Getting emotional with evolutionary simulations: the origin of affective processing in artificial neural networks
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Good Vibrations Switch Attention: An Affective Function for Network Oscillations in Evolutionary Simulations

Abstract
A new hypothesis on the neural mechanisms linking affect to attention is brought forward by evolutionary simulations on agents navigating a virtual environment while collecting food and avoiding predation. The connection strengths between nodes in the networks controlling the agents were subjected to random variation and the fittest agents were selected for reproduction. Unexpectedly, oscillations of node activations emerged, which drastically enhanced the agent’s fitness. Here we analyzed the mechanisms involved in the modulation of attention and found that oscillations acted on competitive networks. Response selection depended on the connection structure, but speed and efficacy of switching between selections was modulated by oscillation frequency. The main focus of this study was the differential emergence of stimulus-specific oscillation frequencies. Oscillations had a higher frequency in an appetitive motivational state than in an aversive state. We suggest that oscillations in biological networks also mediate the affective modulation of attention.

2This chapter is a modified version of Heerebout & Phaf (2010b).
3.1 Good Vibrations Switch Attention

The method of computationally simulating evolutionary processes provides a unique opportunity for the automated development of models and hypotheses on cognitive and affective processes and their underlying neural mechanisms. The role of the modeler is limited to setting up the evolutionary selection procedure (e.g., a genetic algorithm; Holland, 1975), the initial state, and the environmental conditions. This has several advantages of which the opportunity for innovation is not the least. Novel models with mechanisms and functions that had not been previously considered may emerge from these undirected optimization procedures.

In previous simulation work (Heerebout & Phaf, 2010a) we serendipitously discovered ‘artificial neural oscillations’ in agents that inhabited a virtual environment (see Figure 1). The oscillations were an emergent property, not intentionally built in, and not even thought of beforehand, which proved to be highly adaptive. These simulations extended our investigation of LeDoux’s (1996) evolutionary justification of his dual-pathway model for the processing of emotional stimuli (den Dulk, Heerebout & Phaf, 2003). The agents, which were controlled by artificial neural networks, increased their chances of reproduction and survival by collecting food while avoiding predators. Analyses of the oscillating agents showed that the evolutionary advantage was conferred by an enhanced capacity for attentional switching when in an oscillatory mode.
To test the switching efficacy of an oscillating agent, it was compared to a non-oscillating agent from a control simulation with a simpler network. Both agents responded to a plant, placed in front of them at an angle of 45 degrees to its left, which would, as the agent approached the plant, suddenly be replaced by a predator. Their phenotypic behavior was described in terms of speed of movement and rotational speed, and revealed distinct approach and avoidance behaviors. The oscillating agent would
first ‘cautiously’ approach the plant following a swerving, ‘zigzag’, trajectory and then, as it detected the predator, make a sharp turn (at 0.042 degrees per time step) and accelerate strongly (the speed increased 87% in the first ten time steps). The non-oscillatory agent kept a more constant speed. When it would detect a predator, it accelerated only slightly (its speed increased only 13% in the first ten time steps) while turning away (with 0.034 degrees per time step). In addition, this appeared to be a robust finding, because fast switching oscillating agents turned up in five out of the seven replications.

Although the behavioral consequences of the oscillations were evident, the underlying mechanism demanded further analysis. Moreover, the networks from the replicated simulations exhibited oscillations at different frequencies. If the oscillations were adaptive because they enhanced the ability to quickly switch between competing behaviors, then the evolutionary demands imposed by the two types of stimuli might induce different oscillation frequencies. After all, increased flexibility may be advantageous when searching for food, but when fleeing from a predator foraging constitutes a distraction with potentially fatal consequences.

The present study aimed to address these two issues. First, we will briefly reiterate the method of evolutionary simulations. This is followed by the discussion of a simplified connection scheme, newly abstracted from previously evolved agents with oscillations in their networks. This simple connection scheme operated according to a winner-take-all competitive process, of which the switching speed was modulated by oscillation frequency. Similar competitive processes are often assumed to be involved with attentional selection in biological neural networks. More specifically, in our evolved networks the competitive mechanism seems to be responsible for selection-for-action (cf. Allport, 1989). We further investigated how the oscillations are able to modulate selection speed without influencing the specific outcome of this selection process. In addition, the simulation was replicated another 25 times to test whether positive stimuli indeed yielded faster oscillations than negative stimuli. Finally, the results from the evolutionary simulations are combined with empirical data on attentional selection and affect into the hypothesis that also in biological neural networks positive affect is associated with higher neural oscillation frequencies and more efficient attentional switching than negative affect, which conversely fosters the maintenance of attentional focus.
3.2 Evolutionary Simulations

Computer simulations allow researchers to perform experiments that would otherwise be impossible because of temporary, spatial, monetary or ethical constraints. Our evolutionary history is not directly observable and, therefore, empirically investigating evolutionary explanations is a difficult task. To address this problem with computational means, we applied a Genetic Algorithm (Holland, 1975) to agents navigating a virtual environment while collecting food and avoiding predators. Genetic Algorithms (GA’s) are traditionally used as an optimization method, inspired by natural selection. Starting from an initial population that consists of a random combination of gene values, the search for optimal solutions proceeds through selection and reproduction. Fitness is defined as some measure of how well the parameter set solves the problem. Thus, better solutions get a higher chance of survival and reproduction. When a specific solution gets to be reproduced, its parameters are subject to mutations and crossovers. Mutation may improve the performance of the population by occasionally suggesting a new partial solution. With 'crossover', two individual solutions selected for reproduction are recombined. The new solutions replace the less fit solutions in a population. From generation to generation, this leads to a higher overall fitness.

The evolutionary inspired optimization technique has been fruitfully applied to real-world problems. For example, the Aircraft Aerodynamics and Design Group at Stanford employed GA’s for optimization of aircraft design (Gage, 1995). A novel wing design was sought that minimized drag. The initial population resembled simple solutions, encoding the wing as a collection of tapered and twisted elements. Next, the solutions were slightly mutated, adding or removing a few random elements. The drag for each solution was then calculated using a vortex lattice analysis. This ‘fitness function’ determined which designs were selected for reproduction (i.e., which were copied with slight alterations). Multiple repetitions of the process quickly led to the discovering of winglets, small vertical additions at the wingtips (a standard CO₂ emission reducing measure on passenger jets nowadays). Later on, the algorithm found even more efficient “C”-shaped wingtips. This design concept was patented and its application to future aircraft models is under investigation. Although the fitness function guided the evolutionary process, the random variations allowed for the emergence of a fundamental, innovative design concept.
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Due to their innovative power, GAs stand in stark contrast with more conventional cognitive modeling approaches. Connectionist models, but also models constructed with a symbolic formalism like ACT-R or SOAR, are usually analytical models constructed to explain empirical data, formalizing some cognitive theory. The evolutionary simulations, consisting of a GA applied to the agents’ neural networks, on the other hand, automatically synthesize models that produce the goal-behavior, as specified in the fitness function. It should be emphasized that the modeler does not construct a model, but merely sets up conditions conducive to the evolution of the model that performs a particular function. When considering different models that explain behavioral data equally well, the model that has been shown to be more likely to develop in evolutionary simulations should be preferred above the others. Moreover, due to the innovative power of the GA even new models and hypotheses, not previously considered by neuroscientists, may emerge.

The conventional neural-network modeling of affective processes (Armony, Servan-Schreiber, Cohen, & LeDoux, 1995; Den Dulk, Rokers, & Phaf, 1997; Phaf, den Dulk, Tijsseling, & Lebert, 2001) has been strongly inspired by the neurobiological work of LeDoux (1986, 1996). According to LeDoux, the mammalian brain processes fear stimuli via two parallel pathways, running from the sensory thalamus to the amygdala. One pathway projects directly from the sensory thalamus to the lateral nucleus of the amygdala, the other indirectly, first passing through the cortex before reaching the amygdala. LeDoux suggested that these pathways might have evolved to functionally supplement each other. The direct pathway can produce a fast fear response, consisting of autonomic, endocrine and motor (e.g., avoidance) reactions, to a potentially threatening stimulus. The slower indirect pathway processes the stimulus more extensively and may strengthen the initial response if appropriate in case of an actual threat, or inhibit the direct reaction in case of a false alarm. LeDoux (1996) argued that the different functions of the two pathways are adaptive, because the evolutionary cost of a miss exceeds the total costs of the many false alarms produced by the direct pathway.

The straightforward formulation in terms of evolutionary benefits and costs by LeDoux (1996) facilitated the translation by den Dulk et al. (2003) into evolutionary simulations, which indeed resulted in the emergence of dual-processing networks. The setup largely followed the simulations of Beer (1990), in which Beer used Braitenberg
(1984) vehicles (i.e., the agents) to collect plants through chemotaxis. For the present study, the same software for the simulations was used as in the study den Dulk et al. (2003) but the networks of the agents were extended with an extra recurrent layer (see Figure 2) to investigate the adaptive value of such recurrent connections.

Figure 2. The four layers of the network architecture used in the simulations. The layers were potentially fully connected (i.e., all connections in the indicated direction could evolve to non-zero values in the course of the simulations). The arrows depict the direction of the connections. The context layer was added by Heerebout and Phaf (2010a) to allow for recurrent processing.

The present study completely followed the original design choices made by den Dulk et al. (2003). The oscillations, thus, resulted from a ‘design’ process by the GA, but not from the part of the modelers. Relative to this previous study no parameter adjustments were made and the space of possible fitness functions was not explored in any manner to arrive at these results. Insofar as the range of parameter values was
explored by den Dulk et al., it mostly proved of little influence when the parameters remained within reasonable bounds. For instance, whether the number of plants that were simultaneously present in the environment was four, six, or eight, the agents would always evolve to approach plants. The choice for the number of six plants, which was also used in our simulations, was therefore arbitrary. After initialization the simulations followed a simple three-stage procedure, the gist of which will be described here in brief, but more details can be found in Appendices A, B and C.

During initialization a population of agents was created with all the agents’ network connection weights set to zero. The potential network connections, which could evolve to nonzero values, specified a simple multi-layered architecture with an input layer of four nodes projecting to two output nodes and to four hidden nodes. The hidden nodes projected to the output nodes and also to another layer of four hidden nodes, which recurrently projected back to the former hidden nodes. The connections between the two layers of hidden nodes could develop independently (i.e., they did not have symmetrical weight values). One time step was defined as the duration of the calculation of a node’s activation. Therefore, the signals a node received at time t determined its activation at time t, but this activation would be propagated over its sending connection at t+1 (see also Appendix D).

In the first stage the algorithm would select agents to create offspring until the population size had tripled. With the initial population the selection is arbitrary, but with subsequent generations the agent’s fitness (measured in the second stage) determined the agent’s probability of being selected (see Appendix A for details on the selection and reproduction process). In the second stage, the fitness of each agent would be determined individually in twelve different random virtual environments, which always contained ten plants and six predators. The movement of the predators was governed by networks similar to those of the agents. These networks, however, were pre-configured to let the predators approach the agents. This configuration would not change (i.e., there was no ‘arms race’ between prey and predator).

The agents had olfactory sensors, located on the front left and right of their round bodies, which picked up the smells emitted by the plants and predators. The agents could utilize the lateral difference in smell intensity to estimate the direction of the source. The sensors relayed the detected intensities to the input nodes of the agent’s network. After processing, the output nodes’ activation would drive the agents’ left and
right motor actuators, giving the agents tank-like propulsion. Appendix B describes the
details of the smell distribution.

If an agent collided with a plant, the food was considered eaten, and one unit
would be added to the agent’s energy level. The plant would subsequently reappear at a
randomly selected location. Movement by the agent led to a reduction of energy (the
exact energy cost was calculated from the force an agent exerted on the environment;
also see Appendix B for details). An agent would be removed from the environment if it
collided with a predator, if its energy was depleted or if the maximum of 10,000 time
steps had passed.

When the agent was removed, its fitness was calculated as its energy level
multiplied by the total number of time steps spent in all environments divided by the
number of times it had been tested. In the third stage agents are removed from the
population, whereby the lowest scoring agents have the highest probability of being
removed. Appendix C explains how the agents’ fitness is used to calculate this
probability.

After cycling through the stages described above 10,000 times, den Dulk et al.
(2003) obtained weight configurations that had a functionality similar to LeDoux’s dual
pathway model. This architecture was found only in simulations, when (a) the plants
and predators were hard to distinguish, (b) processing via a hidden layer took more time
than direct processing, and (c) both plant and predator were relevant to the agent’s
fitness. The qualitatively different types of processing in the two pathways were further
supported by lesion studies of the separate pathways (i.e., setting all the weights in one
path to zero) in the artificial neural networks. These findings support LeDoux’s
hypothesis that the dual pathway model is adaptive and that it can evolve over time
through small mutations, when there is an exchange between time pressures and need
for accuracy.

3.3 Oscillations in Competitive Networks

Heerebout and Phaf (2010a) subsequently extended the simulation setup to investigate
the adaptive value of recurrent connections via a new hidden layer in the indirect
pathway. The recurrent processing could hypothetically lead to a working memory
capacity for previously processed stimuli by allowing activations from previous time
steps to contribute to the present network state. Unexpectedly, the added layer caused
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the networks to oscillate (e.g., see Figure 3). These oscillations clearly had an adaptive function, more than doubling the agents’ performance relative to agents from the control simulation, without recurrent connections.

In comparison to the LeDoux’s dual-pathway model, an alternative type of dual-processing dynamics emerged in these simulations. The direct route was no longer biased towards avoidance, but had a general energizing function. After lesioning the direct route, approach and avoidance tendencies could be distinguished in the indirect route, but the actions were not actually performed. For the action tendency to actually develop into an action, ‘arousal’ from the direct route was needed. The nodes in the indirect route entered into a competitive process whenever input was delivered to them. The selection of specific approach or avoidance action tendencies was determined by the evolved weight configuration. The oscillations added speed to this selection to a similar extent as was added by preparation through the direct route in the classical dual-pathway model.
Figure 3. An example of oscillating activations in the nodes of the network of a last-generation network. The nodes’ activations are shown over time, separated per layer. The activations shown in panel (A) were recorded when the agent was confronted with a plant and in panel (B) when the agent was confronted with a predator. In this example the period of the oscillation was two time steps with the plant stimulus and six time steps with the predator stimulus.
In classical competitive network models (e.g., see McClelland & Rumelhart, 1981; Rumelhart & Zipser, 1985) input causes the nodes in a network to compete for activation and a steady state can mostly be reached through a process of multiple constraint satisfaction, in which the connection weights constitute the constraints. Although networks of this kind have been applied to model visual attention (e.g., Phaf, Van der Heijden & Hudson, 1990), the inability of competitive networks to swiftly leave a winning state remains a major problem. Switching in these networks usually requires a period of activation decay or even manual intervention by the modeler. The oscillations might suggest a solution to this switching problem by providing a supplementary mechanism to reset the competition. With oscillating competitive networks the winning state could easily shift to another set of nodes in the troughs of the periodical activations. To examine how the oscillations influenced response switching, we distilled an abstract connection structure (see Figure 4) from the oscillating agents. Because the competitive behavior was preserved in the abstract network, even when the oscillation-generating connections were removed, the impact of the oscillations on the competitive process could be investigated.
Figure 4. The network configuration distilled from the evolved agents that generates the oscillations. The ‘I’ nodes provide inputs of scent ‘a’ and scent ‘b’. The solid lines with the arrowheads depict excitatory connections (with weight = 5) and the dashed lines with the globule heads depict inhibiting connections (with weight = -10). Without the grey nodes N3 and N6, the nodes N1 and N2 simply compete with nodes N4 and N5, resulting in the attentional selection of one of these pairs. With the indicated connections to the nodes N3 and N6 added, the network oscillates which modulates the competitive process.

The abstract network was constructed by identifying the connection sets that produced the oscillations in the networks. To this end, negligible and non-effective weights (without which the oscillatory properties of the remaining network did not change) were set to zero and nodes that consequently did not receive any activation were omitted from the abstract network. With these steps the idealized symmetrical connection scheme of Figure 4 (for reasons of computational parsimony all networks were symmetrical with respect to the left and right nodes) was formed. Activations were
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mirrored with respect to input from node I_a and I_b. Activation of N_1, by input node I_a, for instance, triggered activation of N_2. Excitatory feedback from N_2 to N_1 helped to sustain the activation in both nodes. The excitatory connection to the inhibitory node N_3, however, implemented a “flip-flop” mechanism and caused these activations to oscillate. Interestingly, this type of recurrent inhibition has also been identified as a neural oscillation generator by Ritz and Sejnowski (1997; see also Dupret, Pleydell-Bouverie, & Csicsvari, 2008). In addition, the strong inhibitory crossed connections from N_2 to N_4 and from N_5 to N_1 caused N_1 and N_4 to compete for activation. For the inhibitory mechanism to successfully overrule the excitatory input, all inhibitory connections were, in this idealized model, exactly twice the strength of the excitatory connections (-10 and 5 respectively). When context nodes N_3 and N_6 are removed from the connection scheme, a classical competitive network remains. The N_1 and N_4 nodes compete for activation when input activation is applied, and only the most strongly activated node (i.e., the ‘winner’) can preserve a non-zero activation.

The switching efficacy was examined by comparing performances of oscillatory and non-oscillatory competitive networks in a switching task (see Figure 5). The non-oscillatory network had the same connection weights as the oscillatory network, but the connections involved in the generation of oscillations were lesioned (i.e., set to zero). So, both types of networks were derived from the evolved agents that showed oscillatory activations. Non-oscillatory agents evolved in the simulations may have developed other switching mechanisms, presumably involving less mutual inhibition in the first place, but from their fitness scores we know that these mechanisms were less effective than oscillations (see Heerebout & Phaf, 2010a). For the switching task, input consisted of a monotonically increasing signal to the input node I_a, which would be replaced instantaneously by a strong signal to the I_b input node (see upper panel A of Figure 5). Panels B and C of Figure 5 show the ensuing activations of the nodes N_1, N_2, N_3, and N_4 of the non-oscillatory and oscillatory competitive networks, respectively. It is clear that the non-oscillatory network was unable to overcome the winner-take-all mechanism after the switch and remained stuck. Because the oscillatory network never completely settled, it did not take a large change in input to tip over to another winner. Due to the inhibitory pulses from node N_3, which caused the intermittent deactivation of node N_2 and provided an opportunity for N_4 to become activated, the oscillatory network smoothly switched in a few time steps. The abstract
model demonstrates that because its winning ‘steady’ state consists of oscillations, it is able to switch to another ‘steady’ state in the periodically occurring troughs of near-zero activation.

The different abilities of oscillatory and non-oscillatory competitive networks to switch winners clearly support our hypothesis that oscillations increase behavioral flexibility. Inhibition may have been exaggerated in the non-oscillatory networks relative to non-oscillatory networks evolved in actual simulations, but still in the latter networks switching ability is inferior to that of evolved oscillatory networks (Heerebout & Phaf, 2010a). In addition, the abstract network distinguishes the specific underlying mechanisms for selection and switching. In both oscillatory and non-oscillatory agents action tendencies (i.e., approach or avoidance) compete with each other, which according to the ‘selection-for-action’ framework (e.g., Allport, 1989) can be characterized as an attentional process (cf. Desimone & Duncan, 1995; Duncan, 1996; Phaf et al., 1990). In the abstract network the modulation of competition by oscillations is superimposed on the process of attentional selection. The oscillations, thus, enable the switching between winning representations without affecting the nature of the response that is being selected.
Figure 5. The input activations to both networks (A), activations in the non-oscillatory network (B), and in the oscillatory network (C). The scale of the x-axis (time steps) and the y-axis (activation) are the same for the three panels.
In a similar evolutionary-computation study by Ward and Ward (2008) agents evolved to actively direct attention to successive falling targets in order to ‘catch’ them. They found that to be able to focus on the first falling target, the activations from the second falling target, which was simultaneously present, needed to be inhibited. This inhibition subsequently caused difficulty in redirecting attention to the second target after the first one was caught. As a result the agent showed a moment of hesitation after the first target was caught. If the targets were closer together, the inhibition required to stay focused on the first target was more powerful, and the cost in terms of hesitation was larger. Switching cost thus increased with level of competition. These findings are remarkably consistent with our own (Heerebout & Phaf, 2010a) in showing that evolution in most real-world situations not only needs to solve the problem of attentional selection but also of how attention should be subsequently redirected. The artificial neural networks in Ward and Ward’s setup had bilaterally symmetric weights, which prevented the emergence of the flip-flop mechanism (i.e., requiring asymmetrical excitatory and inhibitory connections) responsible for oscillations. To be sure the actual simulations should of course be done, but we would guess that letting loose the constraint of bidirectional symmetry in their simulations would lead to a strengthening of mutual inhibition and competition and to a reduction in switching costs due to the emergence of oscillations.

3.4 Oscillations in Biological Neural Networks
The oscillations emerging in the evolutionary simulations can probably be associated with, relatively high-frequency, gamma oscillations (30-80 Hz) in biological neural networks (for an overview, see Buzsáki & Draguhn, 2004). From the different frequency bands gamma oscillations have most consistently been associated with attention (Womelsdorf & Fries, 2007; Bauer, Cheadle, Parton, Müller & Usher, 2009). The relevance of these oscillations, if any (Pareti & DePalma, 2004), remains a matter of debate. Because evolutionary simulations optimize the genotypic neural networks given particular environmental conditions, they may be in a unique position to shed light on the adaptive function of the emerging oscillations from a computational angle. Our previous work, at least, strongly argues in favor of an adaptive (i.e., fitness-enhancing) function of oscillations (Heerebout & Phaf, 2010a).
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Neurobiological research has suggested a large variety of roles for the oscillations in different areas of the mammalian brain. Possible functions include the binding of cell assemblies (Gray, König, Engel & Singer, 1989), biasing input selection through neuronal resonance (Hutcheon & Yarom, 2000), providing a sense of time (Buhusi & Meck, 2005), selective amplification (Lengyel, Huhn, & Erdi, 2005), and sequence learning (Ulanovsky & Moss, 2007). The enhanced ability of the agents to reorganize behavior in response to specific stimuli in our simulations may correspond to the suggestion of Schaefer, Angelo, Spors, and Margrie (2006) that oscillations serve to discriminate between stimuli (see also Brody & Hopfield, 2003, who showed that simple oscillating network models implemented sensory segmentation). In groundbreaking research, Sohal et al. (2009) even demonstrated in genetically modified mice that light-induced gamma oscillations enhanced information transmission in neocortex by reducing circuit noise and amplifying signals through the circuit. Increased flexibility and switching ability would indeed imply that the information carried by the neural output is more strongly related to the input signal. The mice with induced gamma oscillations, thus, seemed to be able to switch attention more easily than the mice without gamma oscillations.

According to Fries, Nikolić, and Singer (2007) stimuli can be distinguished more easily because the interaction between excitatory pyramidal neurons and inhibitory interneurons results in a time-critical competition during the gamma cycle. The few pyramidal cells that are able to spike first, are the only ones to spike at all. Subsequently, the activity of these pyramidal cells is suppressed by strong inhibitory interneurons which are themselves activated by the initial activation of these cells. The mechanism closely resembles the flip-flop mechanism we encountered in the agents’ networks from our simulations. They suggest this mechanism enables fast processing and flexible routing of activity, supporting fast selection of responses. The correspondence between the neurobiological findings of Fries et al. (2007) and our results further strengthens the association of the oscillations emerging in our simulations with gamma band oscillations in biological neural networks.

In contrast to our hypothesis, Börgers, Epstein, and Kopell (2008) argued on the basis of their (non-evolutionary) simulations, that oscillations increase stimulus competition, help to suppress distracters, and more narrowly focus selective attention. Their oscillations resulted from the interactions between fast-spiking interneurons,
which were periodically subjected to a ‘bath of inhibition’ due to cholinergic activation by a second class of inhibitory interneurons. During this ‘bath of inhibition’ all neural activation was suppressed. Particularly activation from potential distracters could not reach threshold values. Subsequently, only the strongest representation in the network could peak before inhibition started all over again. In their view, only the selection resulting from competitive processes is strengthened by the oscillations. The increased focusing of attention due to oscillations in the Börgers et al. (2008) model would decrease, rather than increase, behavioral flexibility and reduce the amount of information transferred by a network (e.g., see Sohal et al., 2009). In contrast to Börgers et al., in our simulations a distinction between attentional selection and attentional switching emerges, with oscillations only affecting the latter. The further finding of affect-specific oscillation frequencies, which will be discussed hereafter, provides additional support for the distinction and this specific role of oscillations. The evolutionary motivation, which can be distilled quite easily from the simulations, and the experimental evidence supporting the hypothesized link between affect and attentional switching, makes it likely that a similar setup can also be found in biological neural networks.

3.5 New Simulations Reveal Stimulus-specific Frequency

According to LeDoux (1996) the faster, more coarsely grained, direct pathway is biased to evoke an aversive response, because the costs of hesitation are higher when confronted with a threat than with food. This evolutionary reasoning suggests that threatening stimuli should quickly capture and hold attention (cf. Öhman, Flykt, & Esteves, 2001). We wondered whether a similar bias towards focusing attention on negative stimuli could be found in the oscillating networks, even when they did not have the classical LeDoux type of dual-route architecture. While moving away from an approaching predator, there is little need to heed to other stimuli. A high degree of distractibility caused by high-frequency oscillations seems a disadvantage in this situation.

A plant stimulus, on the other hand, should enable rapid behavioral switching, if a predator would appear suddenly. This increased behavioral flexibility, moreover, is supported by ample empirical research in which positive affect was found to increase cognitive and behavioral flexibility (Baumann & Kuhl, 2005; Das & Fennis, 2008;
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Dreisbach & Goschke, 2004; Fenske & Eastwood, 2003; Isen, 1999; Luu, Tucker, & Derryberry, 1998; Tan, Jones, & Watson, 2009). The broaden-and-build theory of Fredrickson (1998), for instance, generalizes these ideas even further by assuming that positive emotions serve to broaden an individual’s momentary thought-action repertoire by expanding the attentional focus. If indeed attentional flexibility is modulated by oscillations, it is only a logical step to expect higher oscillation frequencies for foraging agents than for fleeing agents in the simulations.

To investigate stimulus-specific oscillation frequencies, we replicated the simulations with the recurrent connections of Heerebout and Phaf (2010a) an additional 25 times. This resulted in a total of 32 simulations. The new simulations were exact replications, but new pseudo-random numbers were used in the stochastic decisions (e.g., the weight mutations) for each simulation. We found 430 agents with oscillating networks in the last generation of 27 out of 32 simulations (totaling 547 agents). The oscillation frequencies, both with food and predator stimuli, ranged from zero to 0.5 time step\(^{-1}\) (frequency was measured as the inverse of the number of time steps in a complete activation cycle; periods ranged from infinite, 6, 5, 4, 3 to 2 time steps). Some \((n = 347)\) networks oscillated both with plant and predator, sometimes with different frequencies, whereas 54 networks showed only plant oscillations and 29 networks showed only predator oscillations.

The presence of oscillations had a clear effect on the agents’ fitness. The oscillating agents \((n = 430; \text{average fitness } = 20,112; \text{SD } = 17,833 \text{ energy x time step})\) reached significantly higher levels of fitness \((F(1, 546) = 7.67; p < 0.01, \eta^2_p = 0.014)\) than non-oscillating agents \((n = 110; \text{average fitness } = 15,220; \text{SD } = 12,493 \text{ energy x time step})\) demonstrating that the oscillations have clear functional advantages in these simulations. Over the total of 547 agents the average frequency was significantly higher \((F(1, 547) = 25.27, p < 0.0001, \eta^2_p = 0.044)\) when an agent detected a plant \((f = 0.22, \text{SD } = 0.19 \text{ time step}\(^{-1}\))\) than when an agent detected a predator \((f = 0.18; \text{SD } = 0.17 \text{ time step}\(^{-1}\))\). The extrapolation of these results to biological neural networks, of course, remains hazardous, but if we assume that a time step (i.e., the time needed for activation transfer by a neuron) is about 5 ms, this would result on average in 44 Hz oscillations with the food and 36 Hz oscillations with the predator (c.f. the two frequency bands in Dupret et al., 2008). The frequency difference between stimulus types supports the conclusion that oscillations increase the agents’ ability to switch behaviors, and that the
difference arises from the differential environmental demands posed by food and predators.

An anonymous reviewer to a previous version of the manuscript suggested that the dynamic properties of the plants and predators could be confounded with their valence. The plants were always stationary, but the predators actively pursued the agents. To test whether this dynamic property could cause the difference in oscillation frequency we performed a further set of 22 simulations, in which the plants also moved through the environment, albeit in random directions. The speed (0.3 length units per time step) approximated the average speed of the predators. For the remainder, all conditions and parameters remained the same. If the speed difference is responsible for the differential processing of plants and predators, no frequency difference should emerge in these simulations.

The total number of agents in the last generations of all simulations equaled 377. Oscillations were again recorded in response to plants and to predators. Of the 377 agents 113 showed oscillations only in response to plants and 17 only to predators. The majority, 209 agents, oscillated both with plants and with predators. A small group of 38 agents did not show oscillations with either stimulus. Similar to the previous simulations, the oscillating agents \( n = 339; \text{average fitness} = 16,977; SD = 14,752 \) energy x time step reached significantly higher levels of fitness \( F(1, 375) = 10.9; p < 0.01, \eta^2_p = 0.026 \) than the non-oscillating agents \( n = 38; \text{average fitness} = 9,282; SD = 6,738 \) energy x time step. The difference in oscillation frequency was significant \( F(1,376) = 67.98, p < 0.0001, \eta^2_p = 0.153 \) and even larger than with the previous simulations. When an agent detected a plant the average frequency was 0.25 (SD = 0.18) cycle per time step and when an agent detected a predator the average frequency was 0.16 (SD = 0.17) cycle per time step. If we again assume that a time step lasts 5 ms, the plant frequency corresponds to 50 Hz and the predator frequency to 32 Hz. These results do not seem to support alternative interpretations in terms of stimulus dynamics.

### 3.6 Frequency Reflects Affective and Motivational State

Specific stimuli have acquired their positive affective value, because they generally raised fitness levels throughout evolutionary history. Inversely, negative stimuli are characterized by their recurrent potential to lower fitness. Positive and negative affect indeed appear to be generated by the nervous system as a neural code “to those aspects
of the environment that were a consistent benefit or threat to gene survival in ancestral environments” (p. 173, Johnston, 2003). Affective states in the networks are thus inferred from the consequences specific stimuli may have for fitness level. During evolution the network ‘learns’ to predict these consequences and to prepare for appropriate actions. Appetitive-approach tendencies towards positive stimuli and aversive-avoidance tendencies away from negative stimuli have likely developed in evolution to maximize fitness benefits and to minimize fitness costs, respectively. Such action tendencies, at least, emerged from the undifferentiated initial networks in our simulations as a response to fitness-relevant stimuli. Fitness costs are minimized by a focusing of attention on the negative stimulus and low distractibility. Fitness benefits are maximized by an approach to all positive stimuli and a high level of distractibility by other stimuli. The level of distractibility in our simulations was positively related to oscillation frequency. On average, oscillations had a higher frequency when the agent was foraging than when it was trying to escape from a predator. We suggest that a specific oscillation frequency sets the network in a suitable attentional mode to deal with affectively valenced stimuli.

The aforementioned, highly comparable simulation study by Ward and Ward (2008) also addressed attentional switching, but did not investigate affective influences on switching. Interestingly, Ward and Ward linked the reactive inhibition of the second target to the attentional blink (AB) phenomenon, and referred to recent neurocognitive studies (Hommel et al., 2006; Kessler, Gross, Schmitz, & Schnitzler, 2006) that also relate attentional dwell time to reactive inhibition. The inhibition of the second target when it is sufficiently close to the first target in the Ward and Ward simulations can of course easily be transposed to interference in the attentional blink task. The comparison can even be taken one step further, because also affective influences have been found on the attentional blink (Olivers & Nieuwenhuis; 2006; see also Most, Chun, Johnson, & Kiehl, 2006; Todorović, 2009, recently obtained similar affective modulation of the attentional blink in our laboratory). Not only for the attentional blink task, but also for other experimental tasks there is substantial evidence for the hypothesized link between affect and attentional switching (Baumann & Kuhl, 2005; Das & Fennis, 2008; Dreisbach & Goschke, 2004; Fenske & Eastwood, 2003; Isen, 1999; Luu et al., 1998, Tan et al., 2009). In comparison, the empirical evidence for a relationship between affect and oscillation frequency is much scarcer.
The extrapolation of the simulation results to biological neural networks remains a big step, and surely needs to be supported by empirical evidence. There is some research to suggest that the frequency differences emerging from the evolutionary simulations may have a similar biological function. A motivational role of gamma oscillations is, for instance, suggested by a study of Rougeul-Buser and Buser (1997). They observed 40 Hz oscillations in a cat’s motor, parietal, and visual cortices when it was waiting in front of a hole in the wall from which at times a mouse could pop out and then quickly disappear. When the cat was simply watching the mouse in a perspex box, however, only lower frequencies of 10-15 Hz showed up. We would argue that the cat at the hole is in a positive affective state, full of expectations of a nice meal, and is prepared to quickly switch from immobility to vigorous attack. With the box, however, where the cat cannot reach the mouse, both the need for this preparation and the corresponding oscillation frequency is lower. In the mouse, on the other hand, we would expect the oscillation frequency to be much lower when it is being predated by the cat than when it, for instance, detects a piece of cheese.

A causal relationship between gamma oscillations and positive affect has to our knowledge only been demonstrated very recently by Tsai et al. (2009). They showed with their highly innovative optogenetic method (also see Sohal et al., 2009) that trains of high-frequency light flashes (50Hz) applied to the ventral tegmental area (i.e., containing many dopaminergic neurons) of optogenetically manipulated mice served as a strong reward signal in place conditioning. In the trial, mice were exposed to both high-frequency light trains in one room and low-frequency light trains in another. The total amount of light the mice were exposed to was equal in both rooms. Afterwards, when the mice were given the choice, they all preferred the room where they had been exposed to the high-frequency light trains. If the high, but not the low, frequency light trains can substitute a reward signal, normally produced by a positive stimulus, then this shows that, at least in some cases, high frequency oscillations correspond to positive affect.

The other optogenetic study we mentioned (Sohal et al., 2009), which was performed by the same group and published simultaneously with the study of Cardin et al. (2009), showed the induced gamma oscillations enhanced information transmission. Our evolutionary simulations suggest that the two observations are connected and that high neural oscillation frequencies facilitate efficient attentional switching and high
levels of information transmission, whereas low frequencies foster the maintenance of attentional focus to negative stimuli. Although at the outset of their research these authors have not formulated specific hypotheses about the relation between oscillation frequency, attention, and motivational state, their results provide converging evidence for our hypothesis.

Two different hypotheses were brought forward by the evolutionary simulations in this study. First, oscillations have a modulatory role which is superimposed on attentional selection by means of competition. Second, oscillations have a higher frequency in an appetitive state, associated with positive affect, than in an aversive state associated with negative affect. Particularly the latter hypothesis appears to be new and may provide the missing neurobiological link between affect and attention, which has often been investigated in psychological research. There are only few ideas about the neurobiological mechanisms underlying affective influences on information processing and in view of these simulation results the oscillations seem a likely candidate. Computational simulations can only show that a particular hypothesis is more probable than another (i.e., the likelihood of its emergence is higher), but not that it necessarily holds true in biological neural networks. Evolutionary computation takes a special position within the modeling approaches, because it can create new models and thus form the starting point of the empirical cycle. Of course, novel hypotheses can only be successful if the good vibrations generated by the computer simulations resonate in empirical work and eventually lead to a switching in neurobiological research perspective.