aspect of Huxlin et al. (2009) results is the circumstance that they observed a difference in learning in the intact hemifield compared to the damaged hemifield of the patients: In the intact field (small) performance increases in the direction range taks transferred to new stimulus locations whereas in the blind field every location had to be trained starting from the scratch. This circumstance let the authors to the conclusion that "intact islands of V1" (Huxlin et al. 2009, p. 3989) might contribute substantially to the learning rather than the area MT with its larger receptive field sizes. However, although the performance of the patients dropped again to Zero upon

each new location tested within their blind field a substantial decrease in the overall time to learn the direction task for subsequent new locations is observable.

In terms of our neuronal model this decrease in learning time would be explainable in either higher initial weight values, higher initial stimulus values or a combination of both. This implicates that the learning gain achieved with training in one location transferred to a certain extent as well to new locations within the blind field and hence reopens the possibility that MT contributed to a major extent to the perceptual learning of the patients.

Discussion

In this work we presented a detailed neurodynamical model capable to simulate and explain challenging experimental results obtained with respect to perceptual learning (especially Watanabe et al. 2001; Huxlin et al. 2009).

Astonishingly the results of Watanabe et al. (2001) were not reproduced by later work of the group (especially Seitz et al. 2005; Tsushima et al. 2008). Nevertheless, the results appear to be ground breaking in various respects and still find reference in many overview theories (Seitz and Watanabe 2005; Yotsumoto and Watanabe 2008; Seitz and Watanabe 2009) although the performance deviations are not explicitly addressed. Hence, several open issues remain: Watanabe et al. (2001) did not report a performance increase for stimuli *below* the detection threshold of 8.3% but the way Tsushima et al. (2008) presented their results indicates that an increase in task performance is possible substantially below the reported detection threshold. Moreover, Seitz et al. (2005) reported the detectability of very weak motion signals, comprising only 5% of coherently moving dots, though, overall, the comparability of the stimulus material appears to be difficult to judge.

Quite independent of the question of detectability—and hence visibility—of weak motion signals is the question of potential higher attentional mechanisms which might be used to actively suppress strong and hence *disturbing* motion signals when they are not relevant, as indicated as well by the study of Tsushima et al. (2008) for a motion signal comprising 50% of coherently moving dots. In this case obviously no learning took place when this strong motion signal was task irrelevant and presented in the periphery.

Altogether the considerations outlined so far indicate that the question of "conscious percepts" accompanying motion signals is to be handled with care. But, nevertheless, in conjunction with the simulations they reopened the possibility that perceptual learning only takes place when accompanied with conscious percepts. The correlation between conscious perceptions and the detection rate of a motion stimulus, however, appears to require further investigation: If participants show increasing detections rates on a certain stimulus it appears to be necessary to assume that they actually *saw* these stimuli to a certain though maybe varying extent. The variation however, might be understood with the support of the neurodynamical simulations: Variations in the spiking rates, either due to (random) variations in the stimulus material itself or due to continuous cortical strain might well account for variations in the perception of the participants.

But moreover the studies considered in this work open the question regarding the role of attention in perceptual learning. Leaving the question of conscious percepts aside it is in any way quite obvious that the training took place without the *active* attention of the subjects nor an explicit feedback. This aspect actually implicates that it should be possible to train patients in their blind field with stimuli comprising a certain amount of coherently moving dots by sole passive viewing. Hence patients might be trained by random dot patterns presented in the blind field while viewing some more interesting stimuli in their intact hemifield which might promise a great relief.

With respect to the neurodynacmical model itself a range of issues remain to be addressed. One is the question of saturation. The presented learning rule does not comprise an (artificial) upper limit for the increase in weight strength. Hence with intense stimulation and high weights the spiking rates "collapse".

If cortical neurons operate in an at least principally similar manner this opens the question of overtraining. Certainly it is not very pleasant to view random dot patterns at all or for longer periods of time. This behavioral "unpleasantness" might prevent overtraining but appears to be difficult to translate into a natural limit for a neuronal model. Thus it is well possible that a cortical upper limit for the strengthening of connections does not exist at all which would ask for care with the intense usage of random dot patterns. Similar ethical considerations appear to be necessary with respect to the training of single motion directions or retinal locations. Especially the amazing results reported by Huxlin et al. (2009) underline the great flexibility of the brain but put as well the question of potential negative aspects of one-sided and unnatural visual training.

Another open issue especially with respect to the learning rule investigated is the role of behavioral feedback. For "subliminal" training feedback was not provided and hence not relevant for the current model design. The aspect, however, that learning takes place without explicit selective attention and without feedback opens the question whether these two components are closely related. Thus in Stemme et al. (in preparation) we investigate the question whether behavioral feedback operates primarily by

modification of the participants attention. This approach actually obsoletes the requirement to consider artificial reinforcement learning methods and thus promises a major progress for the usage of neurodynamical models to understand behavioral phenomena.

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