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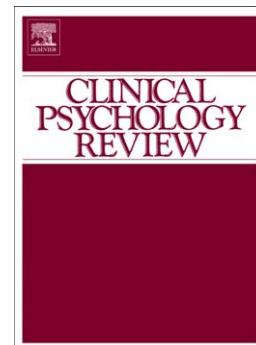
# Accepted Manuscript

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**Selective Attention to Threat versus Reward:**

**Meta-analysis and Neural-Network Modeling of the Dot-Probe Task**

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**Abstract**

Two decades of research conducted to date has examined selective visual attention to threat and reward stimuli as a function of individual differences in anxiety using the dot-probe task. The present study tests a connectionist neural-network model of meta-analytic and key individual study results derived from this literature. Attentional bias for threatening and reward-related stimuli is accounted for by connectionist model implementation of the following clinical psychology and affective neuroscience principles: 1) affective learning and temperament, 2) state and trait anxiety, 3) intensity appraisal, 4) affective chronometry, 5) attentional control, and 6) selective attention training. Theoretical implications for the study of mood and anxiety disorders are discussed.

**Selective Attention to Threat versus Reward:**

**Meta-analysis and Neural-Network Modeling of the Dot-Probe Task**

Theoretical constructs and research methodologies derived from cognitive psychology figure prominently in current emotion research, including investigations into the nature and function of anxiety. For example, cognitive researchers have been studying how individuals visually attend to threatening stimuli, and how between-subject variability in the functioning of attentional systems may correlate with individual differences in anxiety-related traits and disorders (e.g., Williams, Watts, MacLeod, & Matthews, 1997).

Evolutionary models of emotion and attention hypothesize that nature may have programmed the visual-attention system to attend selectively to stimuli of biological significance, including both to cues of possible impending threat (e.g., predators), on the one hand, and to cues of potential reinforcement-reward value (e.g., food, mates), on the other (e.g., LeDoux, 1996; Panksepp, 1998; Rolls, 1999). Attentional mechanisms procuring the rapid detection of sources of potential environmental threat are therefore presumed to afford an obvious survival-facilitating mechanism (A. Mathews & Mackintosh, 1998; A. Mathews, Mackintosh, & Fulcher, 1997; Mogg & Bradley, 1998). However, an equally integral attentional function to the biological fitness of organisms is to orient toward stimuli of potential reward-value in their environments (Panksepp, 1998; Rolls, 1999).

It may be that reward- and threat-detection are performed by distinct attentional systems [1]. Specifically, threat detection attentional mechanisms may represent secondary *interrupt* programs that continuously perform a background analysis of stimuli regarding their likelihood of representing a source of danger, attaining foreground and conscious significance only to the extent that this analysis results in the detection of relatively significant sources of danger (e.g., LeDoux, 1996). Otherwise, the default and primary orientation of attention may be toward reward-relevant stimuli. Thus threat-detection would seem adaptive when operative in the presence of stimuli signifying veritable danger, but maladaptive when consistently interfering with reward-directed behavioural engagement (e.g., such as when reliably 'misfiring', coding

objectively non-threatening stimuli as sources of threat; e.g., A. Mathews & MacLeod, 2005; Williams et al.,

1997). Distinguishing between reward- and threat-detection in this way also shows how the deficient

allocation of attentional resources toward positive-reward stimuli, independent of anxious or fear-related

interference, may represent a distinct form of abnormal emotional information processing, perhaps uniquely

underlying behavioural manifestations of apathy, anhedonia, and clinical depression  (e.g., Keedwell,

Andrew, Williams, Brammer, & Phillips, 2005; Watson, 2005).

*The Dot-Probe Task: Methodology*

The hypothesis that selective attention to threatening stimuli plays a role in anxiety has been the

subject of intensive research investigation in a number of recent studies using a visual probe-detection task

originally developed by Posner and colleagues (Posner, Snyder, & Davidson, 1980), commonly referred to

in the clinical psychology literature as the '*dot-probe task*'. In the dot-probe task, two words, facial

expressions, or pictures that vary in emotional significance (threat vs. neutral, or positive vs. neutral) are

simultaneously presented to participants in different locations of a computer monitor (typically top vs.

bottom or left vs. right), after which a neutral object (the 'probe') appears in the space previously occupied

by one of the two words, faces, or pictures. Participants are instructed to press a response button

immediately upon perceiving the probe, and their reaction time is recorded. A methodological assumption

of this task is that participants' reaction time will vary across trials partly as a function of the stimulus to

which they were attending at probe onset. Specifically, participants are thought to be faster to detect probes

appearing in the location of stimuli that they were viewing at the time of probe onset, relative to probes

replacing stimuli in an unattended visual field, because of the additional time required to shift one's

attention toward the location of the probe in the latter condition (see Bradley, Mogg, & Millar, 2000 for

empirical justification). Figure 1 illustrates these processes in representations of three facial dot-probe-task

trial conditions (A, B, C). From Figure 1 several ways in which individuals with high anxiety (HA) and low

anxiety (LA) might differ with respect to their selective attentional processing of threat cues are readily

discernible, and one of the tasks of the present review is to evaluate these differing hypotheses about dot-probe task performance in HA and LA individuals, as detailed below.

The seminal finding of MacLeod, Mathews, and Tata (1986) that adults with HA were faster to detect probes that replaced threatening words relative to neutral words, whereas this effect was not observed in LA adults, has since been replicated in numerous experiments (previous reviews by Bar-Haim, Lamy, Pergamin, Bakermans-Kranenburg, & Ijzendoom, 2007; Bögels & Mansell, 2004; Mogg & Bradley, 2005; Williams et al., 1997). Moreover, the dot-probe methodology has since been adapted in a now substantive literature as a means of testing increasingly sophisticated theoretical hypotheses about individual differences in selective attentional processing of threatening stimuli and its bearing on an understanding of anxiety and depression. However, an integrative, computational-mechanistic, and biologically-grounded account of selective attentional processing of threatening and reward stimuli as a function of anxiety and depression on this task has not yet been advanced. In this regard, a model that could help resolve the differing conceptualizations about performance in this task by HA and LA individuals (i.e., between Conditions A, B, and C in Figure 1) would be particularly helpful.

*Connectionist Modeling and Amygdala Functioning in Anxiety*

Accordingly, the present work develops and tests a connectionist (neural-network) model of individual-differences in information-processing on the dot-probe task as a function of anxiety. In brief, connectionism provides a theoretical and computational framework for modeling the information-processing parameters underlying the performance of both simple and complex psychological tasks, and may provide a basis for a formal understanding of complex information-processing phenomena of clear relevance to clinical psychology (e.g., Caspar, Rothenfluh, & Segal, 1992; Siegle, 2001). Indeed several theorists have recently considered ways in which connectionist principles might model attentional mechanisms associated with anxiety and negative affect (e.g., G Mathews & Harley, 1996; A. Mathews et al., 1997; Siegle, 2001;

Williams & Oaksford, 1992), although none of these previous treatises have directly modeled the type of selective attentional-processing hypothetically involved in performance of the probe-detection task.

A particular theoretical advantage of connectionist modeling is that it provides a framework for integrating cognitive and neurobiological perspectives regarding the information-processing underlying psychological task-related behavior. This integration is possible because connectionist models capture certain fundamental principles of neural systems (for overview see McLeod, Plunkett, & Rolls, 1998; O'Reilly & Munakata, 2000). A movement toward integrating neural and cognitive processes may be particularly justified, in the case of the probe-detection task and anxiety research, on the basis that a number of studies have identified differences in the neural response to threatening versus non-threatening visual stimuli within and between individuals varying in anxiety levels. Specifically, neuroimaging research has uncovered functional circuits in the human central nervous system that appear to be uniquely devoted to the task of rapidly encoding the presence of threatening environmental stimuli, and that processing in these neural circuits correlates with individual differences in anxiety levels. A robust finding within this literature is that neural pathways linking early stages of processing within the thalamus with response in the amygdala partially mediate the rapid identification of environmental sources of potential threat in humans (recent reviews by: Phelps, 2006; Shinnick-Gallagher, Pitkanen, Shekhar, & Cahill, 2003; Vuilleumier & Pourtois, 2007; Zald, 2003). For example, neuroimaging studies have consistently shown that the human amygdala responds more strongly to threatening than to neutral faces and complex scenes (Murphy, Nimmo-Smith, & Lawrence, 2003; Phan, Wager, Taylor, & Liberzon, 2002) and words (e.g., Kiehl, Smith, Mendrek, Forster, Hare, & Liddle, 1998; Maddock, Garrett, & Buonocore, 2003; Tabert et al., 2001), all of the stimuli thus far studied within the dot-probe task. Moreover, two recent neuroimaging studies confirm the involvement of the amygdala in the processing of threatening stimuli as presented specifically within the context of the dot-probe task (Armony & Dolan, 2002; Monk et al., 2004; see also Amin, Constable, & Canli, 2004). Furthermore, although it is beyond the scope of this article to review these neuroimaging literatures

in detail, later sections of this article will demonstrate that many of the parameters that have been found to

characterize and modulate the form of the human amygdala response to visual threat stimuli, as measured

by functional neuroimaging, bear resemblance to those that have been found to moderate attentional

biases as measured by reaction time on the dot-probe task. Accordingly, differences in amygdala

functioning between high versus low anxiety individuals represent a plausible neural-mechanism for partly

explaining individual differences in selective attentional behaviour for threat on the dot-probe task.

Specifically, increased amygdala responsiveness to threat stimuli, along with its associated functional

outputs, has been implicated. These outputs include modulation of representations in areas known to be

involved in visual attention, such as anterior cingulate, medial and lateral prefrontal, and occipital cortices

(e.g., fusiform gyrus; see Vuilleumier & Pourtois, 2007, and Zald, 2003, for reviews).

*The Present Work*

Accordingly, in ensuing sections of this article, we present a neural network model of selective

attentional processing of threatening and reward-related stimuli as a function of individual differences in

anxiety. The modeling data demonstrate that attentional bias for threatening and reward-related stimuli can

be accounted for by a limited number of theoretical principles, each derived from mainstream clinical

psychology and affective neuroscience literature: 1) affective learning and temperament, 2) anxiety state

and trait effects, 3) appraisal of stimulus intensity, 4) 'affective chronometry', 5) attentional control, and 6)

selective attention training. Putative neural mechanisms underlying these effects within the present model

focus on responses in a threat-detection module that is hypothesized to represent activity within the

amygdala to the visual presentation of threat stimuli. The functional output of this model is proposed to

modulate areas involved generally in visual attention and motor response. A summary literature review of

the theoretical significance of each theoretical construct is provided below, followed by elucidation of the

connectionist model implementation of each of these principles. Hypothesized effects are compared with

obtained-results from the connectionist model, and the latter in turn evaluated against meta-analytically

summarized results or key individual-study empirical data derived from the dot-probe task literature.

*General Meta-analytic Methodology*

To ensure the reliability of the results modeled with the present neural-network architecture, meta-

analyses were conducted to quantitatively specify the magnitude of group differences in attentional bias

scores for threatening relative to neutral stimuli, and the degree to which attentional biases are moderated

by experimentally-defined variables of theoretical significance, where sufficient data were available (see

also Bar-Heim et al., 2007). To the best of the authors' knowledge, all English-written published articles up

to August 1, 2006 that used the dot-probe task, and compared selective attention for threatening relative to

neutral stimuli between HA and LA adults, or anxiety-disordered versus non-patient samples, have been

included in this review. The study inclusion and exclusion criteria are discussed in Appendix A.

Attentional bias scores (ABSs, see MacLeod & Mathews, 1988; MacLeod et al., 1986) were obtained

directly from the articles or were calculated from the mean reaction times reported for various dot-probe

trial conditions in the studies cited. In the latter case, ABSs were computed as the difference between the

reaction times to probes occurring in different versus the same location as threat stimuli, given by the

formula: *{ABS = [(RT|LP + LT|RP) – (RT|RP + LT|LP)]/2}*, where *R* = "Right", *L* = "Left", *T* = "Threat", and *P*

= "Probe". Positive ABSs therefore reflect selective attention toward threat cues, whereas negative ABSs

reflect attention away from such stimuli (MacLeod & Mathews, 1988; MacLeod et al., 1986).

Calculation of the ABS averaged across studies afforded an intrinsic measure of effect size.

Specifically, if ABSs average to zero across various independent studies, this indicates that any significant

effects found for individual studies are unlikely to have been reliable. Calculation of the ABS as a measure

of effect size was opted for over traditional meta-analytic statistics because means and standard

deviations, or otherwise appropriate *t* and *F* statistics unfortunately were infrequently adequately-specified

for the ABS in the studies examined, and were generally not available from the corresponding authors' of

the various studies upon request via electronic mail. However, Bar-Heim et al. (2007) opted to take that more traditional approach and the reader is referred to their article in case of interest in these analyses.

## *General Connectionist Model Methodology*

*Network Architecture*

The basic network architecture is illustrated in Figure 2. The model was organized into two feed-forward pathways that correspond to the side of the screen visual information was analogously presented, and input, hidden, and output layers that encoded features relevant to dot-probe trials as depicted in Figure 1. Briefly, the input nodes encode the presence versus absence of threatening, neutral, and positive-reward stimuli, the hidden layer establishes an internal, distributed, and investigator control-free (i.e., model-emergent) representation of these same stimuli, and a threat-detection module, also composed of input units, simulated the activity of the amygdala in this model. Note that the amygdala units were connected directly with the output units rather than via the hidden units as was the case with the other input nodes, which was intended to be consistent with a direct anatomical route for fear-related encoding, as outlined by LeDoux (1996). Finally, the output layer was comprised of two units conceptualized to represent the networks' current selective attentional focus. Specifically, these nodes encode whether the network was differentially 'attending' to the left or right of its visual-attentional field [2]. Accordingly, note that this connectionist model tests the effect on visual attention of a direct modulation of processing of visual input by a threat-detection module, putatively representing the activity of the amygdala. The selectivity in attention evident at output was quantified as the difference between output activations measured from the two respective output nodes. A strength of the simplicity inherent in this model architecture is that it makes readily transparent, in turn, the analysis and understanding of its mechanistic properties, as defined by the model training and testing parameters described below.

*Network Training Methods*

Six different input patterns were used during training, corresponding to teaching the network to 'attend' toward left and right positive, neutral, and threatening stimuli, respectively, when presented individually. In other words, training patterns were composed of the activation of a single input node, and the activation of a single output node corresponding to the same screen-side (left or right) of the input stimulus. This regimen reflected our assumption that, when presented with a single stimulus to one side of one's visual field, the normal human visual process would entail the orientation of attention toward the stimulus (in other words, we assume that the onset of new stimuli capture visual attention and information-processing resources). It is important therefore to note that the network was not trained to "prefer" to look towards any one type of stimulus over another. Rather all input stimuli were presented singly during training, and in each case the network was taught to attend toward the stimulus. The basic training parameters are discussed in Appendix B. In brief, it is noteworthy that since the network's training involved responding to singular stimuli only, the network was therefore *not* trained on the probe-detection task itself.

*Network Testing Methods & Preliminary Testing*

Networks were tested using simulated probe-detection task trials that tested the network's 'attention' when conflicting stimuli (such as threatening vs. neutral) were simultaneously presented to conflicting visual fields (left vs. right). In the case of threatening versus neutral trials, there were two combinations of probe-detection trials: left-neutral and right-threat, and left-threat and right-neutral; the same was true of pairings of positive-reward and neutral stimuli. Analogues of ABSs for the connectionist simulation were modeled as the output activation of the node corresponding to the location of emotional stimuli minus the output activation of the node corresponding to the location of neutral stimuli, multiplied by 100. Note consequently that this score has the same properties as the ABS: positive values reflect attention toward emotional relative to neutral stimuli, and negative values reflect attention away from emotional relative to neutral stimuli [3].

Following training, the connection weights emerging between the amygdala input units and the output units were reset to +1.0 for the same side output unit, and −1.0 for the opposite side output unit (indicated in Figure 2 by the positive [+] and negative [-] signs depicted adjacently to the respective connections). This was performed because these connections were not purposefully trained (i.e., the teaching patterns did not include their activation, noted above). The threat-module (amygdala) connections are assumed instead to be an intrinsic property of the model and of human information processing of threat stimuli, whether innate or universally learned, as proposed by (LeDoux, 1996). The value of one was chosen purely for computational simplicity.

Before implementing specific tests of hypotheses about selective attentional processing of threat and reward stimuli, preliminary testing was conducted to insure adequate performance of the model for the training patterns. Ten replications of the network were tested, with training epochs composed of an equal number of presentations of each of the six training input patterns. Averaging across the ten replications, it was verified that no significant differences were observed in correct output-node activation between any possible combination of similar paired training patterns when presented singly. Moreover, no significant differences in ABSs emerge following this procedure when threat or reward stimuli are presented in combination with neutral stimuli to opposite sides of the model following this general training scheme. Therefore, differences in attentional bias that *do* emerge, in theoretically-congruent ways, can be causally attributed to the additional parameters that are specified within revised model training and testing schemes. Such emergent patterns are now discussed.

<center>**Empirical Hypotheses and Connectionist Model Simulations**</center>

*Hypothesis & Simulation I: Effect of Selective Attention to Threat Covarying with Trait-Anxiety Level at 500 ms may be Mediated by Differential Amygdala Responsiveness to Threat*

Figure 3 illustrates the results of a meta-analysis of probe-detection task ABSs calculated for threat relative to neutral stimuli separately for the HA and LA groups for word, face, and picture stimuli when

presented for 500-ms, the modal presentation duration utilized in probe-detection task studies of HA and LA participants. In Figure 3, ABSs are averaged across all studies reported in the published literature to date (citations are listed in the Figure note). Consistent with predictions, the HA population demonstrates selective attentional biases *toward* threatening stimuli, whereas the LA population demonstrates selective attentional biases *away* from threatening stimuli, although the effect is stronger for HA individuals [4].

To identify the causal mechanisms underlying this effect, one can begin by identifying factors that differentiate the HA and LA groups other than self-reported anxiety levels *per se* [5]. One such putative mechanism, overviewed in the introduction, is the amygdala response to visual threat. Indeed a robust finding in the neuroimaging literature is that individual, group, and clinical differences in anxiety correlate positively with response to threatening relative to neutral stimuli in the amygdala (e.g., Birbaumer et al., 1998; Canli, Zhao, Desmond, Kang, Gross, & Gabrieli, 2001; Fischer, Tillfors, Furmark, & Fredrikson, 2001; Rauch et al., 2000; Stein, Goldin, Sareen, Zorrilla, & Brown, 2002; Thomas et al., 2001). These results suggest that the predisposition toward experiencing anxiety, and to selectively attend toward threatening visual stimuli, may be mediated at the neurobiological level via a common information-processing mechanism. Specifically, increased amygdala responsiveness to threat stimuli, along with its associated functional outputs, has been implicated. The effect of between-participant and between-group variance in amygdala activation to threatening stimuli can be implemented in the connectionist model by inputting positive values of varying magnitude to the amygdala node corresponding to the side of the threat stimulus. Reference to Figure 2 illustrates that the effect of this manipulation is to increase the activation of attentional outputs corresponding to the spatial location of threat, and decrease likewise the activation of attentional outputs corresponding to the location of neutral stimuli.

Reference to Figure 3, however, illustrates that LA individuals, on average, do not simply attend less selectively toward threat sources relative to neutral stimulus sources, in comparison with HA individuals, but in fact may attend *away* from sources of threat or, equivalently, toward neutral or less threatening cues.

Although this effect could be modeled by inputting negative values to the amygdala nodes in the connectionist network, the input of negative neuronal activation values of course would not be biologically plausible.

In order to capture the effect of attentional avoidance of threat in LA individuals then, we believe that it is necessary to reconsider the idea that a plausible primary function of selective attentional behavior, as discussed in the introduction, involves the orientation of attention toward biologically more 'positive' stimuli, such as those of potential reward- or reinforcement-value, examples being food, other material resources, or viable mates (Panksepp, 1998; Rolls, 1999). Inline, threat-detection mechanisms may instead play an interrupt-program role, allocating attention away from more positive stimuli and toward threat sources only when these sources are appraised as being a 'true-enough' threat. In order to implement attentional preferences toward more positive stimuli in the connectionist network, one can give the network more experience during training with attending toward positive and neutral relative to threatening information, when presented singularly. Specifically, when the extent of training for different types of stimuli is not forced to be equivalent, the competition for attentional resources at output between different types of stimuli results in the stimulus that has been more strongly trained winning at output, directly as a function of the differential ratio of training trials inputted for the respective stimulus types (see Figure 4 Condition A for illustration). Moreover differential experience with neutral relative to threatening stimuli during model training intuitively corresponds with the proportion to which individuals are exposed to these different stimuli, on average, during early development and throughout life. However, input activation to the amygdala nodes on the same-side of the treat-stimulus, if sufficiently strong, may reverse this process in favor of selective attention toward threat (see Figure 4 Condition B for illustration).

In order to implement these effects in the current model, a 2:1 ratio of training of neutral relative to threat stimuli was used, initially an arbitrary starting value chosen for illustration (the effect of varying this parameter is tested in *Hypothesis & Simulation II)*. The corresponding amygdala input value necessary to

achieve an ABS between 0 and 5 was then determined which, in reference to Figure 3, plausibly

approximates the ABS of an individual with average anxiety (i.e., at the median [50th percentile] level of

anxiety). This represented a natural starting point given that the anxiety levels of HA and LA groups both

deviate from the population median anxiety level, and their respective ABSs border a low-positive ABS,

indicating a relative lack of selective attention between the threat and neutral stimulus. This hypothetical

50th percentile amygdala input value was determined to be ~ .65 (Network ABS = 14 = 1.4 ms) for

threatening relative to neutral stimuli when the meta-analytic results for word, face, and picture stimuli are

averaged across stimulus type (see Figure 5 for these averaged results [gray bars]; Figure 5 values

represent the mean of those presented in Figure 3 separately for the HA and LA groups after weighting by

the sample size of studies using each stimulus type).

The value of the amygdala node best fitting the results of the empirical data of LA and HA participants

depicted in Figure 5 was then determined. In order to achieve this, an added constraint was implemented

that these values deviated from .65 by a common unit in absolute value, which was subtracted from .65 in

the case of modeling the results of the LA group, and added to .65 in the case of modeling the results of the

HA group. This constraint was implemented on the basis that each of the LA and HA groups differed from

the population median anxiety level on the STAI-T (see Appendix A). This common unit of deviation was

determined to be .25, and therefore the amygdala response to threat in the LA group was inputted as .40,

whereas the amygdala response to threat in the HA group was inputted as .90. Effectively, *this procedure is*

*analogous to a greater amygdala response in the HA model relative to the LA model despite each model*

*being presented with objectively the same threat-relevant stimulus,* which is consistent with the results of

neuroimaging studies as cited above. Thus the threat-relevance or threat-intensity of stimuli in this model is

determined in the 'eye of the beholder', in relation to the stimulus, rather than derived entirely from the

objective features of the stimulus itself.

The ABSs calculated for the connectionist model with these differing amygdala-node inputs are also illustrated in Figure 5 (black bars) to facilitate comparison with the meta-analytic data. It will be noted that the pattern of results for the connectionist model featured in Figure 5 bear significant resemblance to those of the meta-analyzed empirical data also presented in the figure. Consequently, one interpretation is that increased responsiveness to visual threat stimuli in HA individuals within a threat-detection module common to both HA and LA individuals, putatively involving the amygdala, may mediate the HA individual's increased behavioral selective-attentiveness to the threat stimuli relative to LA individuals, as measured by the dot-probe task [6]. In brief, this effect may index group differences in trait anxiety, state anxiety, or both trait and state anxiety [7].

*Hypothesis & Simulation II: Effect of Selective Attention to Threat Covarying with Participant Anxiety Level May be Moderated by Degree of Threat Exposure During Development*

The *Hypothesis & Simulation I* section demonstrated that, within the present connectionist network architecture, differences in the magnitude with which the amygdala responds to threat stimuli can account for differences in selective attentional biases for threat stimuli between HA and LA individuals, given the same degree of exposure to threatening information during development. Given the equivalent degree of training in these models, the effect of the amygdala response seems most appropriately attributed to inherent or inborn differences between HA and LA individuals in the former simulations, such as genetic differences. Thus, although the present model does not explicitly represent any genetic information, the idea is that, given these effects do not emerge as a result of differential training (analogous to 'learning' or 'previous experience' in connectionist modeling), this effect must be assumed to be driven by an innate factors such as genetic variation. For example, researchers have determined that individuals with one or more short allele(s) at the 5-HTTLPR region of the human serotonin transporter gene (SLC6A4) are at increased risk for anxiety and depression as adults, and show increased amygdala responsiveness to the

visual presentation of threatening facial expressions (Hariri et al., 2002, 2005; Heinz et al., 2005; Pezawas et al., 2005; see also Iidaka et al., 2005).

However, whereas a certain proportion of between-individual variance in anxiety symptoms seems appropriately attributed to genetically-prescribed traits, the vulnerability of other individuals to develop anxiety symptoms may be largely determined by the extent to which they were exposed to threatening stimuli during cognitive development. Specifically, research incontrovertibly reveals that individuals who have been exposed to chronically threatening environments, such as to repetitive emotional, physical, and/or sexual abuse during childhood development, exhibit a higher degree of anxiety symptoms, psychiatric disorders, and various abnormalities in brain processing circuits involved in the emotional appraisal and response to threatening events (see Cicchetti & Toth, 2005). Additionally, Pollak and Tolley-Schell (2003) demonstrated that physically-abused children showed increased vigilance to and delayed disengagement from angry faces relative to happy faces in a variant of the standard dot-probe paradigm (the Exogenous Cueing-Task). Moreover, Koster and colleagues (Koster, Crombex, Van Damme, Verschuere, & De Houwer, 2004) demonstrated that selective attentional biases toward inherently non-threatening cues (colour bars) could be conditioned within a single experimental session via the pairing of their presentation with the presentation of an unconditioned aversive stimulus (white noise). The Koster et al. experiment therefore causally demonstrated that repeated pairing of a previously non-threatening stimulus with an aversive experience motivated subsequent selective attention toward the stimulus within a dot-probe stimulus presentational-format. Although not explicitly discussed by Koster and colleagues', their findings are congruent with the hypothesis that repetitive exposure to threatening stimuli (such as in children's rearing environments) might prompt future anxiety-related selective processing of threat-stimuli. This association can be simulated within the present connectionist model.

Specifically, the effects of variability in the extent to which individuals have been exposed to threatening environments during development can be encapsulated within the present connectionist neural-

network model by varying the proportion with which models are exposed to threatening versus neutral stimuli during training. In this case, training is intended to be analogous to the life-experience-mediated learning of various models during development. [8] To illustrate this effect, models were trained with successively increasing proportions of non-threatening relative to threatening stimuli, via the following forms (non-threatening : threatening): 3:1 (*lowest threat exposure*), 2:1 (*low threat exposure* – note that these are the values used for the networks tested in the *Hypothesis & Simulation I* section), and 1:1 (*high threat exposure*) [9].

Figure 6 illustrates the results of models with the varying proportional-training experience with threatening stimuli just noted, and tested with low, average, and high threat-module amygdala-responsiveness to threat, as defined in the *Hypothesis & Simulation I* section (.40, .65, and .90, respectively). This figure demonstrates a graded sum of two main effects: proportional experience with threat during developmental learning and amygdala responsiveness to threat. Models with limited exposure to threatening stimuli during training, and a low amygdala responsiveness to threat, exhibit the least vigilance for (or most avoidance of) threatening relative to non-threatening stimuli. In contrast, models that were highly exposed to threatening stimuli during training, and were also engineered to have high dispositional amygdala responsiveness to threat, exhibited the most vigilance for threatening relative to non-threatening stimuli.

These findings may have significant ramifications for cognitive psychology theories of emotion. Specifically, these data suggest that a greater frequency of exposure to certain types of stimuli during developmental learning may prompt a greater degree of attention to these stimuli subsequently, not unlike the association between repetitive exposure to stimuli and their subsequent deemed likeability (i.e., the mere-exposure effect; Bornstein, 1989; Zajonc, 1968). Unfortunately however, few studies have assessed the outcome of long-term exposure to threatening and aversive experiences on attentional processing for threat during development (for a recent exception see Taylor, Eisenberger, Saxbe, Lehman, & Lieberman,

2006). The present research therefore suggests that additional studies are needed to evaluate the effects of chronic stress-exposure during early learning on the development of selective-attention systems for threat.

*Hypothesis & Simulation III: Selective Attention to Threat May Covary with Stimulus Threat Intensity & Individual Differences in Threat Stimulus Appraisal*

The results of *Simulations I* and *II* indicate that differential response in the amygdala nodes of the present neural-network architecture represents an account of differential selective attention behavior for threat stimuli. A defensible and intuitive interpretation of these effects, if one considers that the amygdala-nodes represent the basis of the recognition of a threatening stimulus *as a threat* in this model, is that HA individuals view threatening stimuli as 'more threatening' than LA individuals (even if this appraisal mechanism may not always be consciously accessible). Accordingly, HA individuals are found to be more likely to attend toward these stimuli, thereby devoting a greater amount of their cognitive resources to threat processing, toward whatever end (e.g., defensive preparation, attempted coping, etc).

However, cognitive theorists have hypothesized that LA individuals and individuals with average levels of anxiety may be progressively more likely to orient toward threat cues as the objective threat-'*value*' or -'*intensity*' of the stimuli is increased (A. Mathews & Mackintosh, 1998; Mogg & Bradley, 1998). In other words, HA individuals may selectively attend to both objectively moderate and highly threatening stimuli, whereas LA individuals may selectively attend only to stimuli that signify a distinctly high threat-value. In these instances, the 'objective' threat-value of stimuli is operationally-defined by properties naturally inherent to the stimulus (e.g., facial morphing stimuli that can systematically alter angry or fearful expressional features in a way that objectively defines a measureable increase in their threat-intensity; Wilson & MacLeod, 2003). As outlined above, these individual difference hypotheses are predicated on evolutionary models of selective attention to threat, in considering that the ability to rapidly detect sources of potential environmental threat should represent a survival mechanism for *all* humans, rather than only for

those predisposed to anxiety (A. Mathews & Mackintosh, 1998; A. Mathews et al., 1997; Mogg & Bradley, 1998).

The results of a number of preliminary studies provide support for theoretical predictions that attentional bias depends on the threat intensity of stimuli (Mogg, McNemara et al., 2000; Wilson & MacLeod, 2003; Koster, Verschuere, Crombez, & Van Damme, 2004; Mogg et al., 2004). Although the results across these studies do exhibit a certain level of heterogeneity, the variability in this initial set of findings may be due, at least in part, to differences in both the threat intensity of the stimuli used and in the anxiety levels of participants across studies. Therefore in order to study the effects of stimulus threat-intensity within the present connectionist network, we simulated the results of Wilson and MacLeod (2003) as a methodologically-rigorous exemplar of this emerging literature. Specifically, the effect of increasing the objective intensity of threat stimuli was implemented in the present connectionist network by increasing proportionately the response in the threat-module (amygdala nodes) of the network. That is, increasing activation values in the model reflects an increased threat-value of the stimulus encoded at the level of the amygdala nodes in the network. This procedure is motivated by well-replicated findings that the amygdala responds in a graded manner to experimentally-varied degrees of threat as depicted in faces (e.g., in the same way as was conducted in the Wilson and MacLeod study; Morris et al., 1996; Irwin et al., 1998).

In brief, activation for LA and HA networks were modeled against the ABSs found by Wilson and MacLeod (2003) for their LA and HA groups (see their Figure 2, p. 216). In brief, input values were subtracted from for the LA network and added to for the HA network in such a way as to simulate differential amygdala activation values in the two forms of the network, as was similarly conducted in *Simulation I*. Specifically, the low and moderate threat stimuli were activated in the HA network to the same degree as the moderate and high threat stimuli were activated in the LA network (0.2 and 0.9, respectively; with the moderate threat stimulus in the HA network entered as 0.90 to be consistent with the value used in *Simulation I*). The high threat stimulus was then inputted within the HA network with the value of 1.0, in

keeping with an upper limit for input activation as a constraint within the sigmoidal distribution, and in turn, the low threat stimulus was inputted within the LA network with the value of 0.0, in keeping with the lower limit of the sigmoidal distribution (i.e., a non-negative value). Figure 7 plots the results of Wilson and MacLeod and the network-simulated data, and reveals that a close approximation between the two data sets was found.

These findings, implemented via a method common to that used for *Simulation I*, consequently provide a biologically-grounded mechanistic account of previous conceptual proposals concerning the nature of attentional processing of threatening stimuli (A. Mathews & Mackintosh, 1998; A. Mathews et al., 1997; Mogg & Bradley, 1998). In brief, the connectionist model is consistent with attentional functioning being oriented toward the processing of non-threatening stimuli except under environmental circumstances where significant sources of threat exist, upon which attentional resources are allocated principally toward the threatening stimulus. High and low anxious individuals, however, are understood to differ with respect to what they perceive to constitute a threat-stimulus worthy enough of directing their attention toward; HA individual's may exhibit a lower objective threat-stimulus threshold for activating their amygdala, thereby resulting in their being more likely to attend toward stimuli as threats that a LA person might fail to take much notice of. In contrast, LA individuals may require the presence of an objectively-higher stimulus-threat intensity before their processing resources are prompted toward attending to its source.

*Hypothesis & Simulation IV: Selective Attention to Threat May Covary with Stimulus Exposure Duration & Indices of Affective Chronometry*

Davidson (1998; see also Davidson, 2002; Davidson et al., 2000) elucidated the concept of *affective chronometry* as a methodologically tractable explanatory mechanism for investigating individual differences in emotionality in cognitive-affective neuroscience. On this account indices of affective chronometry refer to "the temporal dynamics of emotional responding" (Davidson, 1998, p. 310). Davidson distinguishes between individual differences in: 1) emotional *thresholds*, which define a minimal level of stimulus intensity

required to activate a particular emotional behavior, 2) the *peak* or *amplitude* of an emotional response, which define between-subject variance in the maximum amplitude of an emotional response to a series of graded stimuli, or, if represented as a frequency distribution, the modal response, 3) the *rise time to peak*, defined as the rate at which individuals' emotional response systems rise to their maximum level of response, and finally, 4) *recovery time*, defined as the rate at which individuals' emotional response systems recover to their homeostatic baseline values following an emotion-stimulus perturbation. Although Davidson notes that each of these indices of affective chronometry are distinguishable conceptually, he acknowledges that "the general issue of the extent to which these different parameters are orthogonal or correlated features of emotional responding is an empirical question that has yet to be answered" (Davidson, 1998, p. 310).

Davidson's (1998) principles of affective chronometry appear to be relevant to the examination of the dot-probe task literature, as studies have observed ABSs to vary across distinctive presentation durations of the threat stimuli (see Bar-Heim et al., 2007). For example, HA individuals have not only displayed selective attentional biases for threat when presented for 500 ms, but also when the exposure duration is rapid enough to preclude their conscious perception of the stimuli, whereas HA individuals have less consistently demonstrated an attentive bias for threatening relative to neutral stimuli when stimuli are presented for a longer duration prior to probe onset (e.g., 1000 ms or longer). The results of our meta-analysis of these studies is presented in Figure 8 (references are listed in the figure note).

This initial pattern of experimental findings led cognitive theorists to hypothesize that the enhanced processing of threat cues associated with HA may be operative only for an interim span of time (Bradley et al., 1998; Mogg et al., 1995, 2000; Williams et al., 1997). During initial orienting phases of visual attention, HA individuals may be more predisposed to selectively attend to threatening relative to neutral stimuli than are LA individuals. However, at later more executively controlled phases of selective-attentional processing, HA and LA individuals may differ less in their tendency to selectively attend to threatening stimuli.

Consequently, the finding that selective attentional biases may rapidly habituate in HA individuals, and therefore vary not only as a function of the intensity or 'threat-value' of the stimuli but as also as a function of the stimulus presentation duration, suggest that enhanced threat detection may be sub-served by a *phasic* operating sensory system [10]. Within Davidson's (1998) affective chronometry taxonomy, HA individuals may thus exhibit not only a *lower threshold* and higher *peak-amplitude* for amygdala responsiveness to the visual presentation of threat stimuli (as in *Simulations I and IV*), but also a faster *rise time to peak*.

These effects can be modeled within the present connectionist architecture by engineering the amygdala response to stimuli to vary across time, a biologically-plausible effect. Specifically, the amygdala has been shown in some neuroimaging studies to respond to very briefly-presented threat-related facial expressions (e.g., Morris et al., 1998; Morris, Öhman, & Dolan, 1999; Whalen et al., 1998; Phillips et al., 2004), even if the question of whether this structure responds to truly unconscious presentations of threatening stimuli remains presently undecided (e.g., Phillips et al., 2004). Studies have also shown that very rapid presentations of fearful facial expressions activate the amygdala more strongly in individuals high rather than low in anxiety (e.g., in subjects with posttraumatic stress disorder; Rauch et al., 2000). Additionally, although the amygdala responds reliably to the onset of threatening stimuli, it appears to respond phasically, that is, it rapidly habituates firing both across repeated trials and temporally over the duration of longer single trials (Brieter et al., 1996; see Zald, 2003, for review).

In order to model a time-varying (phasic) response in the amygdala, gamma distributed inputs to the amygdala were modeled (see Appendix C; Carter, Neufeld, and Benn [1998] discuss the clinical-psychological significance of the gamma distribution for modeling cognitive information processing phenomena). Specifically, amygdala activation was tested to be faster (shorter *rise time to peak*) and more pronounced (higher *peak-amplitude* [mode of the distribution]) in the network analogue of HA relative to LA individuals by varying the shape parameter *k* of the gamma distribution (see Figure 9 for illustration of the

effect of this manipulation). Note that in the case of the gamma distribution, *rise time to peak* and *peak-amplitude* are inherently non-orthogonal parameters. In addition, a higher tonic-metabolism at rest (i.e., in cases where no threat stimulus is present) was modeled for the HA network by the addition of constants to the gamma distributions.

The results of connectionist networks with varying gamma distributed inputs to the amygdala nodes of the networks, intended to reflect responses in HA and LA networks, were tested (please see Appendix C for parameters used in these simulations). The network results are contrasted with the meta-analytic empirical data for probe-detection studies in Figure 10 (after averaging the meta-analytic data across word, face, and picture types, as was conducted for *Hypothesis & Simulation I*). From Figure 10 it is clear that the network with amygdala nodes incorporating a gamma-distributed more rapid *rise time to peak*, which also inherently constitutes the network with the greater *peak-amplitude* response within the present gamma-distributed system, demonstrates a greater attentional bias to briefly presented visual threat stimuli than does the network with the lower *rise time to peak*. However, these differences between the networks dissipate to their respective baseline values (the constants) of a relative absence of attentional bias over time. Importantly, a comparison of the results of the connectionist networks with the meta-analytic results of previous empirical studies, via Figure 10, suggests an identifiable concurrence between the two sets of data.

It is notable, however, that at the longer 1000 ms duration, the connectionist model predicts a somewhat higher ABS for HA individuals than has been identified in the behavioural results, and a somewhat lower ABS than has been found for LA individuals. Certainly the form of the gamma-distribution does not predict a *vigilance followed by avoidance* pattern, as this distribution does not result in a negative value (see Figure 9). However, several recent studies have found that HA individuals exhibit not only less vigilance but *avoidance* of threat at especially long presentation durations (Hermans et al., 1999; Koster, Verschuere, Crombez, & Van Damme, 2005; Luecken, Tartaro, & Appelhans, 2004; Rohner, 2002; Tolin,

Lohr, Lee, & Sawchuk, 1999; Rinck & Becker, 2006). The vigilance-avoidance pattern may be due in part to

compensatory attentional mechanisms that come into effect at later presentation durations to correct for

attentional biases. Modeling of the vigilance-avoidance effect is considered further below in the *Hypothesis*

*& Demonstration VI* section.

In summary, these simulation results suggest that the present connectionist network can capture not

only the effects of individual and group differences in anxiety level and stimulus threat intensity on

selective-attentional processing of threat, but also how these effects may vary non-linearly with time. The

results strongly support the relevance of Davidson's (1998) affective chronometry framework to the study of

selective attentional processing of threat, but suggest the possibility that when formally implemented in

mathematical terms, parameters specifying the concepts of *emotional response peak* or *amplitude, rise*

*time to peak*, and *recovery time* may be found to be integrally-related constructs [11].

*Hypothesis & Demonstration V: Selective Attention to Threat May Be Modulated by Attentional Control*

A question of emerging theoretical significance in selective attentional processing of threat research

has been whether attentional biases for threat in HA individuals principally reflect an orienting bias toward

threat, versus an inability to disengage attentional resources away from threat once allocated, or dually

reflect the operation of each of these sub-processes to a certain degree (see Figure 1; Derryberry & Reed,

2002; Koster, Crombez, Verschuere, & De Houwer, 2004; Yiend & Mathews, 2001). Indeed, it has long

been recognized that the ABS derived from the probe-detection task fails to distinguish between these two

potentially unique sub-processes of attentional functioning for threat. Studies that have presented stimuli at

very rapid and preconscious presentation durations, thereby presumably precluding the time necessary for

a significant amount of attentional shifting to occur, provide strong ground for hypothesizing the existence

of early attentional-orienting biases (Bradley et al., 1997; E. Fox, 2002; A. Mathews et al., 1996; Mogg &

Bradley, 1999b, 2002; Mogg et al., 1994, 1995, 1997). However, it may be that only those who also exhibit

deficiencies in attentional control will continue to exhibit a selective attentional bias toward processing

threat over longer presentation durations. For example, in accordance with this prediction, Derryberry and Reed (2002) showed that whereas HA individuals cumulatively revealed an early attentive bias at 200 ms in the exogenous cueing task (a task that involves presenting only a single emotional or neutral stimulus to the left or right of the screen), only HA individuals who also scored low in attentional control (measured by self-report) continued to exhibit selective attention toward threat stimuli at a 500 ms presentation duration.

Importantly, researchers have found that individual differences in attentional control in the context of attending to or away from threatening stimuli may be associated with a distinctive set of neural substrates in comparison with attentional orienting to threat. For example, A. Mathews et al. (2004) demonstrated that whereas individual differences in self-report psychometric measures of behavioral inhibition (an anxiety-related trait) correlated *negatively* with BOLD response in ventral anterior cingulate cortex (ACC) during visual processing of threat, individual differences in *Attentional Control Questionnaire* scores correlated *positively* with BOLD response in the ventral ACC. This finding suggests that ventral ACC functioning may partly underlie individual differences in the ability to consciously-volitionally direct attentional resources toward the performance of targeted goals when this goal entails *not* attending toward the threatening nature of a stimulus (see also Most, Chun, Johnson, & Kiehl, 2006). The finding is also in accord with demonstrations of a functional dichotomy within ACC where emotional ("hot") cognitive-attentional processing is particularly associated with activation in ventral ACC, whereas non-emotional ("cold") cognitive processing is differentially associated with dorsal ACC activity (Bush, Luu, & Posner, 2000; Steele & Lawrie, 2004). Furthermore, Mathews et al.'s findings are consistent with those of Pezawas and colleagues' (2005) that amygdala activity during visual threat processing is positively correlated with ventral ACC activity whereas activity in dorsal ACC correlates negatively with amygdala activity. Furthermore, Bishop, Duncan, Brett, and Lawrence (2004) demonstrated that reduced ventral-ACC and left lateral-PFC activity in the context of a task requiring the direction of attention toward neutral stimuli in the presence of threatening distractors was associated with increasing participant-reported state-anxiety evoked during the

task. Bishop et al. interpreted their results as implying a greater need to recruit cognitive-control structures to maintain sufficient task-related performance in more state-anxious individuals (see also Bishop, Duncan, & Lawrence, 2004; Most et al., 2006). Indeed several studies have identified that conscious, goal-directed, and verbal processing of threat stimuli relative to passive viewing of the same stimuli decreases amygdala response and is associated with increased response in both lateral and medial frontal-lobe structures, the latter including medial prefrontal cortex and ACC (reviewed by Ochsner & Gross, 2005). Additionally, a reduced between-participant negative correlation between functional activity in the amygdala and regions of the medial frontal lobe (including ACC) correlates positively with increases in anxiety-related traits as assessed by self-report (Pezawas et al., 2005; see also Heinz et al., 2005).

This literature suggests that individual differences in attentional control may moderate selective attentional biases on the probe detection task, particularly when stimuli are presented for longer exposure durations. Indeed, the rapid response to threat stimuli in the amygdala is regarded as being key to the function of this structure as a "*fast* or *low-pass*" pre-analysis or filtering of stimuli along a dimension of 'behavioural-emotional relevance', perhaps particularly with respect to danger-threat value (LeDoux, 1996). In contrast, later executively-controlled phases of attention (or '*high-pass appraisals*', see Kalisch et al., 2006) presumably are influenced by first-pass fear-appraisals of stimulus relevance, although may minimize this influence when cognitive resources are applied specifically to this task. Thus high-pass appraisals may ultimately force different conclusions regarding the priority of further stimulus processing, overriding low-pass filtering, in order to be congruent with task-related goals (Cohen, Dunbar, & McClelland, 1990). The inability to inhibit low-pass fear-related processing when required as a means of achieving behavioral goals (e.g., sufficient performance in an experimental task) may be particularly distinctive of clinical-diagnostic manifestations of anxiety (Williams et al., 1997).

In the present connectionist model, output nodes are envisioned to reflect the differential activation of one's visual representational field immediately prior to probe onset, and therefore most appropriately are

construed as reflecting attentional orienting when stimulus presentation is fast. It should be noted however, that output activations at any point in time represent the consequence of non-linear processing occurring across time, such that processing at time *t* is most appropriately modeled as being partially determined not only by stimuli present at time *t* but also by processing occurring at time *t - 1.* Therefore at probe onset, information processing may reflect the ability to suppress amygdala activation to threat as a means of maintaining instructional-goal set, that is, effecting competition between the mental rule '*Scan for Threat & Attend To if Present'* (represented in the amygdala) and the mental rule '*React Only to Probe*' (possibly encoded and maintained in dorsal and ventral ACC and LPFC regions, as competition between the emotional and task-relevant signature value of various stimuli compete for attentional resources; Duncan & Owen, 2000). Plausibly performance of the rule *'React Only to Probe'* will depend directly on the degree to which attention has been preferentially drawn toward the threat stimulus initially at *t - 1* (i.e., the effect of the amygdala), but may also reflect an exterior process to amygdala activity, that is, the strength of processing centers to inhibit or 'disengage' from amygdala-threat processing upon presentation of the probe.

Related to this point, Luecken, Tartaro, and Appelhans (2004) observed that ABSs on the dot-probe task predicted self-reported emotion regulation behaviors, although not in the direction to which they predicted. Specifically, measures of anxiety were uncharacteristically associated with attention *away* from threat in their study when presented at 500 ms, as were negative emotion regulation behaviors (e.g., disengagement coping), although more anxious individuals were subsequently *more* likely to selectively attend toward subliminally-presented threat-stimuli (Luecken, Tartaro, & Appelhans, 2004). This effect may have been due to anxious individuals successfully attempting to disengage from sources of threat when presented for 500 ms, but unable to exert cognitive control over their disposition to attend toward threatening stimuli when presented at faster presentation durations. This would be predicted by the gamma distributions depicted in Figure 9.

In the present connectionist architecture, these effects can be implemented by instituting an attentional control module or high-pass appraisal mechanism that acts to minimize the influence of amygdala response (i.e., low-pass appraisals) over time. It is presumed within the present model that attentional control mechanisms would exert increasing influence with increasing presentation durations given that this psychological process, on the basis of its complexity relative to low-pass appraisal, may occur over a more prolonged time scale.

Figure 11 illustrates, for a high amygdala response, the outcome of two possible pathways through which attentional control mechanisms could conceivably modulate the outcome of responding in the amygdala. In the first case, attentional control may directly attenuate amygdala response. This input, if time-dependent, can be represented as the subtraction of two gamma distributions, the first representing response in the amygdala with a rapid *rise time to peak*, and the second representing emotional attentional-control responses inhibiting amygdala response (here effected by simple subtraction), for example as occurring in ACC, but exhibiting a slower *rise time to peak*. The effect of this inhibitory subtraction is demonstrated in Figure 12 [12]. It may be interesting to note that, given the non-overlap in time ($t$) over which these distributions exert their effects, an early amygdala-mediated threat-vigilance is found to incur a subsequent threat-avoidance over longer presentation durations. Indeed this model predicts a positive association between speed of *rise time to peak* (lower $k$) for threat-vigilance responsiveness and greater subsequent threat-avoidance responsiveness, provided a common distribution effecting emotional attentional-control behavior (see Figure 12). Notably, this pattern of effects can be construed as an explanation of the results of Luecken, Tartaro, and Appelhans (2004).

The hypothesis that a dynamic relation might exist between initial threat-vigilance and later threat-avoidance in the cognitive behaviour of individuals with anxiety disorders has until now been largely predicated on clinical observations and has historically proved difficult to demonstrate in the cognitive-psychology laboratory (e.g., Mogg, Bradley, de Bono, & Painter, 1997; Bradley, Mogg, Falla, & Hamilton,

1998; Williams et al., 1997). However, recent studies using temporally-continuous measures of selective attention, such as number of eye fixations across stimulus presentation (in comparison with the 'snap-shot' index of selective attention that is afforded by simply manipulating the duration of stimuli on the probe task and measuring reaction time to probes), have demonstrated that such a pattern indeed characterizes individuals with anxiety disorders provided the stimulus presentation is prolonged (Hermans et al., 1999; Kosteret al., 2005; Rohner, 2002; Tolin et al., 1999; Rinck & Becker, 2006). However a theoretical understanding of this often observed clinical phenomenon in formal information-processing terms has thus far proved enigmatic. In contrast, the present neural network provides one readily testable mathematical explanation of this phenomenon, which may warrant further empirical testing. Thus implementing this pattern of input response to the amygdala nodes of the HA network decreases the ABS it outputs at 1000 ms relative to the standard gamma distribution, more closely approximating the behavioural results of HA individuals at this presentation duration that were depicted previously in Figure 7.

A second pathway through which attentional control mechanisms could modulate the outcome of amygdala responding, depicted in Figure 11, is that attentional control may attenuate the effect of the amygdala at output (e.g., on occipital regions) by correcting discrepancies between the salience of representations within the two primary visual fields when probes are not present. This can be achieved in the present model either by increasing the activation of representations in fields with low cumulative input, or decreasing (inhibiting) representations in fields with high cumulative input prior to probe onset (see Cave & Batty, 2006, for relevant discussion). Importantly, these two case conceptualizations of the effects of attentional control are not mutually exclusive, and may interactively contribute to the role of ACC and dorsolateral PFC as attentional control mechanisms in the context of threat processing and emotion regulation (Ochsner & Gross, 2005). Accordingly, as working memory requirements increase, threat-related interference may decrease where attentional control is successfully employed (Pessoa, McKenna, Gutierrez, Ungerleider, 2002).

Figure 13 synthesizes the proposed interactive effects of three information-processing dimensions we hypothesize to be implicated in responding to threat-stimuli in HA vs LA individuals that are identified in Figure 11, our elaborated connectionist neural-network model. Testing of this model may provide an integrative-unified account of the processes proposed to underlie differences in dot-probe task performance in HA and LA individuals, as first described in Figure 1 (please see note to Figure 13 for outlining of specific hypotheses and results) [13].

*Hypothesis & Simulation VI: Selective Attention to Threat Can be Causally Induced and Terminated by Attentional Training*

Studies of the association between selective attentional biases favoring threat vigilance and anxiety-traits have almost exclusively been correlational, thereby precluding statements regarding the directional and causal status underlying their association. Accordingly, researchers have recently become interested in the extent to which causally-inducing vigilance toward versus away from threatening relative to neutral stimuli may affect self-reported anxiety (A. Mathews & MacLeod, 2002). In two studies using the probe-detection task (Harris & Menzies, 1998; MacLeod et al., 2002), researchers observed that attentional biases could be induced on subsequent test trials after training average-level anxious individuals either to orient toward or away from threat. Specifically, these researchers required participants to perform a probe task fixed such that probes repeatedly occurred in the place of either threatening or neutral words for two respective experimental groups, causing these individuals to selectively attend toward or away from threatening stimuli post-training. Moreover, MacLeod and colleagues observed that this training predicted self-reported distress levels in response to a subsequent difficult cognitive task (insolvable anagrams coupled with negative performance ratings). The finding that a straightforward adaptation of a simple experimental procedure such as participating in a dot-probe task could (at least temporarily) causally effect changes in an attentional process related to anxiety was theoretically important, and was thought possibly to be clinically-relevant to the development of future psychological interventions for anxiety disorders.

It is noteworthy that attentional training-effects can also be captured within the present connectionist model. To parallel this experimental training in the present connectionist modeling framework, networks were trained, following the regimen used for *Simulation I*, for an additional ten epochs of trials composed only of the simultaneous presentation of threatening and neutral stimulus pairs. For these additional training trials, networks were instructed to attend toward the source of threat. Figure 14 plots the effects of this training for three levels of amygdala activation before and after the additional 10 training epochs, corresponding in the above simulations to low anxious (0.4), average anxious (0.65), and high anxious (0.9) individuals. Figure 14 also plots the results of MacLeod et al.'s average-anxious participants pre- and post-training averaged across their Studies 1 and 2 for their *'attend threat'*-trained participants, and demonstrates that the pattern of findings for MacLeod et al.'s average-level anxious participants fall closely between the average- and low-anxiety network values. Note further that exactly the opposite results obtain if networks are trained to attend toward neutral stimuli, as would be expected (data not shown).

These connectionist network findings, consistent with MacLeod and colleagues' (2002) speculations, are therefore consistent with the assumption that a brief experimental training-intervention based on an adaptation of the probe-detection task may have the capacity to alter attentional behavior for threat in a significant way, and therefore that priming attention away from threat (or more properly, toward neutral information in the presence of weak threat information) may be a promising avenue for future anxiety-disorder treatment applications (e.g., Wells & Mathews, 1994). Specifically, priming individuals to attend toward neutral- or more positive-stimuli in the presence of threatening stimuli of fairly minor significance may promote positive approach-related behavior by decreasing unnecessary interference and distraction by threat-stimuli.

*Hypothesis VIII: Selective Attention for Reward-Reinforcement Stimuli Covaries with Participant Anxiety and Depression Levels*

Although the processing of threatening stimuli has thus far received greater theoretical and research attention in selective attention research, a number of recent studies have concurrently examined selective attention for positive relative to neutral stimuli (i.e., pleasant or reward-relevant stimuli, e.g., happy facial expressions) in addition to threatening versus neutral stimuli using the probe-detection task. These studies generally observed that LA individuals selectively attended toward positive relative to neutral stimuli, whereas this effect was less prominent and occasionally reversed in HA and depressed individuals (Bradley et al., 1997; 1998; 2000; E. Fox, 2002; Keogh, Dillon, Georgiou, & Hunt, 2001; Ioannou et al., 2004; Mogg & Bradley, 1999, but see Bradley et al., 1999). Figure 15 verifies that such effects are robust across studies via a meta-analysis of the ABSs of HA and LA individuals across these studies.

Interestingly, however, less has typically been made thus far of the theoretical significance of these findings in researcher's discourse than has been made of the threat-detection findings. In contrast, as discussed previously in our introduction, there are theoretical grounds to surmise that the principal role of selective attention systems is to orient toward sources of potential reward and reinforcement, with a secondary-system interrupting this primary attentional function only in the presence of detectable threats to the safety of the organism. Consequently, the observed lack of a *normal* biasing of attentional orientation toward positive and reward-reinforcement related stimuli likely has important theoretical and clinical significance of its own (e.g., McCabe & Gotlib, 1995).

Importantly, these effects can be encapsulated within the current connectionist model in two ways. One possibility particularly relevant to facial expression stimuli is that, in HA individuals, neutral faces may be processed as threatening, particularly when presented repeatedly within the context of the co-presentation of positive expressions; this has been documented in at least one neuroimaging study (Somerville et al., 2004). In this case, input to the amygdala nodes on the side of neutral relative to positive stimuli would result in directing attention away from positive stimuli and toward the neutral stimulus as a perceived potential source of threat.

A second alternative possibility is that HA individuals and depressed individuals may be exposed proportionally less on average to positive emotional stimuli during development, and accordingly differences in proportional training account for these effects, as presented and analyzed analogously in the *Hypothesis & Simulation II* section for degree of threat exposure. Specifically, LA and non-depressed individuals may be exposed to proportionally greater positive and rewarding experiences relative to neutral and threatening experiences during early development, in comparison with HA and depressed individuals, which may mediate the depleted motivation and lack of approach-directed behavioural engagement with the environment that seems particularly related to depression (e.g., Beevers & Bjorn, 2002). However, little research has investigated the frequency of positive early-life experiences as predictors of depression and attentional biases later in life, and this is therefore an important question for future study. In summary, implemented imbalances in network training regimens with respect to positive, neutral, and threatening stimuli reflect the assumption that an adaptive and fundamental function of attentional systems entails the orientation of cognitive resources toward the processing of environmental stimuli of greater potential reward- or reinforcement- value. As analogously demonstrated in *Simulation II* for exposure to threat stimuli, inadequate exposure to positive self- and social-focused experiences during development would result, within the present model, in positive stimuli having less motivational-value, intuitively typifying the hypothesized attentional stance of depressed individuals. This may provide a mechanistic information-processing based account of the lack of motivation, apathy, and low positive affect observed in individuals with unipolar mood disorders, particularly the melancholic subtype of major depression (American Psychiatric Association, 1994).

### General Discussion

The present research tested a neural network model of associations between individual and group-differences in anxiety and selective attentional processing of threatening and reward-related stimuli on the probe-detection task. The connectionist model simulated a number of theoretical principles derived from the

clinical psychology and affective neuroscience literatures. Specifically, the model provides a mechanism for testing the effects of dispositional traits (variability in amygdala responsiveness; *Hypothesis & Simulation I*) and affective learning and development (proportional training with threatening relative to non-threatening stimuli; *Hypothesis & Simulation II*), and for examining how threat stimulus intensity (*Hypothesis & Simulation III)* in combination with threat stimulus duration (see *Hypothesis & Simulation IV)* moderate the primary effects of anxiety on selective attentional-processing of threat. Importantly, the model also demonstrates how selective attentional biases favoring threat vigilance might be reduced in HA individuals, via psychological or pharmacological reduction in state-anxiety and associated amygdala reactivity (see footnote 7), by increasing attentional control (*Hypothesis V*) or by selective attention training (*Hypothesis & Simulation VI)*. Moreover, it contrasts ways by which reduced selective attentional-processing of positive or reward-related stimuli may be linked to anxiety (i.e., threat-related interference, e.g., threat-related amygdala response to neutral stimuli in the context of the dual presentation of positive stimuli), or a more primary deficit in reward-motivated information-processing that may be a unique effect of depression, possibly rooted in inadequate exposure to positive and/or reward-related stimuli during early learning-development (*Hypothesis VII)*. A putative neural architecture and set of information-processing mechanisms underlying these effects was laid out, with a particular emphasis on responses in a threat-detection module intended to signify the amygdala response to the visual presentation of threat stimuli, and the functional output of this system on areas generally involved in visual attention and attentional control (ACC and LPFC). In general, the model effectively simulated meta-analyzed results of previous probe-detection and related experiments that have compared attentional biases for threatening and reward-related stimuli in HA and LA individuals.

The present connectionist simulations therefore appear to provide a useful theoretical account of the structural and functional properties underlying attentional bias processes associated with anxiety. As discussed in the introduction, this model presupposes that all humans are equipped with threat detection or

"fear" processing systems that operate in accordance with phasic sensory principles. The ability to rapidly detect signs of possible threat represents a biologically adaptive mechanism that has also motivated previous conceptual models of selective attention for threat associated with anxiety (A. Mathews & Mackintosh, 1998; Mogg & Bradley, 1998). The present connectionist model would suggest that such evaluative scanning is a natural component of visual object recognition; visual stimuli are hypothesized to be analyzed following two separate coactive and interactive routes: standard visual-processing pathways, for the elaborative identification of salient visual properties that primarily function to orient the organism toward positive and potentially rewarding stimuli in the external environment, and a threat-detection route, for rapidly identifying the 'safety' relevance of stimuli. High- versus low -anxious individuals were hypothesized to differ in the extent to which a visual stimulus of the same putative threat-*'intensity'* activates the threat-processing route. The framework tested in this study represents an integration of experimental cognitive-psychology findings with investigations of underlying neurobiological and psychophysiological processes. Consequently, it makes several predictions for further clinical, developmental psychology, and neuroimaging studies of attention to threatening/reward stimuli.

In conclusion, the results of our model simulate what has been observed in the literature (both directly and in our meta-analyses presented here) and are suggestive of future, novel directions for experimental research studies. It is hoped that these future studies will shed further light on the nature and function of anxiety, and relationships between emotion, cognition, and the brain.

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*Figure 1*

*Illustration of dot-probe task trials and putative mechanisms of vigilance for, difficulty disengaging from, and*

*initial avoidance of threat stimuli*
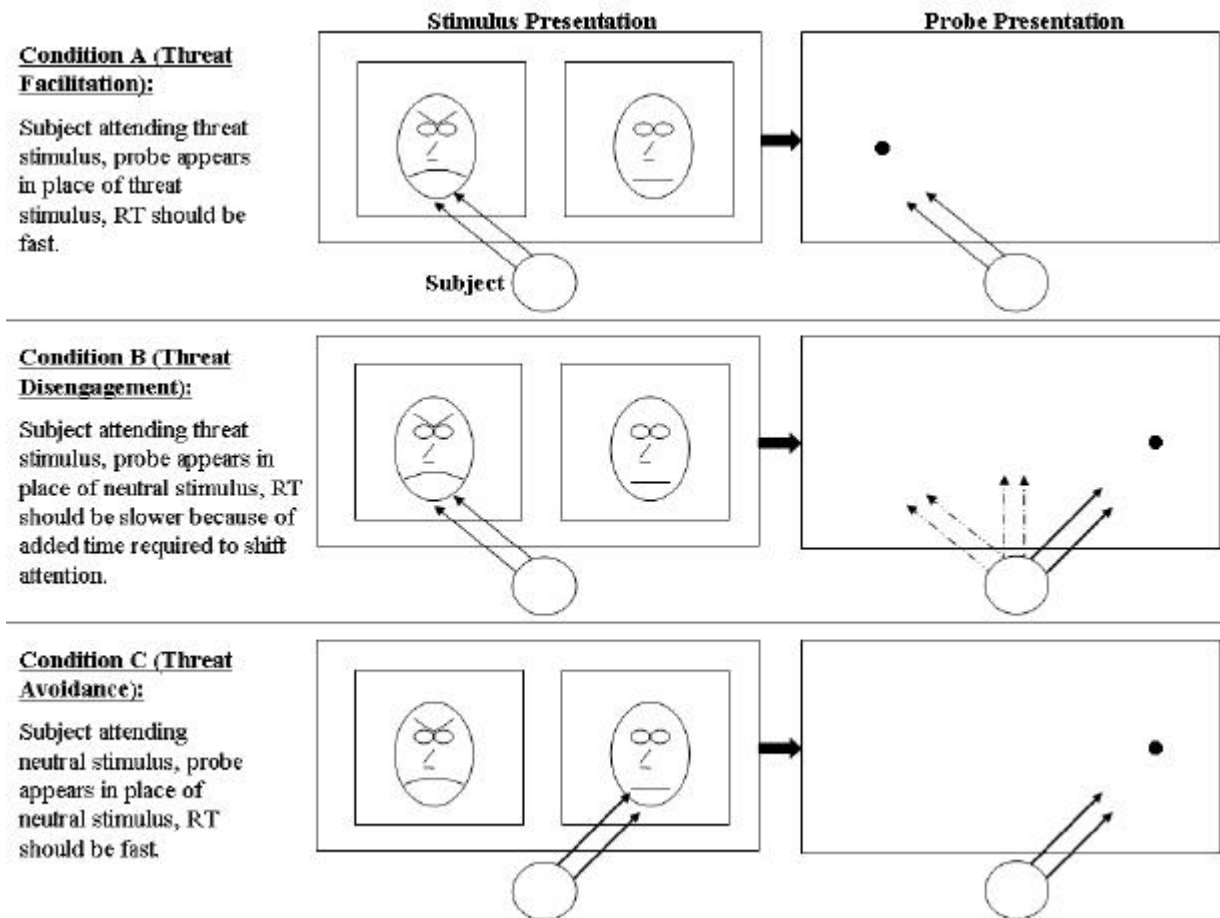


Note: Within a dot-probe task trial, HA individuals may be more likely to initially orient toward threat

(Conditions A & B) than LA individuals (Condition C). Alternatively, both HA and LA individuals may initially

orient toward threat, although HA individuals may be more likely to experience difficulty in disengaging from

threat once their attention has been allocated toward it (Condition B).

*Figure 2*

*Connectionist Neural-Network Architecture (Basic Model)*
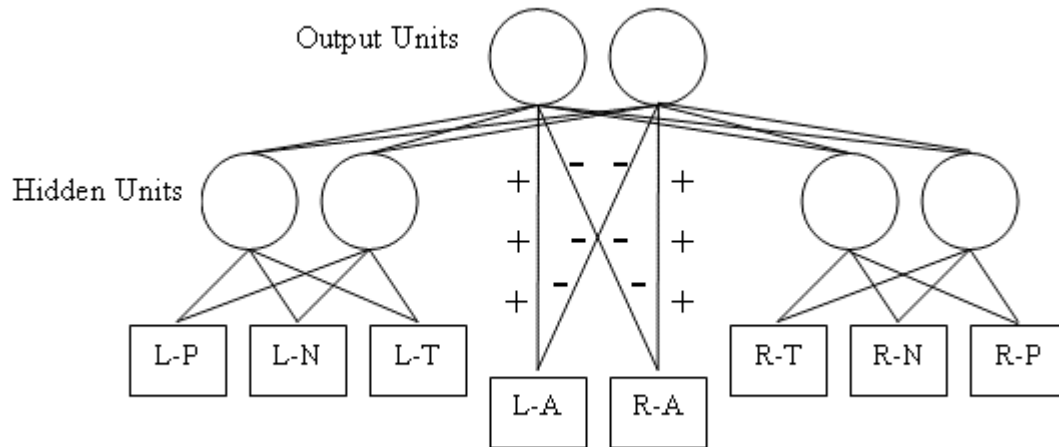


Note: Positive and negative signs between amygdala and output nodes reflect the direction of the weighting of the connections. Input Layer: L-P = Left Positive, L-N = Left Neutral, L-T = Left Threat, L-A = Left Amygdala, R-P = Right Positive, R-N = Right Neutral, R-T = Right Threat, R-A = Right Amygdala.

*Figure 3*

*Meta-analysis of attentional bias scores for threatening words, faces, and pictures calculated across*

*previous studies using a 500-ms presentation duration*
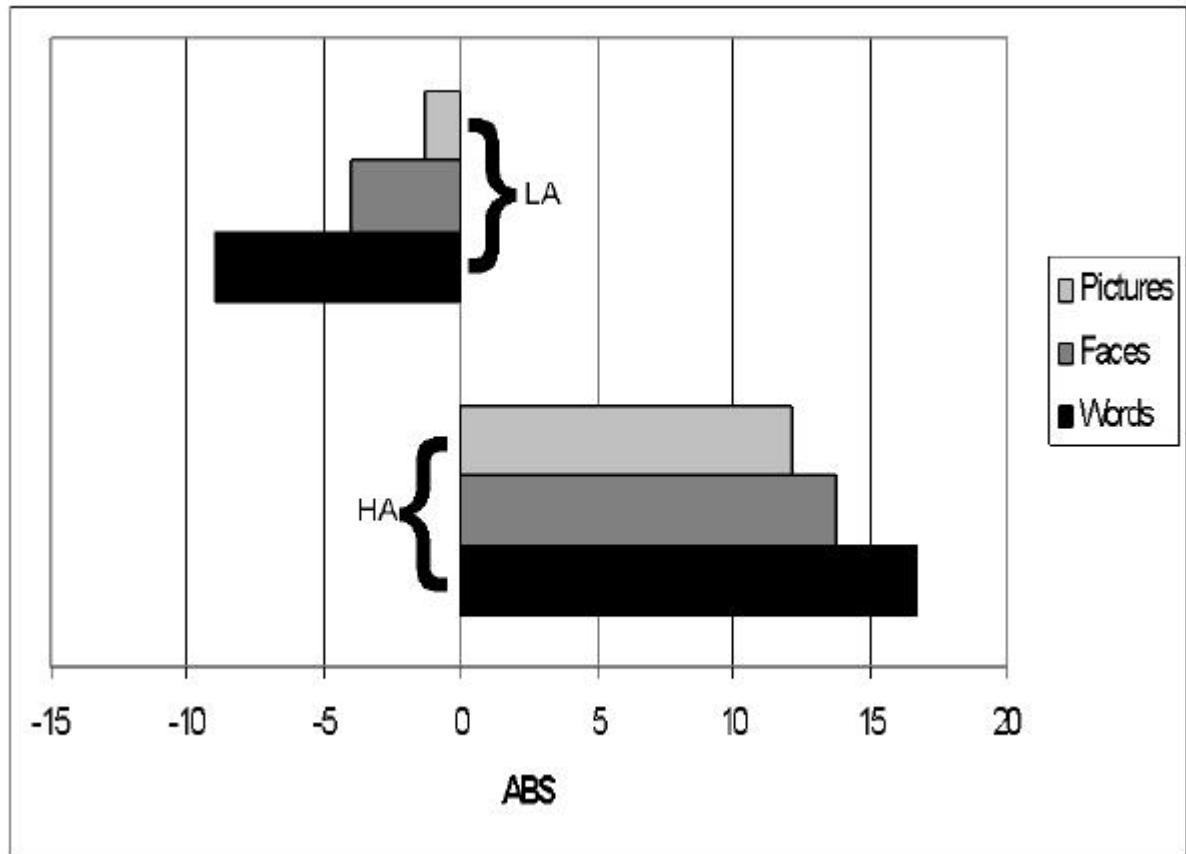


Note: ABS = Attentional Bias Score. Positive values reflect attention toward threat stimulus, negative values

reflect attention away from threat stimulus. This meta-analysis is based on data from the following citation

lists, categorized by stimulus type: *Words:* Bradley, Mogg, & Lee, 1997; Broadbent & Broadbent (1988,

Study 1); Brosschot, de Ruiter, & Kindt, 1999; E. Fox, 1993; Keogh, Dillon, Georgiou, & Hunt, 2001;

MacLeod & Mathews, 1988; MacLeod, Mathews, & Tata, 1986; Mathews, Ridgeway, & Williamson, 1996;

Mogg, Bradley, de Bono, & Painter, 1997; Mogg, Bradley, Dixon, Fisher, Twelftree, & McWilliams, 2000;

Mogg, Mathews, & Eysenck, 1992; Musa, Lepine, Clark, Mansell, & Ehlers, 2003; Tata, Leibowitz, Prunty,

Cameron, & Pickering, 1996; Horenstein & Segui, 1997; Pishar, Harris, & Menzies, 2004; Vassilopoulos, 2005; _Faces:_ Bradley, Mogg, Falla, & Hamilton, 1998; Bradley, Mogg, & Millar, 2000; Bradley, Mogg, Millar, Bonham-Carter, Ferguson, Jenkins, & Parr, 1997; Bradley, Mogg, White, Groom, & De Bono, 1999; E. Fox, 2002, Study 1; Ioannou, Mogg, & Bradley, 2004; Mogg & Bradley, 1999; Mogg, Philippot, & Bradley, 2004; Wilson & MacLeod, 2003; Pishar, Harris, & Menzies, 2004, Studies 1 & 2; _Pictures:_ Mogg, Bradley, Miles, & Dixon, 2004; Mogg, McNama, Powys, Rawlinson, Seifter, & Bradley, 2000, Studies 1 & 2; Koster, Verschuere, Crombez, & Van Damme, 2005; Pineles & Mineka, 2005; Yiend & Mathews, 2001, Study 1).

*Figure 4*

*Connectionist Neural-Network Processing of Threat Stimuli*



**Condition A:**

Neutral stimuli are more frequently trained than are threat stimuli, resulting in stronger connection weights (indicated by bold lines). Therefore, when presented in combination, neutral stimuli activate their corresponding outputs more strongly than do threat stimuli (indicated by black circle).
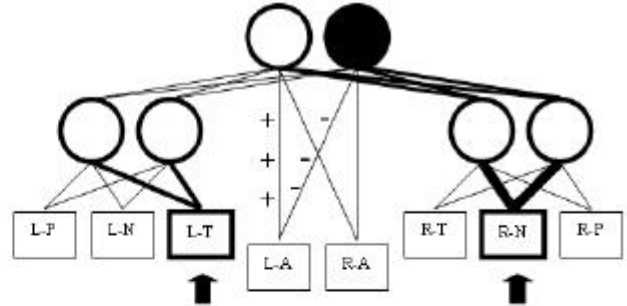
**Condition B:**

However, if the amygdala node is sufficiently activated in combination with the threat stimulus, this increases the activation of the threat-side output node, and decreases the activation of the neutral-side output node. If sufficiently strong, amygdala activation causes the threat-side output node to be the most highly activated.
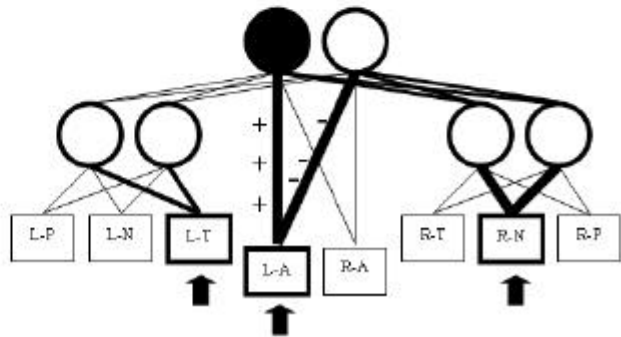
Note: Positive and negative signs between amygdala and output nodes reflecting the direction of the weighting of the connections. Input Layer: L-P = Left Positive, L-N = Left Neutral, L-T = Left Threat, L-A = Left Amygdala, R-P = Right Positive, R-N = Right Neutral, R-T = Right Threat, R-A = Right Amygdala.

*Figure 5*

*Mean attentional bias scores calculated across previous studies using 500-ms presentation duration and*

*the results of the connectionist neural-network model*
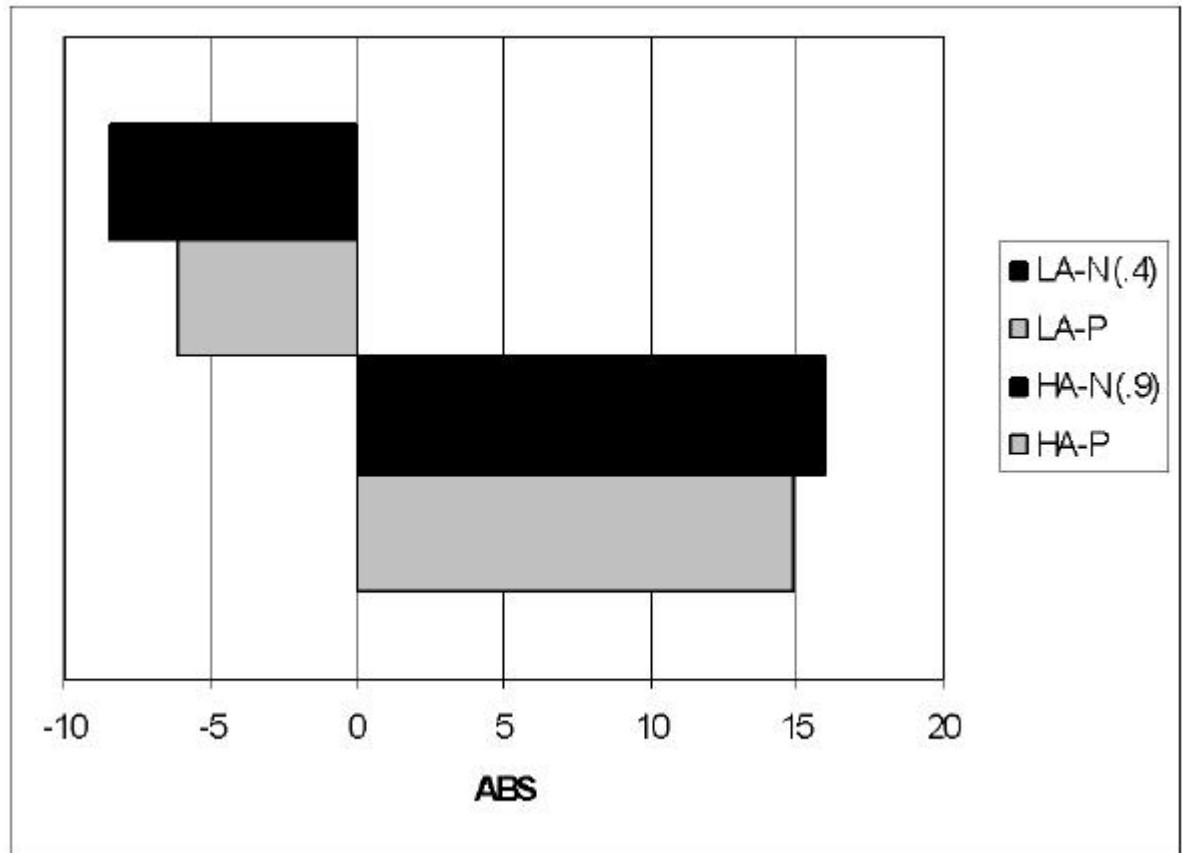


Note: ABS = Attentional Bias Score. Positive values reflect attention toward threat stimulus, negative values

reflect attention away from threat stimulus. LA-P = Low Anxiety Participants, LA-N = Low Anxiety Network,

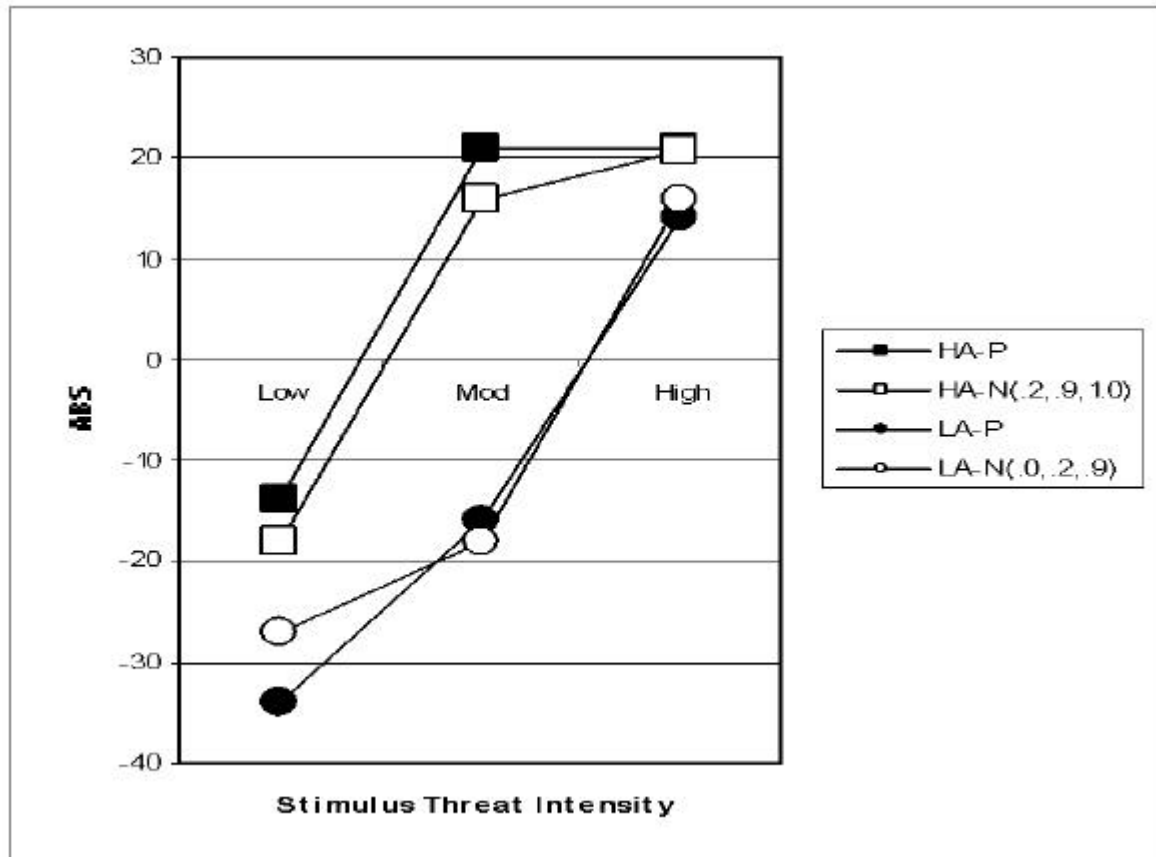HA-P = High Anxiety Participants, HA-N = High Anxiety Network.

*Figure 6*

*Effects of increasing proportional-training with threatening stimuli in the connectionist neural-network model*
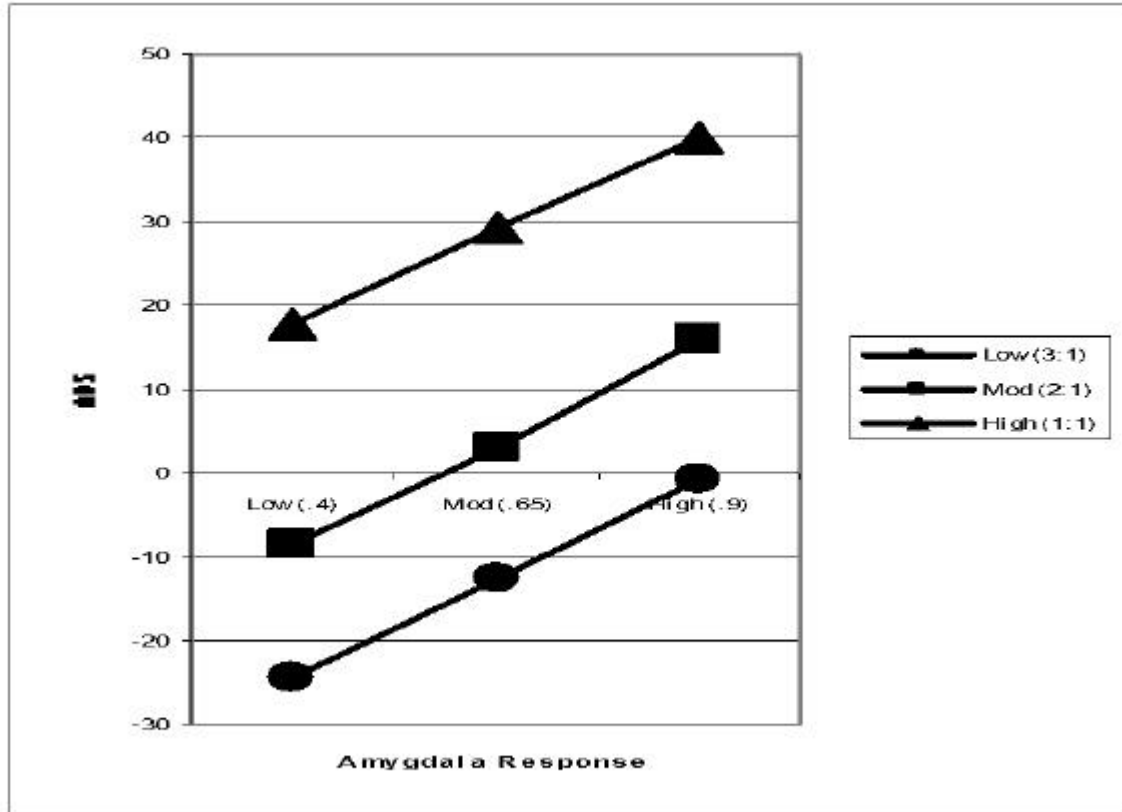


Note: ABS = Attentional Bias Score. Positive values reflect attention toward threat stimulus, negative values reflect attention away from threat stimulus.

*Figure 7*

*Effects of stimulus threat intensity on selective attention in Wilson & MacLeod (2003) and the connectionist*

*neural-network model*

*Figure 8*

*Meta-analysis of effects of threat stimulus duration on mean attentional bias scores for threatening words,*

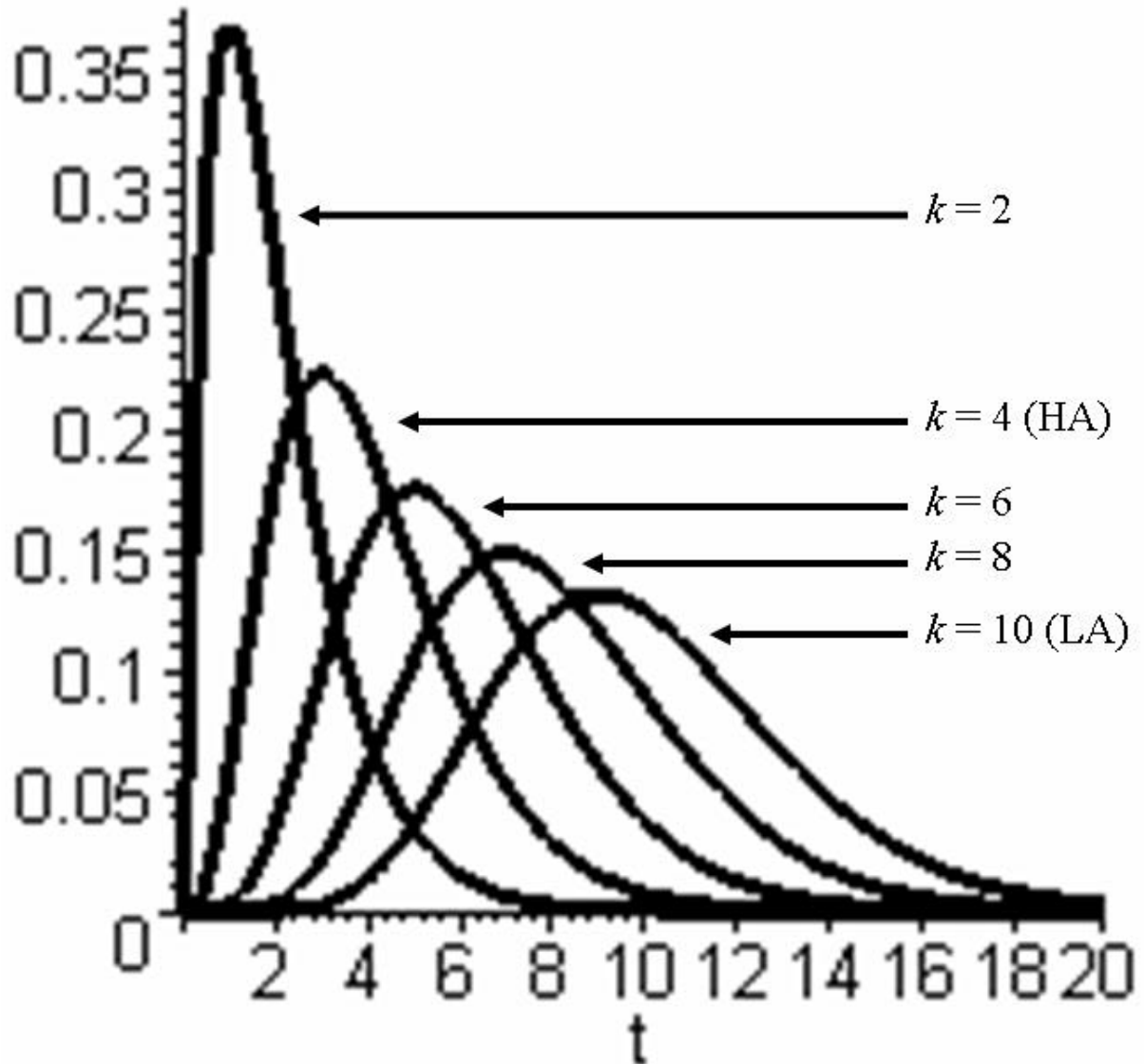*faces, and pictures calculated across previous studies*
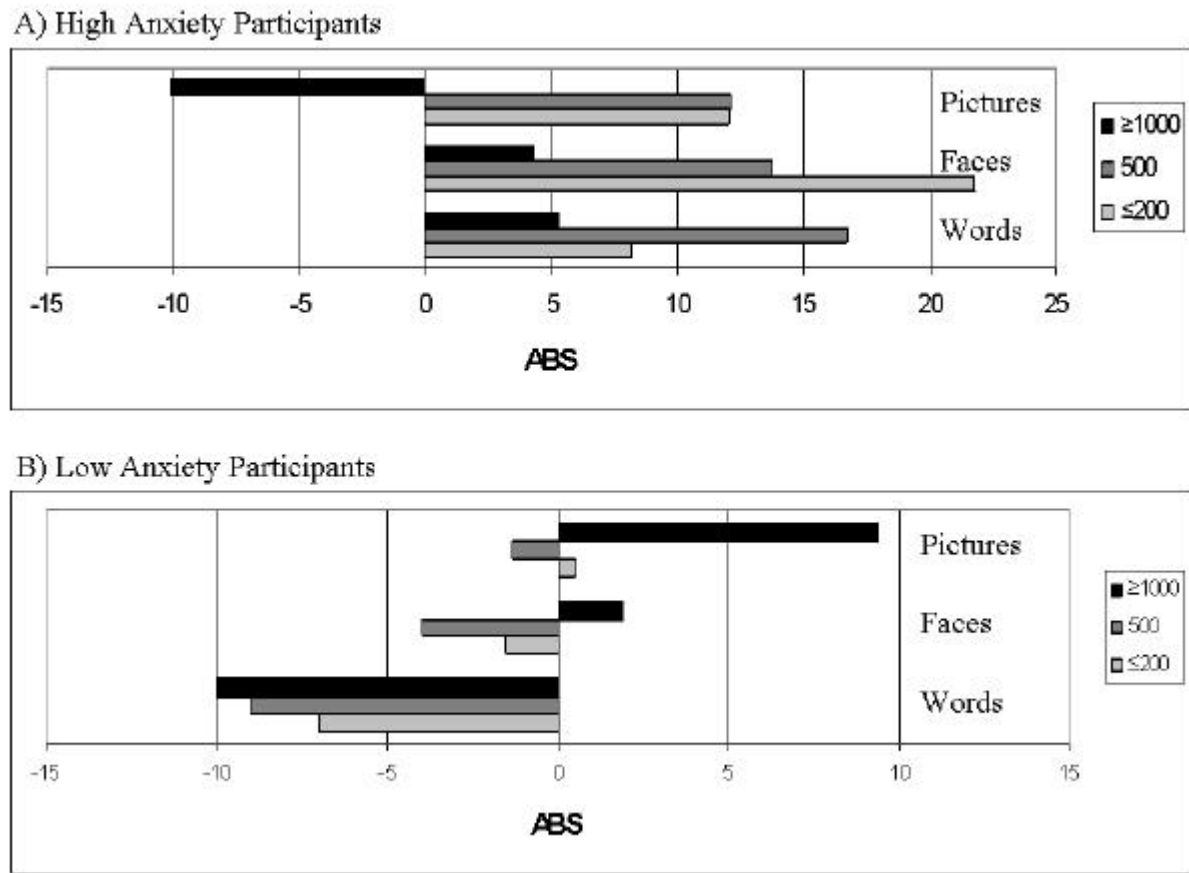


Note to Figure 8: ABS = Attentional Bias Score. Positive values reflect attention toward threat stimulus,

negative values reflect attention away from threat stimulus. This meta-analysis is based on data from all

studies previously cited in the note to Figure 3, for the 500 ms condition, incorporating data from the other

presentation durations utilized in those studies. In addition, the results of the following studies have been

incorporated, which did not utilize the 500 ms presentation duration and hence were not cited in the note to

Figure 3: *Words:* Mogg, Bradley & Williams, 1995; *Faces:* E. Fox, 2002, Study 2; Gotlib, Kasch, Traill,

Joorman, Arnow, & Johnson, 2004; Gotlib, Krasnoperova, Yue, & Joorman, 2004; Mogg & Bradley, 2002;

Mogg, Millar, & Bradley, 2000).

*Figure 9*

*Gamma-distributed responsiveness in the amygdala nodes of the connectionist neural-network*



Note: t = time, HA = High Anxiety, LA = Low Anxiety.

*Figure 10*

*Mean attentional bias scores calculated across previous studies using different threat-stimulus presentation durations and the results of the connectionist neural-network model*
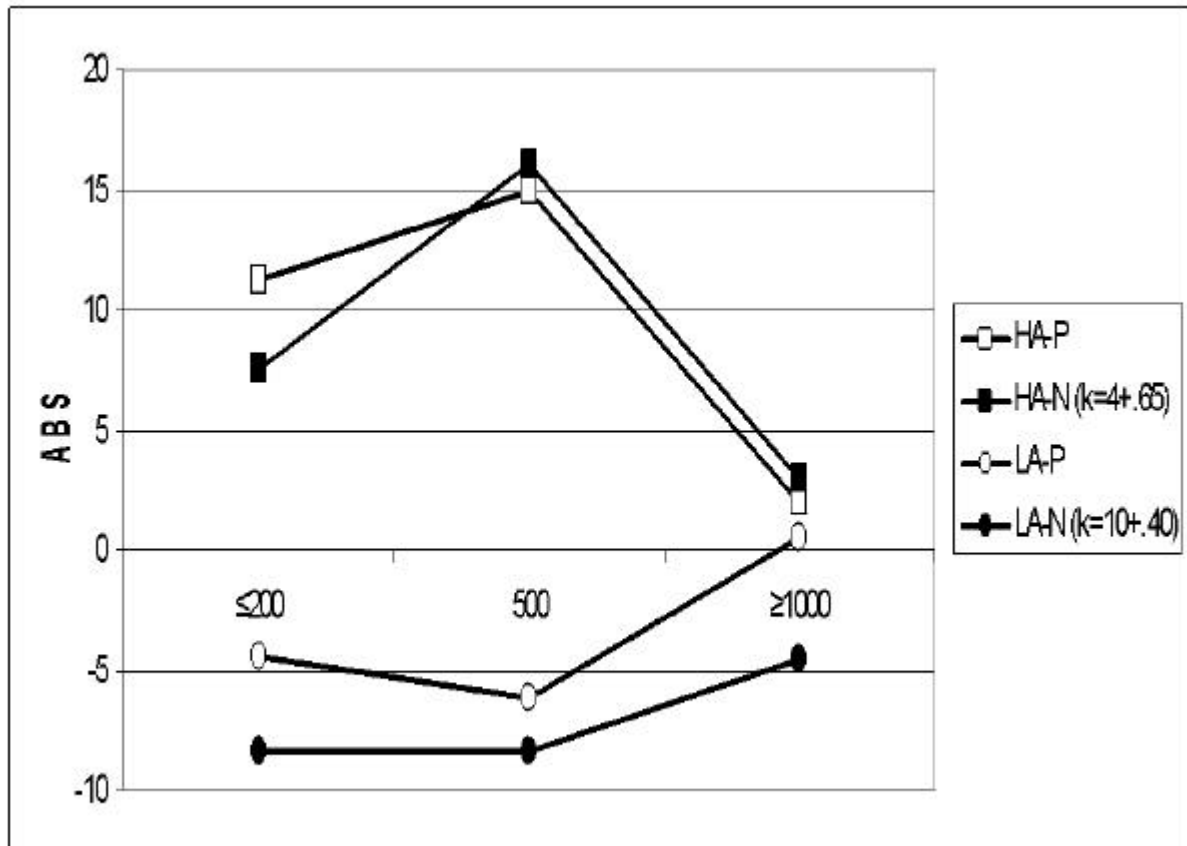


LA-P = Low Anxiety Participants, LA-N = Low Anxiety Network, HA-P = High Anxiety Participants, HA-N = High Anxiety Network.
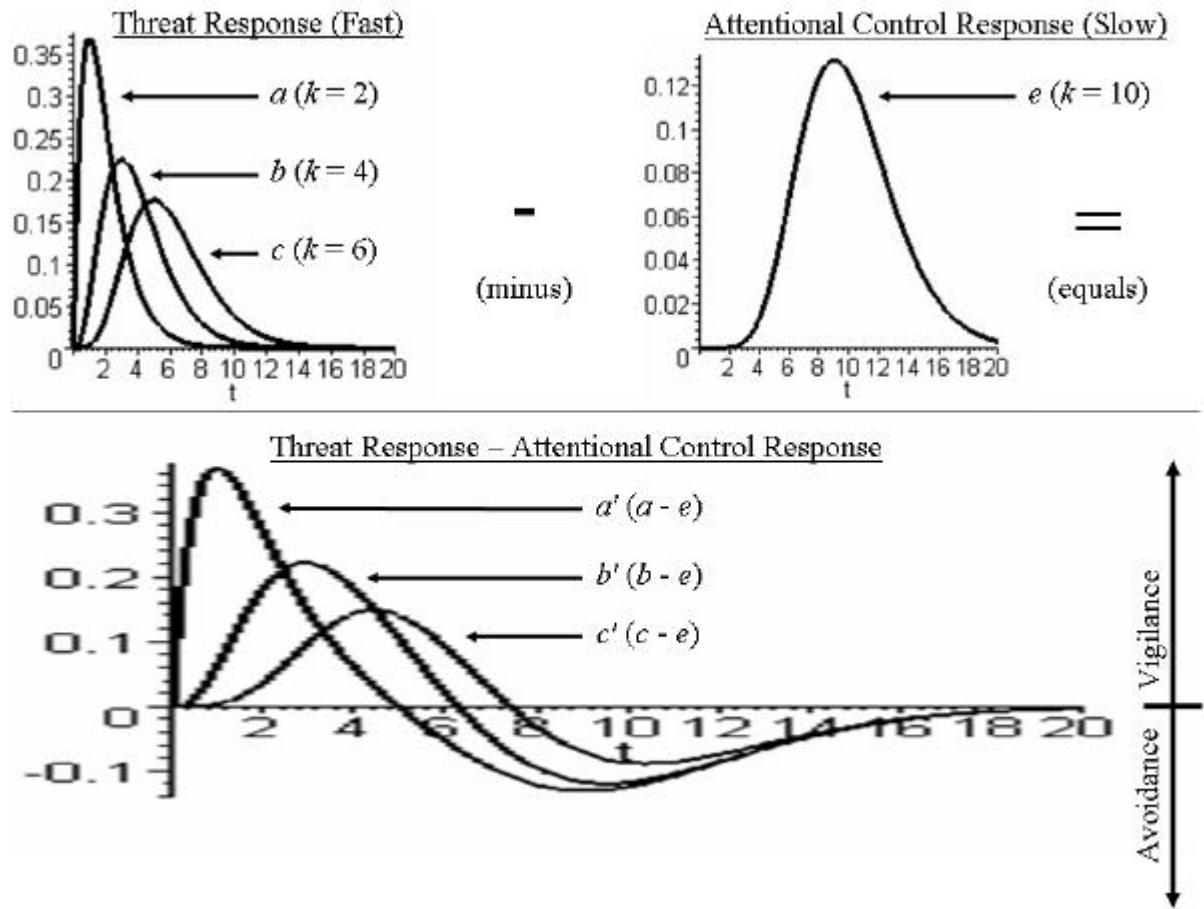
*Figure 11*

*Connectionist Neural-Network Architecture (Elaborated Model)*
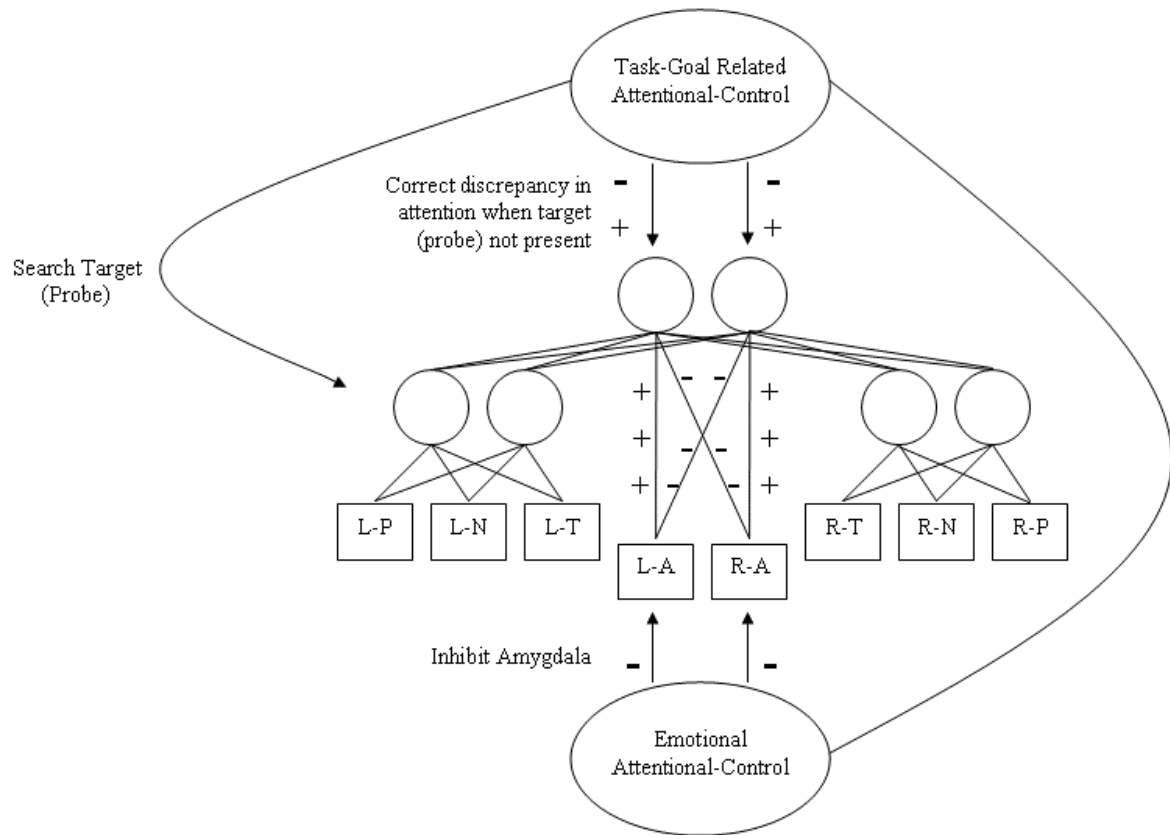


Note: Positive and negative signs between amygdala and output nodes reflecting the direction of the weighting of the connections. L-P = Left Positive, L-N = Left Negative, L-T = Left Threat, L-A = Left Amygdala, R-P = Right Positive, R-N = Right Negative, R-T = Right Threat, R-A = Right Amygdala.
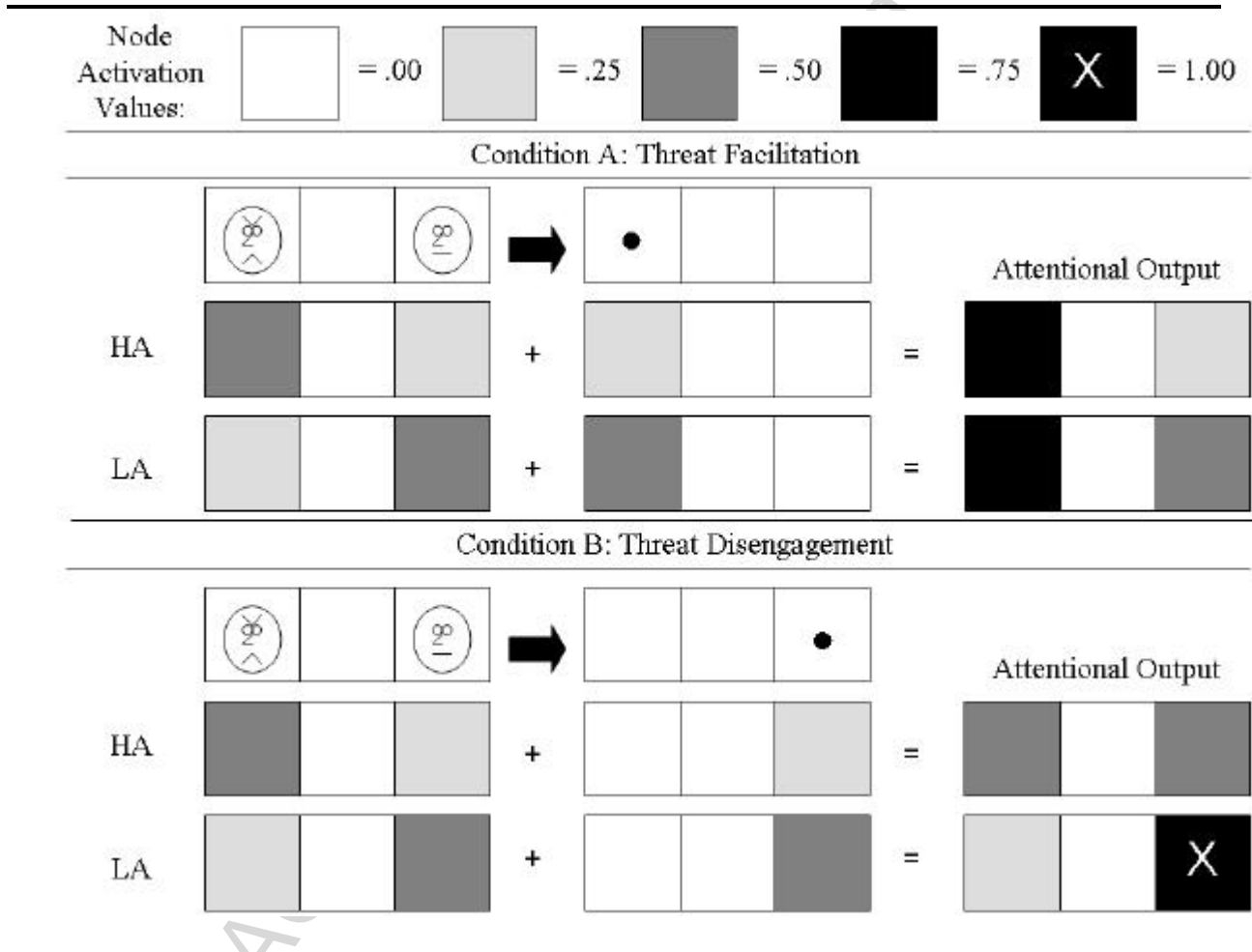
*Figure 12*

*Vigilance-Avoidance Hypothesis of Emotional Attentional-Control*



Note: This model predicts that early threat-vigilance is associated with later threat-avoidance if attentional control is constant across various models.

*Figure 13*

*Three-Dimensional Structure of the Connectionist Neural-Network Architecture (Elaborated Model)*



Note: Values are deemed significant only in an ordinal sense. This model demonstrates the interactive effects of three model dimensions: threat-responsiveness, reward-motivation, and task-goal-related attentional control. The HA model is tested as high in threat-responsiveness (Node Activation Value [NAV] = .50) and low in reward-motivation (NAV = .25) and task-goal-related attentional control (NAV = .25). The LA model is tested as low in threat-responsiveness (NAV = .25), and higher in reward-motivation (NAV = .50) and task-goal-related attentional control (NAV = .50). The hypothesized effects of these dimensions on threat-facilitation, threat-disengagement, and threat-avoidance, as discussed in *Figure 1* are illustrated. The

LA model illustrates initial threat-avoidance (higher response to neutral/reward stimuli in comparison with threat stimuli). The HA model illustrates both threat-facilitation (small effect) and difficulties with threat-disengagement (large effect). In the *Threat Facilitation Condition* (Condition A), the activation of the Target-Probe Node for the HA model is [(Target Node Activation)-(Non-target Node Activation)]: [(.50 + .25) − (.25)] = .50, and the activation of the Target-Probe Node for the LA model is [(.25 + .50) − (.50)] = .25; therefore, a small threat facilitation is effect is shown in the HA model in comparison with the LA model. In the *Threat Disengagement Condition* (Condition B), the activation of the Target-Probe Node for the HA model is [(.25 + .25) - .50] = .00, and the activation of the Target-Probe Node for the LA model is [(.50 + .50) − (.25)] = .75; therefore, a large threat disengagement effect is shown in the HA model in comparison with the LA model. Furthermore, within the HA model, an attentional bias toward threat is demonstrated (.50 - .00 = .50), whereas within the LA model, an attentional bias away from threat is demonstrated (.25 - .75 = -.50). In summary, in response to the presentation of *mildly or moderately* threatening stimuli, HA individuals may be more likely to orient toward the source of threat, whereas LA individuals may be more likely to orient away from threat and toward more neutral/positive stimuli (difference between Conditions A and C in Figure 1). This effect is hypothesized as being due to a higher threat-responsiveness in HA individuals, and a higher reward-responsiveness in LA individuals. LA individuals are also hypothesized to exhibit a greater level of task-goal-related attentional control, which translates as a higher activation response to the probe stimulus. The interaction of these effects encapsulates the results of Koster et al. (2004, 2005) that difficulties in disengaging from threat primarily account for differences between HA and LA groups on the dot-probe task as defined by the ABS. However, the model maintains the prediction that threat-facilitation in HA should also be found, although this effect is predicted to be significantly smaller than the threat-disengagement effect when only two stimuli (one threatening and one more neutral/positive) are present. The threat-facilitation effect may be more easily found when spatial attention is more diversely allocated (e.g., a threatening stimulus is presented amongst several neutral stimuli) or where differences

between groups in task-goal-related attentional control may have less influence (i.e., spatial working

memory may be sufficiently taxed in both HA and LA individuals in the latter instances given the increased

number of distractors) (see Cave & Batty, 2006 for review).

*Figure 14*

*Effects of selective attentional training in MacLeod et al. (2002) and within the connectionist neural-network model*
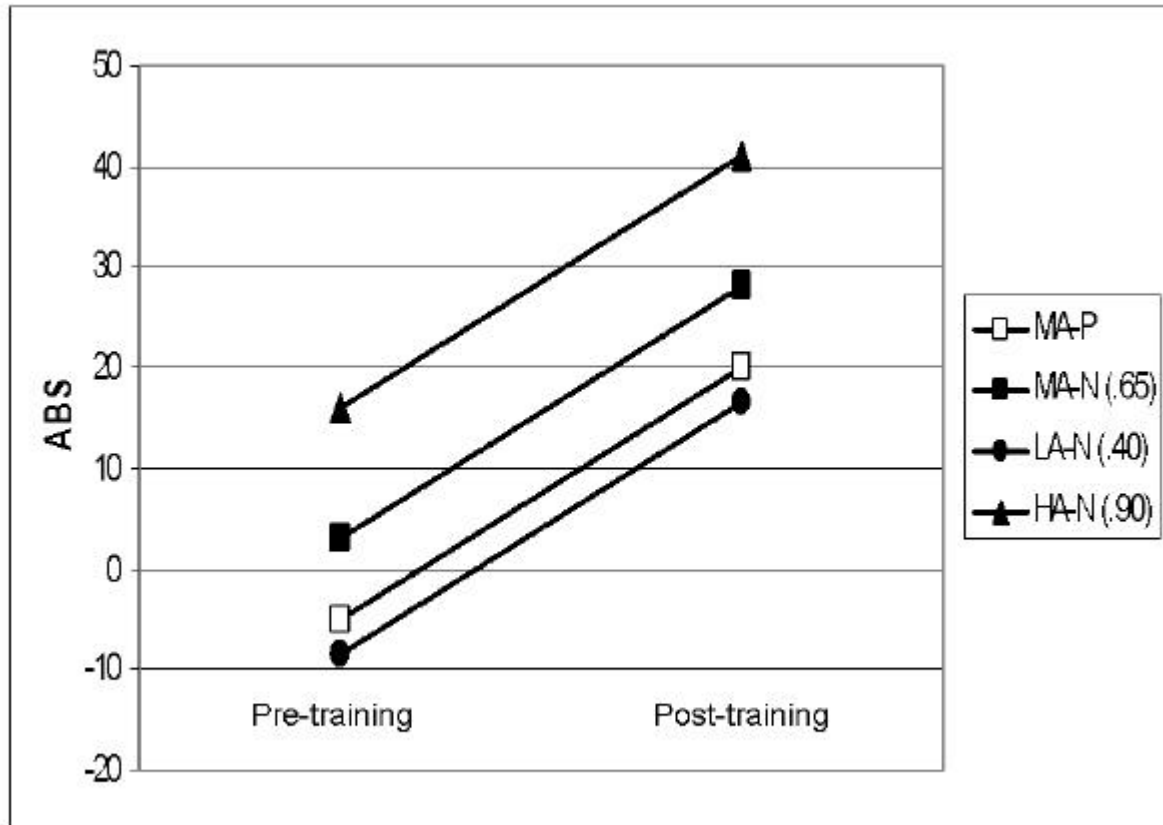


Note: ABS = Attentional Bias Score. Positive values reflect attention toward threat stimulus, negative values reflect attention away from threat stimulus. MA-P = Mean Anxiety Participants, MA-N = Mean Anxiety Network, LA-N = Low Anxiety Network, HA-N = High Anxiety Network.

*Figure 15*

*Meta-analysis of attentional bias scores for positive/reward-related words, faces, and pictures calculated across previous studies for various presentation durations*
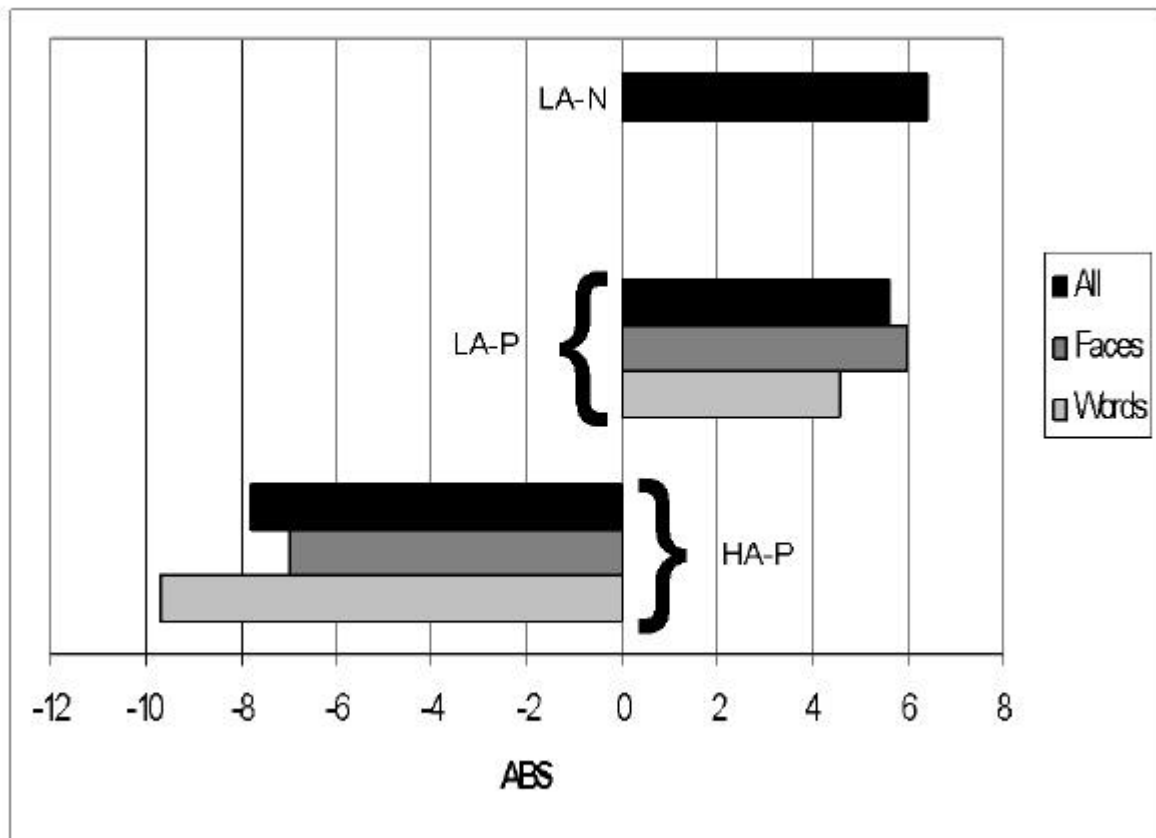


Note: ABS = Attentional Bias Score. Positive values reflect attention toward positive-reward stimuli, negative values reflect attention away from positive-rewarding stimuli. This meta-analysis is based on data from the following citation lists, categorized by stimulus type: *Words:* Brosschot, de Ruiter, & Kindt, 1999; Keogh, Dillon, Georgiou, & Hunt, 2001; Pishar, Harris, & Menzies, 2004; Vassilopoulos, 2005; *Faces:* Bradley, Mogg, Falla, & Hamilton, 1998; Bradley, Mogg, & Millar, 2000; Bradley, Mog, Millar, Bonham-Carter, Fergusson, Jenkins, & Parr, 1997; Bradley, Mogg, White, Groom, & De Bono, 1999; E. Fox, 2002,

Study 1; Ioannou, Mogg, & Bradley, 2004; Mogg & Bradley, 1999; Mogg, Philippot, & Bradley, 2004; Pishar,

Harris, & Menzies, 2004, Studies 1 & 2).

**Appendix A**: **Study Inclusion & Exclusion Criteria & Participant Population Description**

Adult-aged samples were investigated, whereas child and adolescent-aged samples were not included. In the vast majority of non-clinical studies included in this review, participants were grouped on the basis of their scores on the *Spielberger Trait Anxiety Inventory* (STAI-T; Spielberger, Gorsuch, Lushene, Vagg, & Jacobs, 1983) and, accordingly, comparisons reported between groups are considered to distinguish between processing characteristic of high (HA) versus low anxiety (LA) individuals *'in general'*, as opposed to processing of individuals with any specific anxiety disorder or specific subtype of anxiety. Studies were excluded from further review, however, if participants were grouped on the basis of their scores on a measure collectively deemed by the authors as not being central to the general anxiety-spectrum construct of theoretical interest to this article, including eating problems, pain problems, fear of pain as a personality trait, and substance abuse problems.

For studies investigating clinical-psychiatric samples, groups were considered to be representative of HA if they obtained a primary diagnosis of an anxiety disorder (as defined by the *Diagnostic & Statistical Manual of Mental Disorders, Fourth Edition* [DSM-IV; APA, 1994). An exception was that samples with a primary diagnosis of *posttraumatic stress disorder* (PTSD; APA, 1994) were not included, due to the deemed lack of fit of PTSD as a mental disorder primarily reflective of high-anxiety (i.e., PTSD is viewed by the authors as a complex-multidimensional psychiatric syndrome that is improperly reduced to and/or equated with clinically-high levels of anxiety; see Frewen & Lanius, 2006). Individuals with primary diagnoses of mood disorders were not considered to represent anxiety disorder samples, even if a large proportion of such mood disorder samples were also diagnosed with a co-morbid anxiety disorder or exhibited clinically-significant symptoms of anxiety (e.g., Musa, Lepine, Clark, Mansell, & Ehlers, 2003). Although diagnostic and symptom overlap between depression and anxiety disorders is substantial (see Mineka et al., 1998 for overview), this distinction was maintained in the present article given that it is time-honored within the field of clinical psychology and is in keeping with contemporary cognitive theories

regarding the information-processing correlates of these disorders (e.g., Williams et al., 1997; Mogg & Bradley, 2005). All non-psychiatric control groups who took part in these studies were classified as LA in the meta-analysis. Finally, studies were required to group participants in terms of pre-selected inherent dispositions toward anxiety, measured either by current state or trait variables, as opposed to attempting to 'induce' anxiety in one experimental group of participants relative to another in otherwise conceivably dispositionally LA participants.

The uniformity in participant assessment procedures obtained afforded an opportunity to characterize each respective sample in terms of anxiety level via a standardized metric, in the present case normative values for the STAI-T (normative values utilized are the grand mean of those tabulated by Kendall & Sheldrick, 2000, Table 4: $\mu$ = 39.01, $s$ = 10.60, $N$ = 1318). Altogether, the present meta-analytic comparisons are based on a population of 746 HA individuals, who on average scored at the 87th percentile (Z = 1.14 [sample-size weighted]) of the STAI-T, and a comparison population of 767 LA individuals, who on average scored at the 34th percentile (Z = -0.41 [sample-size weighted]) of the STAI-T. It is important therefore to consider that the LA group is, as defined, *low in anxiety*, not only in relation to the HA group, but also in relation to the greater population of adults and college-students from which these participants were sampled. Accordingly, studies encompassed by the present review compared HA and LA groups of individuals, as stated above, and studies that investigated average-anxious individuals only have not been included (Koster, Crombez, Verschule, & De Houwer, 2004; Monk et al., 2004; Schmuckle, 2005).

For the purpose of this review, the dot-probe or probe-detection task was defined as involving the simultaneous presentation of two visual stimuli, one of which was threat- or positive/reward-related, and the other of which was a 'neutral' (putatively less emotionally-relevant) stimulus. A further definitional criteria was that the stimulus properties inherent to the threat, reward, and neutral stimuli were otherwise comparable in sensory characteristics. Studies deemed to involve significant procedural deviations from the standard probe-detection task methodology were excluded. Specifically, two experiments were excluded

because they involved the comparison of processing of neutral and threatening stimuli taken from fundamentally different perceptual/semantic categories (i.e., the processing of threatening facial expressions relative to pictures of furniture, rather than between threatening and neutral expressions; Chen, Ehlers, Clark, & Mansell, 2002; Mansell, Clark, Ehlers, & Chen, 1999). Two excluded studies presented probe-targets simultaneously with threatening words, rather than after a delay (J. G. Beck, Stanley, Averill, Baldwin, & Deagle, 1992; Horenstein & Segui, 1997, Study 2). Other studies presented only a single stimulus per trial (threat/reward or neutral), and examined whether the threat/reward properties of stimuli determined reaction times to probes in stimulus-cued vs. stimulus-uncued regions across rather than within trials (i.e., the *Exogenous Cueing Task*; E. Fox, Russo, Bowles, & Dutton, 2001; Amir, Elias, Klumpp, & Przeworski, 2003; Yiend & Mathews, 2001). The studies by Hermans, Vansteenwegen and Eelen (1999) and Westra and Kuiper (1997) were not included because probe-detection reaction time was not the primary dependent variable. The study by Thorpe and Salkovskis (1998) could not be included due to its incorporation of a second "safety" stimulus that made its comparability with other-probe studies difficult to determine. Finally, a certain number of studies simply did not report sufficient descriptive data to afford the calculation of the attentional bias score, the presently utilized measure of effect size, and hence could not be included in the meta-analysis (Asmundson & Stein, 1994, 1994/1995; Asmundson, Sandler, Wilson, & Walker, 1992; Wenzel & Holt, 1999).

Relevant specifically to word-stimulus studies, in conditions where a study reported an attentional bias score (ABS) for more than a single word-type, such as social-threat words (e.g., *rejected, criticized*) and physical-threat words (e.g., *attack, violence*), the ABS with the highest value for the HA group was selected, and the composite ABS for the LA group selected. This procedure was followed in order to maximize sensitivity to detecting the behavioural effect in HA individuals, given that the threat-'relevance' of these differing semantic categories may vary across different groups of HA individuals. Furthermore,

information-processing of threat-stimuli is presumed by cognitive theorists to partly reflect this content-

relevance (i.e., the *content-specificity hypothesis*; see D. A. Clark, Beck, & Alford, 1999).

**Appendix B: Notes on Basic Network Training**

Networks were trained using the back-propagation algorithm (Rumelhart, Hinton & Williams, 1986), implemented in the connectionist-modeling program *TLEARN* (see McLeod, Plunkett, & Rolls, 1998; Plunkett & Elman, 1997; http://crl.ucsd.edu/innate/tlearn.html). The learning rate was set to 0.1, and RMS error tolerance and momentum were set equal to zero (these values are conventional in the literature and are standard defaults in TLEARN). Activation of units during training was scaled using the standard sigmoid function, which transforms the numerical sum of input values in a way that limits the activation range from 0.0 to 1.0 in units at subsequent processing layers.

The network was trained over multiple training trials that were organized into training epochs. During each epoch the training trials were presented in random order. At the beginning of training, the network's connection weights were random values. As a result, the network generated random outputs for each given input pattern. On each trial, the disparity between the desired and actual output unit activation values (referred to as net error) was computed. Connection strength values were then adjusted in a way that minimized error values for all trials (i.e., back-propagation). Network training was criterion-based; networks were trained until correct inputs were activated to a value = .9.

**Appendix C: Notes on Gamma Curve Modeling**

The gamma distribution is given by the following formula (Evans, Hastings, & Peacock, 2000):

$$f(t) = \frac{(v\,t)^{(k-1)}\, v\, \mathbf{e}^{(-v\,t)}}{\Gamma(k)}$$

where $v$ is a scaling parameter, and $k$ is a shape parameter, with $t$ plotted on the x-axis. In the present case, $t$ models time, whereas $f(t)$ models the intensity of threat-module (amygdala) activation (i.e., the network input value); simplifying the equation via parameter reduction, in the interest of parsimony, $v$ was then inputted simply as 1.0 in all instances. The specific parameters used for the HA network were $k = 4$ and an additive constant of 0.65, the constant implicating the tonic-metabolism in this node at rest. The distribution used to simulate the amygdala response in LA individuals used $k = 10$ and a tonic-metabolic additive constant of 0.40. These specific parameter values were chosen with reference to the pattern of ABSs identified in the meta-analytic results presented in Figure 8, specifically, one with a relatively rapid positive ABS increasing to 500 ms in HA individuals, and attentional avoidance approaching zero over time in LA individuals. Amygdala-unit response to rapid presentations (studies employing a presentation duration = 200 ms) were modeled at $t = 0.75$, to correspond with 75 ms, which was determined to be the mean presentation duration used for this group of studies. The values $t = 5$ and $t = 10$ were used to model 500 and 1000 ms presentations, respectively. The presentation of stimuli to the non-amygdala units used standard binary inputs for a tonic (non-phasic, neural firing-rate constant across time) response: 0 = absent, 1 = present.

**Footnotes**

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[1] Specifically, threat detection processing is conceived of as coding stimuli along a single dimension varying from "No Threat" to "High Threat", while reward detection systems perform a separate analysis for "Non-reward" vs. "Reward". An alternative conceptualization would be that both threat- and reward-detection represents a coding along a bipolar dimension ranging from, for example, "Avoid" to "Approach". One way to disambiguate the explanatory power of these differing conceptualizations is how each would compute instances of 'mixed emotion'. For example, consider a socially phobic individual's attempt to obtain the affectionate and/or sexual interest of another person. He or she is simultaneously motivated and interested in pursuing the other individual's interest, but fearful of rejection and embarrassment/shame, thus experiencing a 'mixed emotion'. Whereas this state is easily codified in the dual attentional-mechanism scheme (i.e., both reward and threat attentional systems score high), it is impossible to capture along the bipolar coding scheme.

[2] Space is determined arbitrarily in this model, thus left vs. right and top vs. bottom designations equally apply. For simplicity, only the left vs. right spatial orientation is discussed.

[3] It is important however to note that the onset of probe stimuli is not modeled explicitly within the present network architecture (i.e., there are no 'probe nodes'; see Figure 2). Rather, probe-onset is modeled implicitly, as probe presentation occurs immediately following stimulus onset (i.e., Stimulus Onset Asynchrony = 0) in the standard probe-detection task procedure.

[4] That HA individuals attend toward threatening stimuli more than LA individuals attend away from the same stimuli (i.e., the ABS in absolute value) may be due to two reasons. One is the fact that the highest within-study ABS demonstrated for HA individuals was always used where multiple types of threatening stimuli were utilized in the studies included, as discussed above in the meta-analysis section. Another

reason may be that the LA group deviates less significantly from the median value of the STAI-T than does the HA group.

[5] In other words, it is assumed that such observed correlations between group differences in subjectively experienced anxiety and selective attentional-processing of threat represent an effect *requiring explanation*, rather than themselves *representing an explanation*, as in 'anxiety causes selective attentional-processing of threat', or vice versa. This is because of the ambiguity left inherent in these expressions to a formal operationalization of 'anxiety' in information-processing terms (i.e., other than as a condition involving selective attentional-processing of threat, obviously a circular argument).

[6] It should be noted that the same effects can be simulated by holding constant amygdala input values between HA and LA connectionist models, but varying the size of the connection weights between amygdala input nodes and the output nodes in these models (specifically, the connection weights between amygdala nodes and output nodes in HA models can be engineered to be larger than in LA models). However, this manipulation would not be in keeping with studies that have found amygdala metabolism itself to correlate with individual and group differences in anxiety. It is possible that the selective attentional behavior of HA individuals derives from a combination of their amygdala response, as well as patterns of differential functional connectivity of their amygdala with other areas of attentional processing and control. It is further possible that functional connectivity relates more to 'trait' anxiety, whereas amygdala activity itself relates more to 'state' anxiety. However, it is difficult to disambiguate these two effects via current methods in cognitive neuroscience. Within the present connectionist architecture, the two effects (threat-module amygdala-input values and connection weights with outputs) are transparently multiplicative. Therefore, in the interest of parsimony, only amygdala inputs rather than amygdala-output connection weights distinguish HA and LA individuals in the foregoing present model simulations.

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[7] It is an accepted view within clinical psychology that environmental challenges or stressors have the power to increase subjectively-experienced anxiety and depression. Studies have determined that such life-event or environmentally-caused increases in subjective anxiety and distress, even in dispositionally LA individuals, are associated with increased attention toward external threat stimuli as measured in the probe-detection task (e.g., Bradley, Mogg, & Lee, 1997; MacLeod & Mathews, 1988; Mogg, Bradley, & Hallowell, 1994; Mogg, Mathews, Bird, & Macgregor-Morris, 1990). Moreover, given that state levels of anxiety may vary considerably over the course of a probe-detection experiment itself, such factors may be important in considering that the probability of observing an attentional bias may depend on the position of blocked task trials (Bradley et al., 1999; Broadbent & Broadbent, 1988; Monk et al., 2004). Such an order effect can be accounted for within the present network, where the threat value of stimuli may be held to decrease over time in the absence of reinforcement. Indeed, repeated presentations of the same threatening stimulus result in decreasing response in the amygdala when the threatening significance of the stimulus is not reinforced (e.g., LaBar et al., 1998; Buchel et al., 1998; Phelps et al., 2001).

It is important to note, however, that in the various probe-detection studies examined, 'trait' and 'state' anxiety have almost invariably been confounded (i.e., the state and trait measures of anxiety of the STAI are routinely significantly and positively-correlated in probe-detection studies; see Broadbent & Broadbent, 1988). It is therefore possible that, whereas previous research has focused primarily on differences between groups in trait anxiety (as defined by the STAI-T measure, or between clinical and control groups), the results obtained as a function of this distinction may nevertheless have been primarily mediated by correlated differences in state-anxiety that equivalently distinguish these groups.

Interestingly, amygdala metabolism also appears to covary with the state anxiety of participants. For example, administration of lorazepam (which reduces state anxiety) significantly reduces response in the amygdala to threatening faces (Paulus, Fernstein, Castillo, Simmons, & Stein, 2005), while

administration of dextroamphetamine (an agent with documented state-anxiety generative effects at high doses) significantly increases response in the amygdala to threatening faces (Hariri et al., 2002). Within the present connectionist neural-network, the selective-attentional effects of transitory increases in state anxiety, studied naturalistically as a function of life-stress or engendered causally by experimental manipulation (Beevers & Carver, 2003; Bradley, Mogg, & Lee, 1997; MacLeod & Mathews, 1988; Mogg, Bradley, & Hallowell, 1994; Mogg, Mathews, Bird, & Macgregor-Morris, 1990), can be captured by temporary elevation in the baseline metabolism of amygdala nodes. This is important as, presenting this association in the reverse, the model is found to predict that reducing state anxiety, via psychological (e.g., relaxation-training) or pharmacological (e.g., Paulus, Fernstein, Castillo, Simmons, & Stein, 2005) intervention should result in a concomitant reduction in biased selective-attentional processing for threat. This effect was recently demonstrated for anti-depressant treatment of anxiety on another selective attention task (the auditory homophone task; Mogg, Baldwin, Brodrick, & Bradley, 2004).

[8] In order to test these effects, however, it is important to hold constant the extent of training overall (such that models do not differ in their amount of 'experience' or learning in general), while experimentally varying the extent to which models are exposed to threatening relative to non-threatening stimuli. In other words, one can effectively alter the *proportional experience* of various models with threatening relative to neutral stimuli. In order to achieve this effect, a common denominator can be determined for various numbers of trials within training epochs (covarying as a function of the different ratios of trials with threatening and non-threatening stimuli), with training continuing until all training trials reach the common pre-determined .9 correct-identification criterion (see Appendix 1). Additionally, the number of training epochs is held to be relatively constant across the various versions of 'proportional-training'.

[9] The sum of trials within epochs for these values is 4, 3, and 2, respectively, and consequently the lowest common denominator equals 12. This common denominator thus served to equally parse the training

epochs, where a 9:3 ratio was used for the *lowest threat exposure* condition, an 8:4 ratio was used for the *low threat exposure* condition, and a 6:6 ratio was used for the *high threat exposure* condition, for neutral relative to threat training trials, respectively.

[10] Response systems displaying phasic sensory-receptivity, an elementary principle in sensory psychophysiology, respond to stimulus onset and/or change but quickly habituate their neural firing to an unchanging stimulus. Phasic sensory systems can be contrasted with sensory systems that are *tonically-receptive*, or exhibit a more-or-less unvarying firing pattern throughout the duration of an unchanging stimulus-presentation.

[11] It might be argued that the *rise time to peak* of the gamma-distributions depicted in Figure 9 are too slow to represent the amygdala response to visual threat stimuli, given that neuroimaging studies have demonstrated amygdala activation to very briefly presented threatening faces that are backward-masked (Morris et al., 1998; Morris, Öhman, & Dolan, 1999; Whalen et al., 1998; although this effect was not extended by Phillips et al., 2004). It is important to clarify here that the distributions in Figure 9 are intended to reflect the *effect* of the amygdala, rather than direct amygdala activation per se. Thus what is hypothesized by the model is that the effect of the amygdala on selective-attentional outputs varies in accordance with the gamma-distributed response profiles depicted in Figure 9.

Additionally, it may be argued that the difference in amygdala responses between HA and LA participants proposed by Figure 9 is too extreme as to be biologically plausible. In response to this it is worth noting that, within a constrained system such as the present neural network architecture, interpretation of the specific values that are arrived at in determining processing effects may be less informative than interpretation of the general principles that are illustrated by varying these values (the same point can be made in regard to the effects of varying the proportional training of models, as in

*Hypothesis and Simulation 1*). Accordingly, the substantive point is that the model hypothesizes a faster gamma-distributed response to threat stimuli in the amygdala module of HA individuals.

[12] Three of the five values of *k* (2, 4, and 6) calculated for the amygdala-response gamma distributions illustrated in the previous Figure 9 are shown, subtracting the gamma distribution with *k* set equal to 10 as an indication of a more sluggishly-acting attentional-control response relative to the amygdala orienting-response.

[13] Several investigators have recently interpreted the results of exogenous-cueing-task studies as challenging the premise that HA individuals demonstrate threat-vigilance, positing instead that the sole attentional characteristic of high anxiety rests in the problem of attentional disengagement (Amir, Elias, Klumpp, & Przeworski, 2003; E. Fox, Russo, Bowles, & Dutton, 2001; Yiend & Mathews, 2001). However, it is important to note that, without presenting simultaneously both emotional and neutral stimuli, no competition for spatial attention is effected at the outset in these studies. This may result in a floor effect that weakens the prospect of identifying possible threat-vigilance effects; indeed, within the present model, as discussed previously in the *General Network Testing Methods & Preliminary Testing* section, when stimuli are presented singly, they activate their corresponding targets very strongly. The method of Koster and colleagues (Koster et al., 2004, 2005) seems to be a more methodologically-sophisticated attempt to separately study threat-vigilance and threat-disengagement as sub-processes causally explaining attentional behaviour on the traditional dot-probe and other visual selective-attention tasks.