Getting emotional with evolutionary simulations: the origin of affective processing in artificial neural networks
Heerebout, B.T.

Citation for published version (APA):

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Affective Modulation of Temporal Attention

Abstract
Evolutionary computation in our research group previously gave rise to the Affect-Gamma hypothesis, which asserts that high-frequency neural oscillations in the gamma band correspond to positive affect and enhance attentional flexibility, whereas negatively valenced, lower-frequency oscillations lock attention to selected stimuli. This behavioral study investigated the influence of affect on attentional switching between emotionally neutral stimuli, and whether this represents the primary form of affective modulation. Experiment 1 showed in a simple switching task that reaction speed to a deviant stimulus increased after suboptimally presented happy faces and decreased after angry faces. In Experiment 2, participants with a dominant global or local spatial bias switched more easily to the opposite bias after suboptimal happy faces than after neutral primes, but less easily after angry faces. Affective modulation of attentional switching was probably incorporated during evolution in many more complex forms of information processing.

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3 This chapter is a modified version of Heerebout, Todorović, Smedinga & Phaf (Submitted).
5.1 Affective Modulation of Temporal Attention

Emotion and attention have co-evolved to deal with priorities in the organism’s environment. These functions are closely linked because the former is about what receives priority, whereas the latter specifies the prioritization process. Evolutionary studies on emotion and attention have been scarce, because it is impossible to observe the evolutionary process from first hand. Recently, however, a number of studies have appeared that studied evolutionary development with a computational method (i.e., genetic algorithms) that mimics evolution (e.g., den Dulk, Heerebout, & Phaf, 2003; Heerebout & Phaf, 2010ab; Ward & Ward, 2008), and that is able to generate novel hypotheses. Evolutionary computation cannot prove these hypotheses to be true, but a hypothesis emerging from a simulation has a clear lead over competing hypotheses of which the evolutionary development has not been demonstrated. The hypothesis that unexpectedly emerged from our evolutionary computation (Heerebout & Phaf, 2010ab) postulates that positive affect facilitates attentional switching, whereas negative affect inhibits disengagement of attention. In this study we wanted to add further weight to the hypothesis and to its biological primacy by showing in Experiment 1 that affective influences can be found in the simplest of tasks requiring a shift of attention, and in Experiment 2 that the affective modulation of spatial attention is derived from the affective modulation of temporal attention (i.e., of attentional flexibility; see also Tan, Jones, & Watson, 2009).

Evolutionary simulations unexpectedly produced a new hypothesis on affective modulation, which primarily applies to the temporal dimension of attention. In these simulations the structure of the models is not designed by the modeler to fit some set of empirical data, but emerges autonomously from the optimization process by the evolutionary algorithm under a set of environmental conditions. The role of the modeler is thus reduced to specifying the initial conditions. Den Dulk, Heerebout, and Phaf (2003) already simulated agents that had to attend selectively to either plants or predators in a virtual environment. In the computational evolution, the connection weights of the agents’ artificial neural networks developed in such a way that the agents would approach plants while avoiding predators. Their performance determined their odds of survival and reproduction, i.e., their fitness. The resulting networks had a dual-
processing architecture with avoidance of predators taking priority over plant approach (cf., LeDoux, 1996).

More recently, when we introduced the possibility of recurrent connections, oscillations unexpectedly emerged in these networks, which almost doubled the agents’ fitness (Heerebout & Phaf, 2010a). The oscillation frequency of the activations of the nodes (i.e., quasi-neurons) in the agent’s network was higher when the agent was confronted with plants than with predators (Heerebout & Phaf, 2010b). The oscillations facilitated attentional switching from plants to predators, and thus led to quicker and more forceful avoidance reactions when a predator appeared suddenly. Attentional switching from predator to plant, however, may be maladaptive, because it would cause distractions when fleeing the predator. If a threatening stimulus appears, harm can best be avoided by locking attention to it. This reasoning was supported by the results of the simulations. The hypothesis that affect modulates attention via oscillations with different frequencies has only very recently received empirical support from neurobiological studies in genetically modified mice (Cardin et al., 2009; Tsai et al., 2009).

In human research, affective manipulations with attentional switching tasks have mainly been studied in the context of individual differences (i.e., with respect to anxiety) and psychopathology (for a review, see Yiend, 2010). The emphasis in these studies generally lies on attentional capture, or engagement, by emotional stimuli and not so much on the affective modulation of attentional switching. There are, however, indications that disengagement effects may even be larger than capture effects, such as in the emotional Stroop task (see Phaf & Kan, 2007) and in the attentional deployment task (e.g., see Yiend & Mathews, 2001). A crucial difference between capture and modulation is, moreover, that the former only applies to emotional material, whereas the latter can also tune attentional processing of non-emotional material. Particularly the affective modulation of, at least not explicitly, non-emotional processing argues in favor of a close intertwinemnt of emotion and attention, and shows that the two cannot be separated as was often done in traditional cognitive psychology.

In the network models evolved from the simulations of Heerebout and Phaf (2010b) a distinction was made between attentional selection and modulation. Input to these networks gave rise to a process of competition between two distinct behavioral outcomes, (i.e., either an approach or an avoidance response). The networks indeed
Affective Modulation of Temporal Attention

revealed strong inhibitory connections between neighboring nodes, which is characteristic of competitive networks. Lateral inhibition and competition have traditionally served as an explanatory mechanism for selective attention (e.g., Duncan, 1996; also Phaf, van der Heijden, & Hudson, 1990). Biased competition towards emotional stimuli, moreover, has been postulated to be responsible for the attentional capture by these stimuli (Öhman & Mineka, 2001). The oscillations, on the other hand, did not influence the specific response being selected, but modulated the speed and efficacy of switching between selections by providing troughs in the activations, in which ‘winners’ could easily change. The switching hypothesis asserts that positive affect corresponds to higher-frequency oscillations, and a higher switching susceptibility, than negative affect. The present study will not investigate the oscillation part of the hypothesis, but focus on the affective modulation of disengagement from non-emotional stimuli on a behavioral level.

The switching hypothesis has been supported by results from at least two experimental paradigms, although both types of findings are open to alternative interpretations. The local-global task (see Baumann & Kuhl; 2005, Tan et al., 2009), which will be discussed in more detail with Experiment 2, for instance, has traditionally been interpreted in terms of spatial attention to either large-scale or small-scale features (e.g., Gasper & Clore, 2002). The attentional blink task (see Most, Chun, Widders, & Zald, 2005; Olivers & Nieuwenhuis, 2006), on the other hand, addresses the interference in identification performance between successive targets, and, thus, must focus on the temporal aspects of attention. Olivers and Nieuwenhuis interpreted their results in terms of the investment of limited-capacity resources during controlled processing. The view of a limited-capacity reservoir, from which attentional resources are drawn at the expense of other processes, however, has been frequently criticized on empirical grounds (e.g., Allport, 1990). Also in our opinion, the limited-resources account can better be replaced by the more neurobiologically plausible biased-competition account (e.g., Duncan, 1995; also Phaf et al., 1990).

The attentional blink arises with rapid serial visual presentation of two targets (T1 and T2) within a stream of distracters. If T2 is presented within 500 ms after T1, the detection of T2 suffers from the detection of T1. Perhaps the nicest example of affective modulation of the attentional blink can be found with Olivers and Nieuwenhuis (2009, Experiment 2a). Positive pictures, presented optimally (250 ms) before the two targets,
reduced the attentional blink relative to neutral and negative pictures. In agreement with our switching hypothesis, the positive affect facilitated switching from T1 to T2. Olivers and Nieuwenhuis, however, interpreted their results in terms of a more diffuse mental state following positive primes, which would reduce the investment of resources in T1 and enhance performance on T2. Their claim that the overinvestment of resources is responsible for the interference was further supported by their Experiments 1 and 3. Both an additional task load and the instruction to concentrate less, improved attentional blink performance.

In Experiment 1, we want to show that affective modulation constitutes a low-level, biologically early, mechanism that is not itself a control process and does not entail the differential allocation of limited-capacity resources. We do so by implementing suboptimal affective priming (i.e., largely non-conscious, cf. Murphy & Zajonc, 1993) to further minimize controlled processing, and by having the task automatized to such a degree that few attentional resources can be said to be recruited by the preceding target. Switching to the subsequent deviant target would of course require resources in the limited-capacity view, but would not suffer in this task from the few resources allocated to the preceding target. According to our hypothesis, which fits in the alternative biased-competition view (e.g., Duncan, 1996; also Phaf et al., 1990) and does not presuppose capacity limits, positive affect facilitates switching from the dominant mode of responding.

5.2 Experiment 1

The attentional blink task not only involves attentional switching but many other cognitive functions, which may also be subject to affective modulation, such as the maintenance of both T1 and T2 in working memory before they are reported at the end of the stream. We, therefore, looked for a purer measure of attentional switching, which would allow for a smaller range of interpretations. The neuropsychological ACE (attentional and cognitive efficiency) test battery developed by Mialet, Bisserbe, Jacobs, and Pope (1996) may provide a suitable measure in the form of the AZE task, which these authors claim to require active switching of attention and an inhibition of motor automatisms. In this continuous choice reaction time task, participants press with the index finger of the dominant hand different keys (the ←, ↑, and → keys, respectively) on the keyboard in response to the letters A, Z, and E. The letters A and Z are presented
Affective Modulation of Temporal Attention

on the left and right side of the screen, respectively, and occur much more frequently than the letter E, which can appear on either side. Due to the spatial stimulus-response compatibility, after a training period the task becomes a highly automatized sensorimotor procedure, which only occasionally requires a switch to a deviant stimulus.

We modified the original AZE-task in a number of respects and introduced affective priming with facial expressions before the switch trials. The suboptimal primes were expected to have only short-lived effects on attention, so that priming could be operationalized as a within-subjects factor. In order to check for longer-term effects, however, we also included conditions in which the primes were presented in the trial preceding the switch trial. To increase the difficulty of switching, we placed the response keys further apart on the keyboard. To prevent interference in responding to the letters from the letters on the keyboard, we substituted the stimulus letters by geometric figures (i.e., square, circle, and triangle). Mialet et al. had two different instructions in separate blocks (one stressing accuracy vs. one stressing speed), but we instructed the participants to react as quickly and accurately as possible in the whole experiment. The overinvestment hypothesis predicts a higher investment of resources and shorter reaction times after negative primes in the switch trials than after neutral primes, and less investments and longer reaction times after positive primes. Because almost no resources are invested in the regular trials, according to this hypothesis differential interference effects are not to be expected when the primes are in the trial preceding the switch. The switching hypothesis gives rise to the opposite predictions with immediate priming, but agrees that the suboptimal primes in the preceding trial will not influence interference.

5.2.1 Method

Participants

Fifty-nine psychology students from the University of Amsterdam with normal or corrected-to-normal vision participated in the experiment for course credit, after signing informed consent. The results of three participants were not analyzed due to not following instructions (e.g., using multiple fingers) or to experimenter error (i.e., with regard to the equipment settings). The remaining 56 participants (43 female) had an average age of 21.3 (SD = 3.6) yr.
Design
The experiment had a 3 x 2 within-subjects factorial design. The first independent variable concerned the primes (happy face, neutral house, or angry face), and the second one prime position (switch trial or preceding trial). The reaction time to the triangle served as the main dependent variable. The longest reaction time per condition was considered an outlier, thus taking a fixed percentile for outlier removal. The proportion of errors could also serve as dependent variable but was too low (less than 2%) to allow for meaningful analyses. Two lists with randomly determined condition orders (minimum distance between triangles four trials) and of couplings of specific faces to conditions were counterbalanced.

Material en apparatus
The targets were a square, a circle, or a triangle with a diameter of approximately 1.3 cm (visual angle 1.13°). Eighteen happy and 18 angry face primes, with equal numbers of male and female faces, were taken from the Karolinska Directed Emotional Faces set (Lundqvist, Flykt, & Öhman, 1998). They were all gray-scaled and cropped to present the faces only from the chin to above the eyebrows. A total of 324 house pictures from the websites of real estate agencies served as neutral primes. Twenty different masks consisting of scrambled parts of faces were cropped in an oval form and presented against a black background to match the size, shape, and contrast of the Karolinska faces. All prime and mask images were resized to 400 x 300 pixels and subtended a visual angle of 16.0° x 11.3°. Primes and masks were presented centrally, and the targets 4.3° left or right from centre.

Stimuli were presented against a white background on a CRT monitor with a 40 cm (15.75”) diagonal with a 1024x768 pixel resolution and a refresh rate of 60 Hz. Participants were seated approximately 50 cm from the screen. Responses were given on the computer keyboard (standard 105 key PC keyboard with US International layout). The ‘z’ served as response key for the circle, the ‘/’ for the square, and the ‘7’ for the triangle. The circle always appeared left of centre, the square right of centre, and the triangle 50% left and 50% right. Participants were asked to hold the index finger of their dominant hand on the space bar at the start of a trial and return to it after having responded. The space bar was labelled with a green sticker, and the ‘z’, ‘/’, and ‘7’ keys, with circle, square, and triangle stickers, respectively.
Figure 1. Timeline of stimulus presentation in Experiment 1.

A trial (see Figure 1) started with the presentation of a mask for 200 ms, which was followed by the prime for 50 ms, and again by the same mask for 100 ms. Immediately after the second mask the target appeared either left or right of centre. The target remained on screen until response. In the 1000 ms intertrial interval an empty screen was presented. Before the experimental session, 50 practice trials were performed with only neutral house primes. The deviant triangle would appear five times in the practice block. The experimental block consisted of 360 trials with 36 triangle trials, of which six were immediately preceded by a happy prime, six by an angry prime, another six by a happy prime in the previous trial, and six by an angry prime in the previous trial. In all other trials, neutral houses served as primes.
Procedure

Participants were informed that the experiment was about attentional switching in a simple task which they would practice extensively. They were instructed that they should react to one of three geometric figures by pressing the corresponding key with the index finger of their dominant hand. Between trials they should rest their finger on the green label of the space bar. They were told that the scrambled picture was there to help them fixate to the centre. They were warned that the triangle would appear only infrequently, and that the targets were presented equally often to the left as to the right, so that they could react the fastest if they would initially keep their eyes at the middle of the screen. They were further instructed to react as quickly and accurately as possible, and were informed that their reaction times and errors would be registered. In the exit-interview, participants were asked for their impressions and whether they noticed something special during the experiment. At the end of the experiment, participants were debriefed about being shown happy and angry faces during the experiment, and were asked directly whether they had seen these faces.

5.2.2 Results

Particularly when primes occurred immediately before the switch, participants were faster to switch to the triangle after the happy prime than after the neutral prime, which in turn led to faster switches than the angry prime (see Figure 2). In a 3 x 2 (prime x position) ANOVA the main effect of prime (F(2, 110) = 5.11, p < 0.01, ηp² = 0.085) was qualified by an interaction with prime position (F(2, 110) = 4.56, p < 0.05, ηp² = 0.076). Only with immediate priming (with priming in the previous trial all |t| < 1) did the priming conditions differ reliably in one-tailed paired t-tests (Happy-Angry t(55) = -5.01, p < 0.0001, Cohen’s d = -0.70; Happy-Neutral t(55) = -2.23, p < 0.05, d = -0.32; Neutral-Angry t(55) = -2.57, p < 0.01, d = -0.36).
Figure 2. Average reaction times (RT) in ms as a function of prime type and prime position in Experiment 1. Error bars denote 1 SE (standard error), which when applicable have been adjusted for within-subjects designs.

Exploratory analyses with gender and handedness (nine participants reported to be left-handed) revealed no effects of these variables. In the exit-interview, three participants spontaneously reported to have seen faces, and another nine responded that they may have seen faces after being asked. The masks were, however, also composed of scrambled faces, which may have led the participants to think that they had seen faces. Even the participants who said they had seen some faces, moreover, reported no awareness of their emotional expressions. When we contrasted the priming in these twelve participants with the other participants, only a group difference emerged with immediate priming. Priming appeared to be larger in the more prime-aware group (Happy 733 ± 22 ms; Neutral 776 ± 22 ms; Angry 781 ± 22 ms; all these and subsequent SDs were adjusted for within-subjects designs, when applicable) than in the prime-unaware group (Happy 753 ± 24 ms; Neutral 757 ± 23 ms; Angry 772 ± 28 ms). A 2 x 3 ANOVA indeed revealed a significant interaction between Group and Prime ($F(2, 108) = 5.57, p < 0.01, \eta_p^2 = 0.094$). This finding does not necessarily mean that conscious priming is larger than non-conscious priming, but may indicate that more
participants in the unaware group than in the more aware group did not process the primes at all, and that the former group showed smaller priming effects for this reason.

5.2.3 Discussion
In this very simple task with a fixed stimulus-response mapping, a sudden switch from an automatized routine to a deviant stimulus was facilitated by barely visible happy faces, whereas it was inhibited by angry faces. Participant reports suggested that there was little conscious processing of the faces and even less of the emotional expressions, so that little controlled processing seems to have been elicited by the primes. There are also indications that affective priming by faces may be stronger with suboptimal presentation than with optimal presentation (Murphy & Zajonc, 1993; Rotteveel, de Groot, Geutskens, & Phaf, 2001), possibly due to the absence of conscious regulation (i.e., a control process). The setup with suboptimal presentation may, thus, have improved our chances of finding these effects. The suboptimal priming effect, moreover, seemed to be short-lived, because it did not extend to switches in a subsequent trial. More importantly, however, if processing of the faces was, at least partially, non-conscious, this may illustrate the bottom-up nature of the affective modulation of attentional switching, which acts before top-down control processes come into play. If one wants to think in terms of limited-capacity resources, it is very unlikely that many resources were allocated to this automatized task. Within the resources framework it seems difficult to explain how an even smaller investment of resources in positive conditions could lead to shorter, instead of longer, reaction times to subsequent, deviant stimuli. The findings in Experiment 1 argue in favor of a low-level modulation process that does not entail resources or control processes.

The prevailing view on the effects of positive emotions is the broaden-and-build theory of Fredrickson (2004), which compounds attentional flexibility with the broadening of attention. Fredrickson and Branigan (2005) showed that positive film clips, on the one hand, increased the selection of global features from ambiguous local-global patterns (see also Gasper & Clore, 2002), and, on the other hand, induced a more flexible action repertoire. Similarly, Rowe, Hirsh, and Anderson (2007) found that positive music enhanced (i.e., broadened) interference by incompatible flankers, and at the same time improved access to remote associates. In this light, however, the finding of a reduced attentional blink with positive affect (e.g., Olivers & Nieuwenhuis, 2006)
Affective Modulation of Temporal Attention

seems rather paradoxical. According to broaden-and-build, attentional focus should have broadened due to positive affect, so that the interference in the detection of T2 should have increased instead of decreased, as was found by Olivers and Nieuwenhuis. In our view, flexibility in the temporal domain (i.e., switching in time) should be distinguished from broadening in the spatial domain (i.e., to large-scale features) and we aim to do so in Experiment 2. We will further argue that the affective modulation of temporal attention has primacy, because increased flexibility can give rise to switching either to a broader or a narrower spatial focus, depending on the dominant attentional set.

5.3 Experiment 2

With regard to the affective modulation of spatial attention, two opposing positions have been taken in the literature. The first, which can at least be traced back to Derryberry and Tucker (1994; see also Basso, Schefft, Ris, & Dember, 1996; Derryberry & Reed, 1998; Gasper & Clore, 2002), and perhaps in part even to Easterbrook (1959), holds that positive affect broadens spatial attention, whereas negative affect narrows it. The reverse has, however, also been postulated in the literature (Moore & Oaksford, 2002), and supported by studies with ambiguous local-global pictures, at least for participants with a default global precedence, by Baumann and Kuhl (2005), and Tan et al. (2009). The latter researchers reduced the hypotheses on the affective modulation of spatial attention to a flexibility account by arguing that participants with a dominant local focus broaden attention, whereas participants with a global focus narrow attention as a consequence of positive affect. With negative affect they observed a slowing of disengagement from the dominant focus. This flexibility account, which agrees well with our switching hypothesis, thus explains the opposite findings in the domain of spatial attention by coincidental differences in dominance of attentional focus, due to different participant samples or to due to the settings of experimental conditions.

Evidence suggesting a broadening of spatial attention with negative affect, has recently been published by Bocanegra and Zeelenberg (2009). In their research, attention to global vs. local features was measured by tilt-detection performance on Gabor patches with low and high spatial frequencies, respectively. Similar to a sound, also a visual image can be analyzed in terms of a superposition of oscillations (i.e., of
lighter and darker pixels with different frequencies, see Schyns & Oliva, 1999). Global (i.e., large-scale) features of a visual image are encoded in the lower part of the spatial frequency spectrum (LSF), whereas local (i.e., small-scale) features are encoded in the high spatial frequencies (HSF). Fearful face primes increased sensitivity to orientation in LSF, low-contrast, Gabor patches compared to neutral face primes, while at the same time decreasing sensitivity in HSF, high-contrast, Gabor patches (Bocanegra & Zeelenberg, 2009). The neutral faces in these experiments seemed to have acquired a positive valence due to their presentation amidst fear faces. Relative to inverted neutral faces, which may well have represented the genuinely neutral prime condition in this study, the upright neutral, but positively tinted, face primes indeed facilitated HSF processing and reduced LSF processing (Bocanegra & Zeelenberg, 2009; Experiment 2). These findings with negative and positively tinted faces, thus, seemed to support the reverse position of Moore and Oaksford (2002).

It may be argued that different stimulus-specific mechanisms are at work in the affective modulation of attention to local or global features (e.g., Gasper & Clore, 2002), and to HSF or LSF components of an image. Bocanegra and Zeelenberg (2009), for instance, hypothesized that fearful stimuli enhanced “quick and dirty” processing in the magnocellular pathway from pulvinar and superior colliculus to the amygdala, which also is the privileged route for the processing of LSF stimuli (see Vuilleumier, Armony, Driver, & Dolan, 2003). This certainly makes evolutionary sense, because threatening stimuli are often encoded in the LSF-parts of the spectrum (e.g., due to their movement, or peripheral location). An alternative evolutionary stance would, on the other hand, posit that a narrow focus on the threat increases the chances of survival, and that interference by distractions is highly maladaptive.

In our view, global and local stimulus features are processed through LSF and HSF channels respectively, and attentional processing of the two types of stimuli should, therefore, be modulated in the same manner by affect. The Bocanegra and Zeelenberg results with the Gabor patches of different spatial frequencies may be due to a relatively high number of participants with a dominant global focus in their sample, whereas the participants in the experiments with ambiguous local-global stimuli may have had a largely local bias (cf., Gasper & Clore, 2002). Different presentation times may have been responsible for the opposite dominant biases in the two types of experiments. It is well-known that short presentation, as in the Bocanegra and
Zeelenberg experiments, generally favours global (i.e., LSF) perception, whereas long presentation, as in most local-global experiments, fosters local (i.e., HSF) perception (e.g., Schyns & Oliva, 1999). In Experiment 2, we implemented intermediate target presentation times, so that the two bias groups (i.e., global vs. local) would approximately have the same size. We wanted to investigate whether similar switching, in opposite directions for the two bias groups, could be observed with LSF-HSF stimuli as was obtained with ambiguous local-global stimuli (Baumann & Kuhl, 2005; Tan et al., 2009).

In order to investigate the affective modulation of attention to LSF-HSF stimuli, we modified Experiment 2 of Gasper and Clore (2002) and replaced the local-global stimuli with hybrid stimuli consisting of superpositions of two different pictures from low and high spatial frequency ranges (for an example see Figure 3). The longer-term mood induction used by Gasper and Clore was substituted by a short-term affective priming manipulation similar to Experiment 1. To investigate the duration of suboptimal affective priming a short and a longer prime-target interval were included. After the hybrid target picture, the two constituent pictures were presented in an unfiltered format, and the participant was asked to indicate with response buttons which of these two alternatives (i.e., corresponding to the local or global features) resembled the target picture most.
Figure 3. Example of hybrid car stimulus (top) in Experiment 2. The stimulus is created by adding the two bottom images, one of which is filtered in the HSF domain (bottom left) and the other in the LSF domain (bottom right). The HSF image is rich in detail but the details are difficult to perceive at a brief glance. When added to a LSF image, the detailed one will always dominate when viewed from a short distance, but the details will be lost as the page is moved further away from the reader. The response alternatives in the experiment were the unfiltered versions of the bottom images. Adapted with permission from www.automobilemag.com.

Next to the number of local or global choices, reaction times (RT) served as dependent variables in the experiment. Relatively faster responses to global (LSF) than
to local (HSF) alternatives reveal a broad focus, whereas slower responses indicate a narrow focus. The reaction time difference with neutral priming was used to determine overall local or global feature dominance. This difference is more suited for this purpose than the relative number of local to global choices with neutral priming, because the latter depends more on arbitrary settings of filtering parameters and viewing distance. Targets were presented for intermediate durations (i.e., between suboptimal and optimal levels), so that the local and global bias groups would have, as much as possible, the same size. If the switching hypothesis can also explain the LSF-HSF results, the direction of affective modulation should be opposite in the two bias groups. If the friction between the two spatial hypotheses, however, depends on the type of stimulus, then, similar to Bocanegra and Zeelenberg (2009), positive primes should overall enhance the perception of HSF features and negative primes of LSF features.

5.3.1 Method

Participants

Sixty Amsterdam University students with normal or corrected-to-normal vision participated in the experiment, after signing informed consent, for either course credit or a financial compensation. The data of six subjects were not analyzed, because they either forgot to take their glasses (and only told so at the end of the experiment), did not remain on the chin rest throughout the experiment, or due to experimenter error (i.e., in the equipment settings). All analyses were run on the remaining 54 participants (40 female, mean age 21.6, SD=3.7 yr, five reported to be left-handed). The participants were divided in local and global bias groups on the basis of their difference in reaction times to LSF and HSF choices after the neutral primes with both prime-target intervals.

Design

The experiment had a 3 x 2 within-participants factorial design. The first independent variable had three levels: happy or angry prime faces, or a neutral empty screen. The second independent variable concerned the prime-target interval (0 ms vs. 300 ms). Dependent variables were the number of choices for either the LSF or the HSF alternatives and the corresponding reaction times. A similar percentile outlier-selection procedure was used as in Experiment 1. With less than six responses per condition no outlier was removed, between 6 and 10 responses the longest RT was removed, and
with every next five responses one outlier more was removed. The trials belonging to these outlier responses were removed entirely, which also entailed removal of the choice scores from these trials. The presentation order, the position of the response alternatives, and the combination of faces, masks, intervals, and hybrid pictures were drawn randomly (without replacement) by the experimental software. Only the 20 masks were repeated in the 240 trials of the experimental session.

Material and Apparatus
Hybrid visual stimuli were constructed using Matlab R2007b (The MathWorks, Inc., Natick, MA) by combining pairs of images filtered in different frequency spectra. The hybrid images were a combination either of two houses or two cars. The car pictures were taken from an online automobile magazine (www.automobilemag.com), while the house pictures were taken from websites of real-estate agencies. The images were paired on the basis of overall similarity of foreground object form and position, as well as background structure. Where possible, the pair consisted of an image of the same car against the same background in two different orientations, or the same house taken from two different angles on the same day. All images were resized to 300 x 400 pixels. House pictures that originally had a greater height than length were first cropped in such a way that the resizing would not introduce distortion. After resizing, all the images were gray-scaled in order to reduce the number of dimensions along which filtering was performed. One of the images in the pair was low-pass filtered with a Gaussian filter with a standard deviation of 12 cycles per image width. The other image was high-pass filtered with a Gaussian filter with a standard deviation of 20 cycles per image width. The images were then combined by linear addition into a hybrid that was well represented in the high and low spatial frequencies (~85%-100%), with progressively fewer frequencies towards the medium range (~ 30% in the mid-range, see Figure 4). The unfiltered constituent images served as response alternatives in the experiment. Of the resulting 123 car pictures and 127 house pictures, 10 were used in the practice trials. The remaining 240 hybrid pictures were divided over two blocks, in which all conditions would occur.
Figure 4. Low and high filtering curves for the two constituent images of the hybrid pictures in the spatial frequency spectrum (in cycles per image width).

The 40 happy and the 40 angry face primes, with equal numbers of male and female faces, were taken from the Karolinska Directed Emotional Faces set (Lundqvist, Flykt, & Öhman, 1998). They were all gray-scaled and cropped to present the faces only from the chin to above the eyebrows. The masks consisted of 20 scrambled faces cropped in an oval form and presented against a black background to match the size, shape, and contrast of the Karolinska faces.

Stimuli were presented against a white background on a CRT monitor with a 40cm (15.75") diagonal with a 1024x768 pixel resolution and a refresh rate of 60Hz. Participants viewed the screen from an in height adjustable chair with their head stabilized in a chin rest positioned one meter from the screen. The rest’s bar held the chin of the participant at the same height as the lower edge of the screen. The hybrids and the response alternatives occupied a visual angle of 5.65° x 8.04°, the primes and masks of 11.60° x 8.50°. Participants operated the mouse with the preferred hand and responded by clicking the left or right mouse button to indicate their choice of the left or right picture, respectively. A trial (see Figure 5) started with the 200 ms presentation of a mask, followed by a 50ms prime and the same mask again for 200 ms. After a 0 ms or 300 ms empty interval, the target hybrid picture was presented for 150 ms and a second
empty interval of 500 ms followed. The response alternatives were subsequently presented until response.

**Figure 5.** Timeline of stimulus presentation in Experiment 2.

**Procedure**

The experiment was introduced to the participants as a study into visual attention, in which the attentional capture by either details or global features was investigated. They should, therefore, respond quickly and in an intuitive fashion. The participants were not warned beforehand that emotional faces would appear between the masks. They were instructed that the masks were there to let them know that the trial is beginning and that
they should focus their attention to this frame. The participants were shown how the hybrid images work, by viewing a printed example of an image where the HSF car faced to the left and the LSF car to the right. The image was shown at a close distance, and then slowly moved away from the participants until they reported seeing only the LSF image. It was then briefly explained to them that there are two images in the hybrid, that the more detailed one dominates from nearby and the less detailed one from afar, and that they may see one or the other when the pictures are presented only briefly on the screen. Participants were reminded to make intuitive choices if they did not manage to see the target clearly. There were first ten practice trials with three car and seven house hybrids, which were not used in the remainder of the experiment. After practice, the 240 experimental trials followed in two blocks of 120 trials each separated by a short break. In the exit interview, open questions (e.g., whether they noticed something special) were first posed, and subsequently the participants were asked directly whether they saw the faces between the masks.

5.3.2 Results
Local and global bias groups were distinguished on the basis of the RTLSF –RTHSF difference scores with neutral primes, summed for both prime-target intervals. Low scores imply a bias towards LSF (i.e., global) features and high scores a bias towards HSF (i.e., local) features. There were more negative than positive scores, which may indicate that more participants had a global than a local bias. It is also possible, however, that relative differences in the speed of perceiving LSF and HSF features in the target picture (response alternatives were unfiltered) were responsible for the majority of negative scores. The histogram (see Figure 6) revealed three separate distributions with the left one representing the global-bias group, the right one the local-bias group, and the middle one the group with only moderate biases. When the extremely biased participants were eliminated from the histogram a distribution resulted with a mean of 235 ms (SD = 68 ms). This mean was taken as the criterion distinguishing global (n=29) and local (n=25) groups. Five participants spontaneously reported to have seen the faces, and another six when asked so. These numbers were too small to involve them in the analysis of group effects.
Local and global groups showed affective modulation in opposite directions, as can be seen both from the number of choices (see Figure 7) and the reaction time differences (see Figure 8). These effects, moreover, only occurred reliably with the short prime-target intervals. A LSF-choice was coded as 1 and an HSF-choice as 2. The final choice score was obtained by averaging over these numbers. The global group overall made more LSF selections (1.154 ± 0.080) than the local group (1.244 ± 0.127), as was evidenced by the main effect of group \( (F(1, 52) = 13.76, p < 0.001, \eta_p^2 = 0.209) \) in a 2 (group) x 3 (prime) x 2 (interval) ANOVA on the choice scores. The group distinction made on the basis of the RT differences is, thus, reflected in the choice results. More importantly, the significant group x prime x interval interaction \( (F(2, 104) = 5.91, p < 0.005, \eta_p^2 = 0.102) \) supported the opposite priming effects for the two groups with the short interval, and the absence of priming with the longer interval. This conclusion was strengthened by the results of separate group x prime ANOVAs for the two intervals. The interaction proved to be significant for the short interval \( (F(2, 104) = 6.30, p < 0.005, \eta_p^2 = 0.109) \), but not for the long interval \( (F(2, 104) = 2.01, NS) \).

Figure 6. The histogram of RTLSF –RTHSF scores with neutral priming summed for the two prime-target intervals.
Planned comparisons showed that only the differences between happy and angry prime conditions were fully significant for the global group ($t(28) = 1.77, p < 0.05, d = 0.33$), and for the local group ($t(24) = -3.17, p < 0.005, d = -0.64$).

A similar pattern of results emerged from the RT differences (see Figure 8). For this dependent variable, the priming effects also seemed to be present with the longer intervals, albeit much smaller. The neutral priming conditions were not further analyzed because the group distinction was based on it. Overall, the RT advantage on the LSF above the HSF pictures was much larger ($F(1, 50) = 10.83, p < 0.005, \eta_p^2 = 0.178$) for the global group (-234 ± 310 ms) than for the local group (-63 ± 113 ms). This main effect was only qualified by an interaction between group and prime ($F(1, 50) = 4.09, p < 0.05, \eta_p^2 = 0.076$). Separate ANOVAs for the two intervals showed the interaction only to be significant for the short interval ($F(1, 52) = 6.61, p < 0.05, \eta_p^2 = 0.113$), but not for the long interval ($F(1, 50) = 1.07, NS$). Planned comparisons for the short interval revealed a significant priming effect for the global group ($t(28) = 2.22, p < 0.05, d = 0.44$), and a marginally significant effect for the local group ($t(24) = -1.62, p = 0.059, d = -0.33$).
Figure 7. Choice scores as a function of prime type and group in Experiment 2 for the short prime-target interval (Panel A) and for the long interval (Panel B). Error bars denote 1 SE (standard error), which when applicable have been adjusted for within-subjects designs.
Figure 8. Average RT differences (RTLSF – RTHSF) in ms as a function of prime type and group in Experiment 2 for the short prime-target interval (Panel A) and for the long interval (Panel B). Error bars denote 1 SE (standard error), which when applicable have been adjusted for within-subjects designs.
5.4 General discussion

The experiments showed that barely visible happy faces facilitated attentional switching, whereas angry faces slowed down disengagement from previously selected responses and stimulus features. In the first experiment, emotional expressions modulated response shifting due to a deviant stimulus. In the second experiment, the expressions did not lead to a bias to process either local or global features per se, as postulated by the spatial modulation hypotheses, but influenced the switching from the dominant spatial bias, which the participant revealed after neutral primes. These findings contradict the notion that the two opposing forms of spatial modulation are stimulus-specific (i.e., depend on global-local vs. LSF-HSF pictures). In addition, both experiments weaken a number of competing accounts, such as the attentional resources and the spatial modulation hypotheses, and provide converging evidence in favor of the switching hypothesis.

In both experiments, the suboptimally presented face primes did not seem to have been processed consciously by the majority of participants. The few participants that reported to have seen faces may also have seen them in the masks, which consisted of scrambled face parts. If processing of the faces was non-conscious, this may emphasize the basic, and evolutionary early, nature of this type of affective modulation and the lack of involvement of higher-level control processes. Enhanced switching during positive affect has even been postulated to be an innate fixed action pattern. Eibl-Eibesfeldt (1970), for instance, observed that both humans and primates involuntarily move their eyes around during eating, and, thus, continuously shift attention in this positive state. Kuroki (2007) reported a similar finding with human infants, who disengage their gaze more often from their point of fixation in a positive than in a neutral affective state. Affective modulation of attentional switching can, thus, not only take place in the absence of consciousness, but also seems biologically engrained, as can be deduced from phylogenetic and ontogenetic continuities.

In our evolutionary simulations (Heerebout & Phaf, 2010b), temporal modulation emerged quite readily in these simple networks, which have little room for more intricate forms of processing. Although the agents in these simulations roamed a two-dimensional spatial environment, a broadening or narrowing of spatial attention due to stimulus type was not observed. Both the results of the simulations and of the experiments show that the temporal and the spatial senses of the broadening and
narrowing of attention should be distinguished, and that the temporal version has evolutionary primacy. The implementation of temporal modulation by different oscillation frequencies only required networks with a few levels of nodes and with recurrent connections between at least two levels. The extrapolation of these simulation results to biological networks also suggests that temporal modulation has developed long before the emergence of controlled and conscious processing, which probably requires much more extensive neural networks.

Once the basic form of affective modulation had developed, it probably was incorporated in other forms of processing that evolved later. A higher flexibility due to positive affect has, for instance, been observed in a semantic remote-associates task (Bolte, Goschke, & Kuhl, 2003; Rowe, Hirsch, & Anderson, 2007), in creative problem solving (Baas, De Dreu, & Nijstad, 2008; Isen, Daubman, & Nowicki, 1987), and in control processes (Dreisbach & Goschke, 2004). Persons in a positive mood state, moreover, tend to have more new, non-obvious insights (i.e., Aha! experiences) when solving a problem, whereas anxious persons employ more deliberate strategies for solving the problem (Subramaniam, Kounios, Parrish, & Jung-Beeman, 2008). The sudden nature of these insights suggests that the solution is first computed non-consciously, and by consequence is also modulated affectively without awareness. In the domain of memory, induced moods differentially modulated illusory familiarity in primed recognition performance, as if level of consciousness for the primes was manipulated, with a positive mood corresponding to more non-conscious patterns of results (Rotteveel & Phaf, 2007). Indicating higher retrieval flexibility, positive affect also lured participants into more false memories in the Deese-Roediger-McDermott paradigm than negative affect (Storbeck & Clore, 2005). The simple concept of attention used in the simulations (i.e., as selection for approach or avoidance actions) thus probably needs to be broadened to domains of functioning that developed later in evolution to cover the full range of affective modulation phenomena.

It is very likely that mutual inhibition, and the ensuing competition, is an architectural feature of most levels in the nervous system. The neural oscillations, which according to our hypothesis are responsible for the affective modulation of attentional switching, present an opportunity for affective modulation at all these levels. They may provide a suitable vehicle for propagating modulatory effects through the nervous system. Recently, Gregoriou, Gotts, Zhou, and Desimone (2009), for instance, observed
long-range coupling between prefrontal and visual cortices of high-frequency gamma oscillations in attentional tasks. In a similar vein, neural oscillations can tune many different levels of processing. The findings in the low-level switching task (i.e., in Experiment 1), and with the switching from a dominant spatial bias (i.e., in Experiment 2) may only be at one end of a broad range of tasks subject to affective modulation.

Attentional engagement and disengagement are complementary processes, for which, in our simulations at least, different mechanisms have evolved. Attentional capture was implemented by the genetic algorithm in the shape of biased competition, and attentional switching as the escape from this competition in the troughs of an oscillation. These mechanisms, however, only address the process of how priority is given, but do not tell us much about what gets priority. The simulations also suggested an answer to the latter question in the form of affect, which can also be accounted for in evolutionary terms. According to Johnson (2003), positive and negative affect are 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). In the course of the simulated evolution, fitness-enhancing stimuli (i.e., food) elicited approach behavior and high flexibility, whereas fitness-reducing stimuli (i.e., predators) led to avoidance and less distractibility.

The close evolutionary relationship between attention and emotion suggests that both attentional engagement and disengagement are influenced by affect. Affective stimuli may be privileged in capturing attention, but they may also increase or reduce the readiness for switching to other stimuli. Although we also plan experiments on the mediation by neural oscillations, this study obtained evidence supporting the affective modulation of attentional switching only on a behavioral level. The convergence of simulation and human experimental results strengthens the claim that the facilitation of switching attention by positive affect and the locking of attention by negative affect has evolved early, not only in virtual, but also in biological evolution.