

Running head:

Inhibition during circa-strike stage: Attention or switching of defensive mechanisms?

Inhibition during circa-strike stage: Attention or switching of defensive mechanisms?

Robin Schraauwers

Applied Cognitive Psychology

Under supervision of:

Joke Baas (UU)

David Terburg (UU)

Experimental Psychology

ECTS: 30

Thesis

14-07-2014



Universiteit Utrecht

Inhibition during circa-strike stage: Attention or switching of defensive mechanisms?

Abstract

Recent studies have shown an inhibition of startle reflex prior to active escape behavior when participants are placed in what resembles the circa-strike stage of the Predator Imminence Model (Fanselow, 1994; Lang et al., 1997; Löw et al. 2008; Richter et al., 2012; Terburg., 2012). In this paper we examine the cause of this inhibition, which could either be attention related or might represent a switch between defensive mechanisms. To examine this cause, we used the circa-strike escape task which manipulates distance to threat (Terburg, 2012). The modality of the startle probe and the threat-signals was kept the same, focussing attention on the startle probe modality. Fear-potentiated startle occurred at every distance to the threat. However, no significant difference were found between a near and a far-away threat or between a near and an unavoidable threat. We can therefore not conclude whether there was inhibition of startle-potentiation or whether there was startle potentiation when a threat was imminent yet avoidable.

We can therefore not conclusively confirm either of our hypotheses. More research is needed to determine the exact cause of the inhibition of startle found by Richter et al. (2012), Löw et al. (2008) and Terburg (2012). Recommendations are given for further research.

Keywords: Fear-potentiated startle (FPS), startle inhibition, attention, defensive mechanism, circa-strike escape task, C-SET.

Introduction

In 2012, Richter et al. conducted a study involving patients with panic-disorder and agoraphobia. They showed that during anxious apprehension an increase of heart rate and skin conductance levels as well as a potentiation of startle-responses occurred. This state of anxious apprehension was induced by placing the participants in a small, dark chamber from which they could escape by pressing an escape-button. Some of the patients exhibited active escape behaviour. The minute prior to this behaviour was compared to the rest of the test-

Inhibition during circa-strike stage: Attention or switching of defensive mechanisms?

period and showed an interesting effect. To assess defensive reactivity, heart rate and skin conductance levels were measured, while the startle eye-blink was measured as an index of amygdala defence system activation. What was shown was that heart rate and skin conductance levels increased linearly in the minute before the button-press, while the eye-blink startle response was relatively inhibited. Since the startle reflex is thought to be a mechanism that protects the body from harm (such as facial muscles protecting the eyes by blinking) and serves to ready an organism for action against a threat (Yeomans, Li, Scott & Frankland, 2002) potentiation of startle was expected. Another reason is that human and animal studies have demonstrated that when a startle evoking stimulus is shown in the presence of a cue that signals an aversive event, the startle reflex is potentiated (Davis & Astrachan 1978; Grillon et al. 1991). Potentiation of this startle reflex also seems to depend on how much the participants fear the threat (Sabatinelli, Bradley & Lang, 2001). However, the opposite pattern (i.e inhibition and not potentiation) was observed in the study by Richter et al. (2012) in what seems to be the most anxious period in their test.

Richter et al. (2012) are not the only ones who found this surprising effect. Löw et al. (2008) have found a similar inhibition of startle eye-blink when a threat is imminent in their study about emotional arousal and reward. In this study, participants could earn or lose money by performing well on a visual task and different modalities were used for the unconditioned stimulus (visual) and the conditioned stimulus (auditory startle probe). Startle was inhibited for both reward and loss cues in the imminent stage of the test.

There are two possible explanations for the occurrence of the inhibition of startle. The first explanation for the inhibition of startle reflexes when a threat is imminent could be that it represents a switch from a state of passive defence to a state of active defence. According to Bradley and Lang, fear and anxiety are necessary for our survival (2000). They state that

Inhibition during circa-strike stage: Attention or switching of defensive mechanisms?

“*Emotions evolved from functional behaviors that facilitated the survival of individuals and species.*” Emotions such as fear and anxiety are therefore an adaptive mechanism to ensure someone’s safety. Up until now, the startle reflex is thought to be such a defensive mechanism (Yeomans, Li, Scott & Frankland, 2002). However, since reflexive blinking does not seem to occur in the study by Löw et al. (2008) when an attack is imminent, this mechanism and its purpose might have to be reconsidered. When the defensive distance becomes this small, the startle reflex might not have the same defensive purpose. The exact defensive purpose might depend on the distance between the threat and the organism. Here The Predator Imminence Model (Fanselow, 1994; Lang et al., 1997) comes in useful. It describes a variety of behaviour that can occur when organisms are being threatened depending on the distance to this threat. There are three stages; pre-encounter defence, post-encounter defence and the circa-strike defence. During the pre-encounter stage, an organism is in a context in which a predator was encountered in the past, but is not present at the moment. The organism will be vigilant, but in a non-specific way. In the post-encounter stage the predator has been sighted, and the organism freezes and selectively focuses its attention on the predator. When the predator comes closer and an attack is imminent, the organism will show strong autonomic arousal and escape behaviour. This is the circa-strike stage.

The potentiation of startle reflexes during post-encounter defence, and the absence of it during circa-strike defence (as in the study by Richter et al. (2012) and Löw et al. (2008)) might perhaps involve a switch from one defensive mechanism to another. The potentiation of startle might no longer be a part of the active defence mode. This way an inhibition of startle might signal a switch between defensive mechanisms.

To examine whether an active escape mechanism was at play in the study by Richter et al. (2012) and Löw et al. (2008) Terburg (2012) has devised a task that was designed specifically to modulate threat levels within a participant by varying the distance between the

Inhibition during circa-strike stage: Attention or switching of defensive mechanisms?

participant and the threat. This task was called the Circa-Strike Escape Task (C-SET), since participants completed the circa-strike stage of the Predator Imminence Model (Fanselow, 1994; Lang et al., 1997). They could escape these ‘attacks’ by pressing a button. Again, as in the study by Löw et al. (2008), the startle probe was auditory while the cues signaling distance to threat were visual. His results showed that there was a relative inhibition of fear-potentiated startle (FPS) when a threat was imminent when the first and second half of the test was compared. He suggests that these results might signal the occurrence of a switch between from a passive to an active defensive mechanism.

The second explanation for the effect found by Richter et al. (2012) and Löw et al. (2008) is focused on attention. Richter et al. (2012) themselves proposed that the relative inhibition of the startle reflex might have been caused by a reduced processing of the external cues so as to facilitate escape behaviour. In their study the threat was an interoceptive one, since the participants all had panic-disorder with agoraphobia. Selective attention was most likely not fully focussed on the external startle probe but rather on one’s own internal state, since this was the actual threat in their study.

Attention is known to have a large impact on the startle reflex, which is the reason that a mismatch in modalities and the attention given to each modality might explain the inhibition of fear-potentiated startle found by Löw et al. (2008) and Richter et al. (2012). The impact of such a mismatch is shown by Anthony, Butler and Putnam, who conducted a study in 1987 in which they manipulated the modalities of a task that participant’s had to perform. At the same time they kept the modality of the startle probe (auditory) the same across all tests. They found that if the task and the startle probe did not have the same modality, startle was inhibited. The amount of attention given to the startle probe can therefore explain the effects found by Richter et al. (2012) and Löw et al. (2008).

Inhibition during circa-strike stage: Attention or switching of defensive mechanisms?

Since different modalities were used for the unconditioned stimulus and the conditioned stimulus in the study by Löw et al. (2008) this could have caused the participants to focus their attention on the visual modality and therefore to pay less attention to the auditory startle probe. The reduced processing of which Richter et al. (2012) proposed that might have brought about the startle inhibition might possibly be similarly explained by a lack of attention given to the startle probe.

When trying to find possible causes for the inhibition of startle when a threat is imminent, the Predator Imminence Model (Fanselow, 1994; Lang et al., 1997) proves insufficient and slightly outdated. McNaughton's and Corr's have since then taken all newly available knowledge and come up with the two-dimensional defence system (2004) (see figure 1). This model takes into account not only the defensive distance but also defensive direction (approach or avoid). It describes a wide range of neurobiological and behavioural responses, depending on availability of flight and distance to threat. They explain that with a large (subjective) distance between threat and organism, chosen behaviour can have a wide range and be highly complex. The closer the threat, the more basic the response will be. The startle inhibition shown by Richter et al. (2012) and Löw et al. (2008) might be a part of the bodily responses to such a specific situation. It might only occur when a threat imminent is and fleeing is possible. In other situations (i.e. other defensive distance and/or direction), startle might be potentiated.

Inhibition during circa-strike stage: Attention or switching of defensive mechanisms?

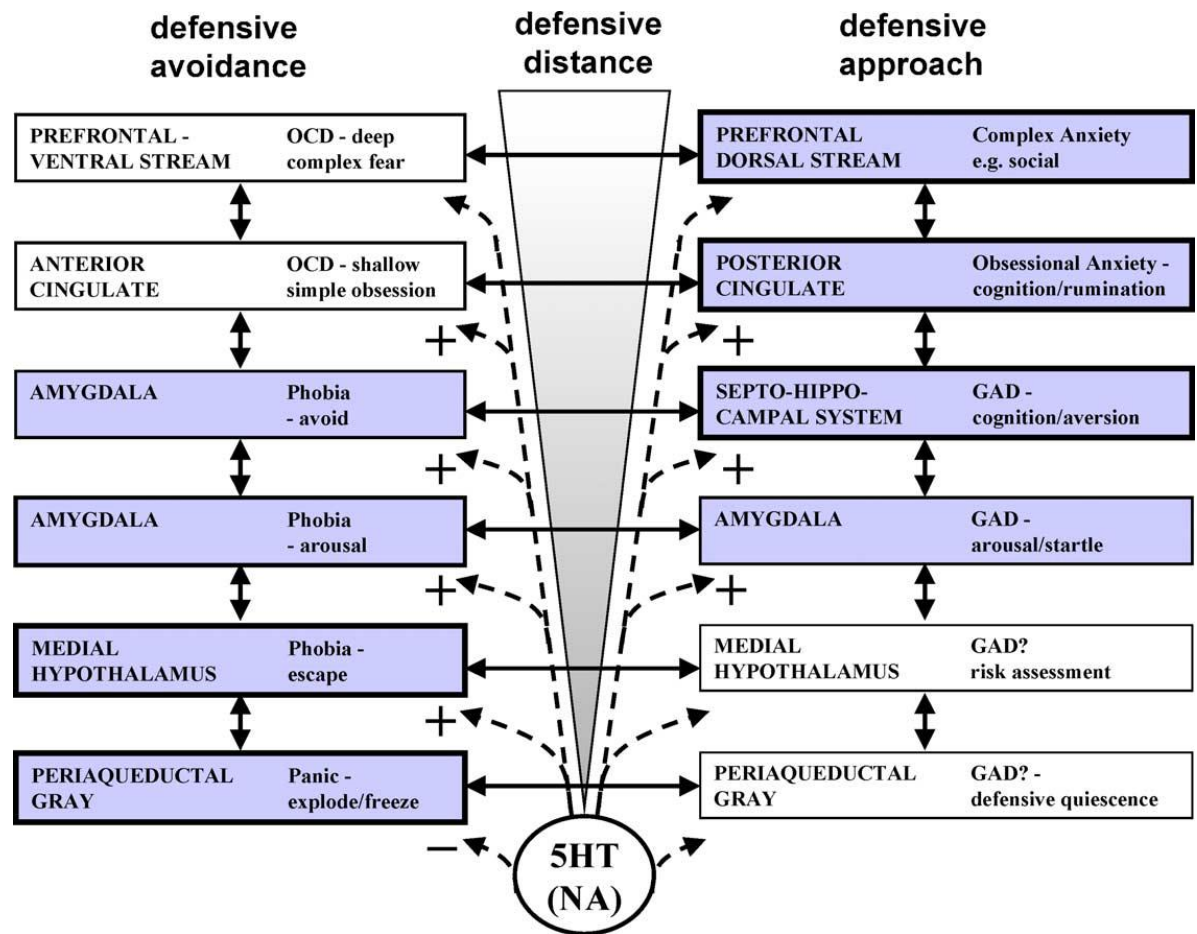


Figure 1, The two-dimensional defence system by McNaughton & Corr (2004).

The mechanism that underlies a possible switch from one defensive state to another might be caused by the neural structures responsible for the specific behaviours during specific situations. For instance, Mobbs et al. (2007) have shown that shifts from prefrontal to periaqueductal grey (PAG) occur, depending on threat imminence. They state that the PAG seems critical during imminent proximal threat, while distal threats elicit more activity in the prefrontal cortices. The potentiation of startle mostly seems to depend on the amygdala. In detail, a state of panic seems to depend on the PAG (McNaughton & Corr, 2004), while the amygdala is involved in fear and anxiety (LeDoux, 1994). The extended amygdala, and in particular the central nucleus of the amygdala and the bed nucleus of the stria terminalis (BNST) are implicated in mediating startle potentiation (Pissioti et al., 2003; Buchanan et al.,

Inhibition during circa-strike stage: Attention or switching of defensive mechanisms?

2004; Funayama et al., 2001). They also state that the PAG may inhibit the higher control processes when threat levels are very high. This is in line with the two-dimensional defence system by McNaughton and Corr (2004) (see figure 1). This system shows that when distance decreases, the responses tend to go from depending more on the prefrontal areas when distance to threat is large, to ultimately depending more on the PAG when a threat is imminent. The amygdala and the medial hypothalamus are responsible for responses at intermediate distances (see figure 1). Recently evidence has been found however that indicates that the basolateral amygdala (BLA) also has an inhibitory function on the vigilance system in humans (Terburg et al., 2012). An explanation for a possible switch between defensive mechanisms might be that it is caused by a specific interplay between certain parts of the amygdala (for instance the BLA), the medial hypothalamus and the PAG.

However, when the inhibition of startle depends on the attention given to the startle probe, it seems reasonable to assume that the startle probe is not fully processed by the defence system. This might then have caused the inhibition of startle found by Richter et al (2012) and Löw et al. (2008).

The purpose of the current study is to try and find out whether the lowering of startle found by Richter et al. (2012) and Löw et al. (2008) may be (at least partially) explained by participants switching attention away from the modality of the startle probe.

In the current study the modality of the startle probe and the distance signalling cues will all be auditory so that no cross-modality effects can occur and all attention is focussed on the modality in which the startle probes are presented. This enables us to specify two hypotheses that are mutually exclusive. Based on the attention interpretation by Richter et al. (2012) and Löw et al. (2008), we would expect that startle will not be inhibited when a threat is imminent since all attention is focussed upon the startle probe modality. Alternatively, if

Inhibition during circa-strike stage: Attention or switching of defensive mechanisms?

the lack of startle potentiation with imminent threat that requires active escape is again found with all attention focused on the auditory pathway then the attention explanation has to be ruled out. The switch in defensive responding then becomes the most plausible explanation.

Methods

Subjects

A total of 20 persons participated in the study; seven participants were excluded for various reasons. One participant was marked as non-responder and was excluded, since he or she had less than 1 artefact-and null-response free trial per condition per time-block. Another three did not pass the awareness check for the condition in which they could expect to receive the shock, even though these conditions were explicitly explained. One participant did not finish the habituation and test-block, and two people were excluded due to missing data caused by technical malfunction. Data from 13 participants (female=8, male=5; mean age 20.7 ± 2.35) were analysed. All received compensation for their participation in our study. None of the participants had any history of or current psychological and/or neurological disorders and all had self-reported normal vision and hearing.

EMG assessment

The startle eye-blink reflex was measured with electromyography (EMG). Two 4-millimetre bipolar Ag/AgCl surface electrodes were placed on the orbicularis oculi and the common mode sensor and ground electrodes were placed on the forehead. The data was DC-amplified by a BioSemi-amplifier and digitalized at a sampling rate of 2048 Hz.

Shock-procedure

Shocks were administered by placing two electrodes on the inside of the wrist a fixed distance from each other and were delivered to the side of the non-dominant hand.

Inhibition during circa-strike stage: Attention or switching of defensive mechanisms?

The participants received moderately painful shocks during the experiment. The level of pain was controlled for such that it was the same for all participants; a 4 on a subjective scale ranging from 1 to 5, corresponding to ‘rather annoying / painful’. This level was set prior to the experiment in a ‘shock work-up’ procedure (this procedure is described in detail by Klumpers (2012)). The shock consisted of a train of 150 2-ms pulses that were administered at a rate of 200 Hz.

Task

Every participant had to perform a practice-block (36 trials), a habituation-block (12 trials) and a test-block (86 trials), in consecutive order. For each of these trials the distance to threat could be either far away and easily escapable (safe), near-by and escapable with great effort (chance level, approach speed adjusted to individual performance on responding to the attack during the habituation-block) or up-front and inescapable. Furthermore, each trial type was presented under both safe and threat-conditions.

Of the 86 test-trials, 72 contained a startle probe and were therefore used in the analysis. Each of the six conditions (threat x distance) had twelve trials, amounting to seventy-two trials in total. Only eight trials within the threat condition contained the possibility of actually receiving a shock (depending on success of the avoidance response). The contingency between the shock and the different conditions was explicitly explained in the practice-block. In the habituation-block, no shocks were administered, but they did receive a startle-probe during each trial. It was signalled on the screen when participants were too slow or too fast when they pushed the button, and whether they would have received a shock at that moment if they would have been in the test-block. The tenth trial (a near-threat trial) of the test-block always contained a reinforcing shock. The timing for this trial was adjusted so that it was impossible for the participant to escape.

Inhibition during circa-strike stage: Attention or switching of defensive mechanisms?

The task was adapted from the circa-strike escape task (C-SET) designed by Terburg (2012).

Stimuli

During each trial, visual stimuli signalled the condition that the participant was in; safe or threat. In the safe-condition participants never received a shock; in the threat-condition they had a chance of receiving an electric shock, which was administered to the wrist.

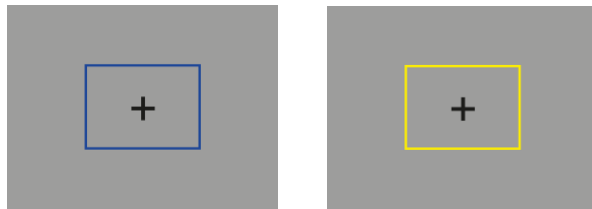


Figure 2. Blue signals a 'safe' condition, while yellow signals a 'threat' condition.

Within both the safe and threat the condition, different sounds indicated the distance condition (see figure 2 for the safe/threat signalling visual cues). This distance could be either far, near or too close to be avoided. Auditory stimuli were used to signal the distance between participant and threat. A far away threat was signalled by a 250 Hz tone, a nearby threat by a tone of 500 Hz and an unavoidable threat by a 1000 Hz tone. The subjective noise pressure levels for the tones were respectively 53, 51 and 54 B, which were all at a similar subjective level of 54 dB. This is in accordance with the equal loudness contour (Vitz, 1972).

Each trial had a fixation-time followed by an attack. An attack consisted of the tone getting higher. It could reach a maximum of a 1000 Hz, which indicated that the attack was successful, and a shock might be expected. In the near-condition when an attack was imminent, participants had an average of 235 ms to react. This time was adjusted for each participant, according to his or hers own average reaction time during the practice-block. The time was adjusted in such a way that participants could respond fast enough only at chance

Inhibition during circa-strike stage: Attention or switching of defensive mechanisms?

level. It could be as fast as 100 ms and as slow as 400 ms in the near-condition. In the far-condition the shock was always easily avoidable. Time to react to the tone started at 1000 ms, but was adjusted to be between 400 and 1600 ms. Since the tone started at 1000 Hz in the unavoidable distance-condition, participants always had a chance of receiving a shock when they were in the threat-condition. The inter-startle interval was 20 ± 3 seconds. See figure 3 for the timing and sequence of events during different trials.

A

Safe			
Fixation	Circa-strike escape task		
1-20 s	4-8 s		
	3-6 s	startle	1-2 s

B

Threat			
Fixation	Circa-strike escape task		
1-20 s	4-8 s		
	3-6 s	startle	1-2 s

C

Threat with shock				
Fixation	Circa-strike escape task			
1-20 s	4-8 s			
	3-6 s	startle	1-2 s	shock

Figure 3, sequence of events during test-trials. The first and second row displays the trial-condition and of which parts this condition consists. The third row shows the duration of the fixation and C-SET. The fourth row presents the duration of each part in the C-SET. A: Sequence of events in safe-condition with startle. B: Sequence of events in threat-condition with startle. C: Sequence of events in threat-condition with startle and shock. Fixation-time depends on the time since last startle. Inter-startle interval was 20 ± 3 seconds.

Anxiety and approach/avoidance scales

Before the start of the test a State Trait Anxiety Inventory (STAI-T), a Behavioural Inhibition System (BIS) and Behavioural Approach System (BAS) questionnaire were

Inhibition during circa-strike stage: Attention or switching of defensive mechanisms?

administered. This was done to help factor out possible effects that could be caused by individual trait anxiety and approach and avoidance tendencies.

Data reduction and analysis

Vision Analyzer software (Brain Products, brainproducts.com) was used to analyse the raw startle data. After that a 28-300 band-pass filter was used on the raw EMG data. The signal was then baseline corrected, rectified, segmented and smoothed offline with a 14 Hz zero phase Butterworth filter.

Segmentation happened on the basis of the conditions (threat x distance) and resulted in 72 epochs per subject. These segments were separated into 2 time-blocks, each containing either the first or second half of the trials. Each epoch started 50 ms before the startle probe onset and ended 150 ms after onset. Startle magnitudes were defined as peak EMG-activity between 25 and 100 milliseconds after startle probe onset. A baseline-artefact rejection (-30 to -20 ms) was performed. Trials with baseline activity greater than 2 standard deviations from mean baseline activity were marked as artefacts and trials with a ratio of <1.55 between standard deviation of signal and baseline were marked as null-responses. All startle data were standardized for use in analysis.

A factorial repeated measures ANOVA with a $2 \times 2 \times 3$ (time x threat x distance) design was used to compare the effects of threat and distance on startle during the first and second half of the test. Besides that, a factorial repeated measures ANOVA with a 2×3 (time x distance) design was used to compare the effects of threat and distance on fear-potentiated startle during the first and second half of the test. Outliers were windsorized so these could not alter the skewness or kurtosis of the data.

In a separate analysis STAI-T and BIS/BAS were entered as covariates to see whether they had any significant influence on the startle-data.

Inhibition during circa-strike stage: Attention or switching of defensive mechanisms?

Results

A factorial repeated measures analysis of variance (ANOVA) was used to examine 13 participants startle magnitude during 6 different conditions, threat (2) x distance (3), over two time periods (2) and for fear-potentiated startle for three distances over two time periods. A paired t-test was used to compare startle magnitude over two threat-conditions during three distances. Boxplots and Shapiro-Wilk indicated that the assumption of normality was not violated; F_{\max} was 3.14 for startle magnitude and 2.54 for the fear-potentiated startle, demonstrating homogeneity of variance. Mauchly's test showed that the assumption of sphericity was not violated for any of the factors.

Threat

There was a significant main effect of threat on startle magnitude, $F(1, 12) = 68.90$, $p < .001$, $\eta_p^2 = .852$. Startle was significantly higher in the threat condition ($M = 0.294$, $SD = 0.038$) than in the safe condition ($M = -0.292$, $SD = 0.036$).

Distance

Distance had a significant main effect on startle magnitude, $F(2, 24) = 23.79$, $p < .001$, $\eta_p^2 = .665$. Startle was significantly higher in the unavoidable condition ($M = 0.25$, $SD = 0.04$) than in the far-away condition ($M = -0.19$, $SD = 0.04$). Startle was also significantly higher in the unavoidable condition than in the near condition ($M = -0.05$, $SD = 0.03$), but there was no significant difference between the near and far-condition.

Threat x distance

Threat and distance had a significant interaction $F(2, 24) = 4.10$, $p = .029$, $\eta_p^2 = .255$. The difference between the safe and threat condition for each distance was examined with a paired t-test. It showed that for all distances, the threat-condition elicited a significantly higher startle than the safe-conditions (see figure 4). There was a significant difference in startle

Inhibition during circa-strike stage: Attention or switching of defensive mechanisms?

magnitude for the safe-condition ($M = -0.52$, $SD = 0.20$) and threat-condition ($M = -0.06$, $SD = 0.14$) during far-away trials; $t(12) = 5.46$, $p < .000$. There was also a significant difference in startle magnitude for the safe-condition ($M = -0.17$, $SD = 0.21$) and threat-condition ($M = 0.29$, $SD = 0.24$) during nearby trials; $t(12) = 4.76$, $p < .000$. Lastly, there was a significant difference in startle magnitude for the safe-condition ($M = -0.09$, $SD = 0.31$) and threat-condition ($M = 0.57$, $SD = 0.34$) during unavoidable trials; $t(12) = 4.15$, $p = .001$.

A far-away threat ($M = -0.43$, $SD = 0.09$) elicited a significantly lower fear-potentiated startle than an unavoidable threat ($M = 0.82$, $SD = 0.14$), $F(1, 12) = 6.53$, $p = .025$, $\eta_p^2 = .353$. No significant difference was found between the far-away and near ($M = 0.51$, $SD = 0.09$) condition, $F(1, 12) = 0.53$, $p = .481$, $\eta_p^2 = .042$ and between the unavoidable and near condition $F(1, 12) = 3.64$, $p = .080$, $\eta_p^2 = .233$.

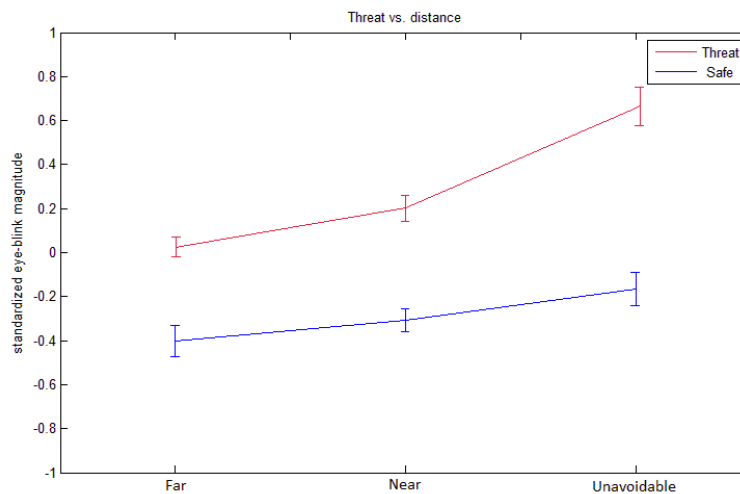


Figure 4, Standardized eye-blink magnitude for threat vs. distance

Time

Time had a significant influence on startle magnitude, $F(1, 12) = 169.43$, $p < .001$, $\eta_p^2 = .934$. Startle was significantly higher in the first half of the test ($M = 0.359$, $SD = 0.032$) than in the second half ($M = -0.357$, $SD = 0.026$). No interaction effects were found between time

Inhibition during circa-strike stage: Attention or switching of defensive mechanisms?

and threat $F(1, 12) = 0.78, p = .395, \eta_p^2 = .061$ and time and distance $F(2, 24) = 0.08, p = .927, \eta_p^2 = .006$. No three-way interaction effect was found between time, distance and threat, $F(2, 24) = 1.29, p = .293, \eta_p^2 = .097$. No significant main effect of time on fear-potentiated startle was found $F(1, 15) = .580, p = .458, \eta_p^2 = .037$, (see figure 5).

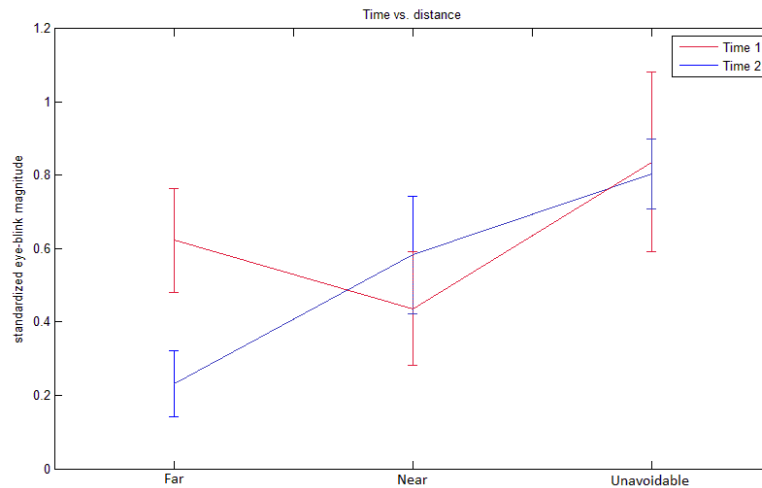


Figure 5, Standardized eye-blink magnitude for the fear-potentiated startle during the first and second half of the test. No significant differences.

Covariates

None of the questionnaires had a significant influence on any of the factors and the interactions between them ($p > .056$ for all factors) when entered into the analyses of startle as covariates. The influence of the STAI-T ($p = .056$) and BIS on time ($p = .073$) were the only ones that approached significance. Furthermore, none of the questionnaires had a significant influence on any of the factors and the interactions between them ($p > .300$ for all factors) when entered into the analyses of fear-potentiated startle as covariates. Due to the small sample size and because the covariates did not have a significant influence on either threat or distance, none of the questionnaires have been added as covariates.

Discussion

The current study investigated whether the relative inhibition of startle found by Richter et al. (2012) and the inhibition found by Löw et al. (2008) were caused by a switch between defensive mechanisms, or because the startle probe was not fully processed due to inattention towards the startle probe modality. The results show that time, distance and threat-level all have a significant influence on startle magnitude. As expected, startle magnitude was higher for the threat condition than for the safe condition for all distances (see Sabatinelli, Bradley & Lang, 2001). The manipulation of distance to threat by means of the C-SET was also successful, since distance to the threat had a significant influence on startle magnitude. Furthermore, distance to threat had a different effect on startle, depending on whether they were in a safe or threat condition.

When we look at the effects of the C-SET on the startle, we can see that for all distances fear-potentiated startle occurs. When we look closer at the FPS, we can see that there is a significant difference between the far- away condition and the unavoidable condition. This shows that when a threat is proximal instead of distal, startle is enhanced. However, no significant difference was found between a far-away threat and a nearby threat, or between the nearby threat and the unavoidable threat.

When we now look at the two hypotheses that were formulated (i.e. attention or a defensive mechanism), we can see that our results are inconclusive. The modality of the startle probe and the distance-signalling cues were both auditory in our study, contrary to the study by Löw et al. (2008). This way it was ensured that the startle probe was fully processed and a possible found inhibition would not depend on attention given to the startle probe. However, our results are inconclusive. The near and unavoidable conditions do not differ significantly, which would support our attention-related hypothesis, since the potentiation of startle seems present. However, the far and near condition also do not differ significantly,

Inhibition during circa-strike stage: Attention or switching of defensive mechanisms?

which would support our hypothesis of a switch between defensive mechanisms. Depending on this result, it seems startle-potentiation is inhibited.

It might be useful to repeat our study with as an extra condition a match or mismatch between startle probe and task modality. This way the original data by Terburg (2012) might be reproduced and direct comparisons between matching and mismatching modality's can be made. Terburg (2012) has shown that an inhibition of fear-potentiated startle occurred when a threat was near in his C-SET. The inhibition occurred in the near condition in the second half of the study, when this was compared to the first half. Just as in the study by Löw et al. (2008), there was a however a mismatch between startle probe and task modality in his study. As of yet no reason has been found for why this inhibition of fear-potentiated startle in the study by Terburg (2012) occurs during the second half of the test. In our study, with startle probe and task both having the same modality, we cannot conclude that this same inhibition of startle-potentiation was found.

Our study did have some limitations. Some of the effect sizes found were small to moderate, which was most possibly caused by excluding a large amount of participants (due to various reasons). These effect sizes might have been greater if the sample size had not been diminished so much.

In this study the modalities of the startle probe and the task were kept the same for the most part. The three tones that signalled distance to threat were auditory, as was the startle probe. However, the cue that signalled whether participants were in a safe or threat condition was visual. The alternative to this was six tones, each one signalling distance to threat in either the safe or threat condition. This was not ideal, since the physical quality of the tones (amount of Hz and loudness) might have interfered with the startle-reflex. A pilot-study would have been necessary to study these effects.

Inhibition during circa-strike stage: Attention or switching of defensive mechanisms?

To make sure that each tone was easily distinguishable, we chose three tones in our study, representing the three distances. At the time it was chosen to use a visual cue to signal the threat condition, since all the distance-signalling tones should always be distinguishable from one another. This proved more difficult if the frequency of the tones were to close together. However, the visual cue might have had some unwanted effects. The effect of distance on startle occurred in both the safe and the threat condition, which might be explained by a generalization-effect (see Baas et al., 2004 for an example of a generalization effect caused by a shock-signalling cue overshadowing a context cue). The visual cue might not have been salient enough in our study to overcome the auditory distance-cues, which might have caused this generalization effect. Different results might be obtained when all cues are auditory (i.e. six tones), because a generalization effect might be prevented.

In conclusion, our results are inconclusive. The current data support do not support the hypothesis that startle potentiation depends on the amount of attention given to the modality of the startle eliciting stimulus. It also does support not our hypothesis that the inhibition of startle-potentiation is caused by a switch between defensive mechanisms.

More research is needed to examine the specific cause for the inhibition of startle-potentiation when a threat is near and active escape is possible.

References

- Anthony, B. J., Butler, G. H., & Putnam, L. E. (1978). Probe-startle inhibition during HR deceleration in a forewarned RT paradigm. *Psychophysiology*, 15(Suppl.), S285.
- Buchanan, T.W., Tranel, D., & Adolphs, R. (2004). Anteromedial temporal lobe damage blocks startle modulation by fear and disgust. *Behavioural Neuroscience*, 118, 429–437.

Inhibition during circa-strike stage: Attention or switching of defensive mechanisms?

Davis, M., & Astrachan, D.I. (1978). Conditioned fear and startle magnitude: effects of different footshock or backshock intensities used during training. *Journal of Experimental Psychology; Animal Behavior Processes*, 4, 95–103.

Fanselow, M.S. (1994). Neural organization of the defensive behavior system responsible for fear. *Psychonomic Bulletin and Review*, 1, 429-438.

Funayama, E.S., Grillon, C., Davis, M., et al. (2001) A double dissociation in the affective modulation of startle in humans: Effects of unilateral temporal lobectomy. *Journal of Cognitive Neuroscience*, 13, 721–729.

Grillon, C., Ameli, R., Woods, S.W., Merikangas, K., & Davis, M. (1991). Fear-potentiated startle in humans: effects of anticipatory anxiety on the acoustic blink reflex. *Psychophysiology*, 28, 588–595.

Klumpers, F. (2012). Fear Not: Neurobiological Mechanisms of Fear and Anxiety. (Doctoral dissertation, University of Utrecht). Retrieved from <http://dspace.library.uu.nl/handle/1874/234624>.

Löw, A., Lang, P.J., Smith, J.C., & Bradley, M.M. (2008). Emotional arousal in threat and reward. *Psychological Science*, 19, 865– 873.

Lang, p. j., Bradley, M.M., & Cuthbert, B.N. (1997). Motivated attention: Affect, activation, and action. Lawrence Erlbaum Associates Publishers: New Jersey.

LeDoux, J.E. (1994). Emotion, memory and the brain. *Scientific American*, 27(6), 50–59.

Richter, J., Hamm, A.O., Pané-Farré, C.A., Gerlach, A.L., Gloster, A.T., Wittchen, H., Lang, T., Alpers, G.W., Helbig-Lang, S., Deckert, J., Fydrich, T., Fehm, L., Ströhle, A., Kircher, T., & Arolt, V. (2012). Dynamics of Defensive Reactivity in Patients with Panic Disorder and Agoraphobia: Implications for the Etiology of Panic Disorder. *Biological Psychiatry*, 72(6), 512-520.

Inhibition during circa-strike stage: Attention or switching of defensive mechanisms?

Mobbs, D., Petrovic, P., Marchant, J.L., Hassabis, D., Weiskopf, N., Seymour, B., et al. (2007). When fear is near: Threat imminence elicits prefrontal-periaqueductal greyshifts in humans. *Science*, 317, 1079–1083.

Mobbs, D., Marchant, J.L., Hassabis, D., Seymour, B., Tan, G., Gray, M., et al. (2009). From threat to fear: The neural organization of defensive fear systems in humans. *Journal of Neuroscience*, 29, 12236–12243.

McNaughton, N., Corr, P.J. (2004). A two-dimensional neuropsychology of defense: fear/anxiety and defensive distance. *Neuroscience and Behavioral Reviews*, 28, 285-305.

Pissiota, A., Frans, O., Michelgard, A., et al. (2003). Amygdala and anterior cingulate cortex activation during affective startle modulation: A PET study of fear. *European Journal of Neuroscience*, 18, 1325–1331.

Terburg, D. (2012). Hyper-vigilance for fear after basolateral amygdala damage in humans. *International Conference of Psychology (ICP), Cape Town, South Africa*.

Terburg, D. (2012). Hyper-vigilance for fear after basolateral amygdala damage in humans. *Translational Psychiatry*, 2, 115.

Vitz, P.C. (1972). Preference for tones as a function of frequency (hertz) and intensity (decibels). *Attention, Perception, & Psychophysics* 11(1), 84–88.

Yeomans, J.S., Li, L., Scott, B.W., & Frankland, P.W. (2002). Tactile, acoustic, and vestibular systems sum to elicit the startle reflex. *Neuroscience and Behavioural Reviews*, 26, 1-11.