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Is threat recognition special? Resistance of threat recognition to perceptual noise

***Abstract**: Perception takes into account the costs and benefits of possible interpretations of incoming sensory data. This should be especially pertinent for threat recognition, where minimising the costs associated with missing a real threat is of primary importance. We tested whether recognition of threats has special characteristics that adapt this process to the task it fulfils. Participants were presented with images of threats and visually matched neutral stimuli, distorted by varying levels of noise. We found threat superiority effect and liberal response bias. Moreover, increasing the level of noise degraded the recognition of the neutral images to higher extent than the threatening images.*

To summarise, recognising threats is special, in that it is more resistant to noise and decline in stimulus quality, suggesting that threat recognition is a fast 'all or nothing' process, in which threat presence is either confirmed or negated.

***Keywords**: threat superiority, object recognition, signal detection, fear module, misperceptions*

Although intuitively the purpose of perception should be to produce as accurate and detailed representation of the environment as possible, high metabolic costs of neuronal computations (Lennie, 2003) and time-constraints imposed on perception (Wilson, 2002) enforce limits on what level of accuracy can be achieved.

In fact, the main purpose of perception, just as any other function or organ, is to increase the organism's chances of survival. This is usually best fulfilled by obtaining a full, detailed and accurate representation of the environment. However, in some situations accuracy has to be sacrificed in order to maximise the rewards or minimise the costs for the organism.

As the embodied cognition approach posits, perception is a tool in service of our goals and needs, a tool that enables and optimises action (Proffitt, 2006). As such, perception should be shaped by the values that different elements of the environment represent to the organism. This view, initially voiced by the proponents of the much criticised 'New Look' approach to perception (Bruner & Goodman, 1947), is now approached again from different perspectives, with a solid theoretical grounding (Geisler & Diehl, 2003; Proffitt, 2006) and sounder empirical evidence (Balcetis & Dunning, 2006).

The purpose of this study is to establish whether recognition of threatening stimuli is special, i.e. whether and how it differs from recognition of neutral stimuli. Specifically, we aim to show how the potential costs related to threatening stimuli change the way threats are perceived and how the task of threat recognition is optimised by adjusting the level of trade-off between speed and accuracy, and increasing the resistance to noise.

Threat detection has been extensively studied as an example of how the value of an object can influence its interpretation. For example, it has been shown that threatening stimuli are detected easier and faster than non-threatening stimuli (March, Gaertner, & Olson, 2017; Rosa, Gamito, Oliveira, Morais, & Saraiva, 2011), even in young children (LoBue, 2010) and infants which suggests a biological basis of this mechanism (LoBue & DeLoache, 2010).

Öhman argued that detection of threats is governed by a 'fear module', which is able to function independently of the cortex and without conscious awareness (Öhman & Mineka, 2001). The fear module tags potentially threatening stimuli which receive preferential processing. Recently, pulvinar neurons have been identified as a candidate for the neurobiological substrate for the rapid detection of evolutionary threats (Van Le et al., 2013).

What is not clear is how the relevant stimuli are selected. Threat-superiority effect has been mainly demonstrated for attentional processes (LoBue & Matthews, 2014; New &

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German, 2015; Öhman, Soares, Juth, Lindström, & Esteves, 2012; Sakaki, Niki, & Mather, 2012), but clearly selection of certain stimuli for preferential processing must be preceded by at least rough perceptual analysis. In other words, if certain classes of stimuli are to be treated in a special way, items must be first recognised as belonging to this class. Therefore, there should be a quick way of assessing the visual stream for presence of threats (Öhman & Soares, 1993).

According to LeDoux (1996), processing of threatening stimuli is served by two pathways: a slower and more accurate cortical route – the 'high road' and a very quick, but more basic subcortical pathway – the 'low road'. The low road conveys only very coarse information, which means that only crude and inaccurate recognition can be obtained. However this is sufficient to pre-select and tag potentially threatening stimuli for further cortical processing.

Gray (1982) calls such mechanism an 'alarm bell', because its purpose is to detect and prompt allocation of attention to potentially threatening stimuli as quickly as possible. To achieve its purpose, such system is likely to sacrifice accuracy for speed, which will result in high rate of false alarms. LeDoux (1986) argues that an unnecessary fear response to a false alarm can always be extinguished when more information is acquired, but delaying the response until the stimulus is properly analysed can be potentially very costly.

This allows expressing threat detection problem in terms of signal detection theory, that is a method of measuring the ability to distinguish between signal and noise (Green & Swets, 1966; Macmillan & Creelman, 2005). Specifically, it allows distinguishing between cognitive and perceptual factors influencing the responses to stimuli contaminated with various levels of noise. The perceiver's ability to distinguish between signal and noise is referred to as *sensitivity* (d'). Higher sensitivity means that the perceiver is able to categorise the stimuli more accurately and she is less likely to mistake one type of stimulus for another. Criteron (c) refers to perceiver's response strategy independent of her ability to distinguish signal from noise and reflects her preference for certain type of response at the expense of other. The criterion is optimal when any further increase in the rate of desirable outcomes is related to an even higher increase in the undesirable outcomes. When the perceiver is more likely to respond 'Signal' than 'Noise', the criterion is called liberal, because higher levels of noise are likely to be tolerated. Liberal criterion is related to high rates of hits, but at the price of elevated rate of false alarms. In contrast, bias to respond 'Noise' rather than 'Signal' leads to a conservative criterion, which is less tolerant to noise and rejection of noisy stimuli is more likely. This means that although the proportion of correct rejections will increase, so will the overall number of misses. Changes in sensitivity are usually considered to affect earlier, perceptual stages of processing, whereas response bias can be changed at the cognitive level. For this reason, Signal Detection Theory provides means of distinguishing between factors influencing cognition and perception.

Many authors claim that a liberal response bias, with small number of misses and high number of false alarms, is the optimal decision making strategy when dealing with threats (Haselton & Buss, 2000; Nesse, 2001; Neuberg, Kenrick, & Schaller, 2011; Stein & Nesse, 2011). Nesse (2001) points out that all hazard- detection systems, e.g. flight, stress, cough or anxiety, behave like 'smoke detectors', that is defence responses are initiated too readily or too intensely. Error management theory (Haselton & Buss, 2000) predicts that whenever the cost of a miss is higher than the cost of a false alarm, or vice versa, a bias towards the least costly error should be manifested. Thus, a liberal bias, when the cost of a miss is high, is an evolutionary adaption that increases the fit of the organism by reducing total cost incurred by the organism, but at the price of increasing the total rate of errors it makes.

Thus, it would be expected that detection or recognition of threatening stimuli should be related to a liberal response bias, but not necesarilly increased sensitivity or accuracy, because the speed advantage might actually come at the expense of accuracy. In support of this hypothesis, several studies found that threatening or emotional stimuli were related to a liberal response bias compared to non –threatening stimuli, but not improved sensitivity or accuracy (Becker & Rinck, 2001; Wiens, Peira, Golkar, & Öhman, 2008; Windmann & Krüger, 1998; Windmann & Kutas, 2001). Similarly, the higher recognition rate related to emotional words is not cause by better recall, but, again, by a response bias (Dougal & Rotello, 2007). In other words, participants were more likely to mistake neutral stimuli for threatening stimuli than the other way round. On the other hand, threat detection may simply be more accurate and resistant to unfavourable viewing conditions. For example, the threat detection advantage may be related to rapid and preferential detection of certain low-level visual features, such as curvilinear shape of a snake (LoBue, 2014). LoBue, Matthews, Harvey and Stark (2014) report more accurate detection of threats, that goes beyond a simple response bias. The motivation for the existence of such mechanism would be its strong evolutionary advantage (Isbell, 2009). There is already some evidence for its biological basis (Van Le et al., 2013, 2016).

In this study, we investigated the effect of increasing levels of noise on recognition of threatening and non-threatening stimuli. We tested whether the threat-superiority effect is related not only to the allocation of attention, but also to object recognition. We paired threatening stimuli with visually similar neutral stimuli and tested how quickly and accurately they would be recognised. We hypothesised that the 'alarm bell' mechanism (Gray, 1982) or the fear module (Öhman & Mineka, 2001), which purpose is to pre-select potenitally threatening stimuli for preferential conscious processing, would lead to shorter reaction times for threatening stimuli, but also to a liberal response bias. In other words, we predicted that neutral stimuli will be more often mistaken for their threatening counterparts than the other way round. This effect should be present even in case of higher levels of noise, when the sensory input is very impoverished, because the fear module is adapted to making extremely quick decision based on fragmentary information.

Method

Participants

Thirty undergraduate Psychology students (21 females, mean age = 21.4, SD = 3.2), took part in the experiment for course credits, after giving their informed consent. The study was approved by the Faculty Research Ethics Committee.

Stimuli

All stimuli were 700 × 700 pixels greyscale pictures, matched in contrast and intensity. The stimuli comprised two sets, representing threats and their neutral counterparts. In each set there were four subcategories of threatening pictures matched with neutral counterparts, i.e. pictures of objects similar in physical appearance but non-threatening in nature. Pictures of spiders were matched with pictures of flowers, cockroaches with ladybugs, snakes with ropes, and rats with squirrels. There were nine different pictures in each threatening subcategory, matched with nine neutral counterparts. Every picture was additionally distorted with noise to various extents. On level 1 of distortion, 70% of all pixels were randomly chosen and replaced with pixels of random intensities, 75% of all pixels were replaced on level 2 and 80% on level 3.

Fifteen (8 females, mean age = 26.3, SD = 8.6) participants who did not take part in the actual experiment were asked to rate all pictures from the experimental set in terms of (1) subjective fear response the pictures evoked in them, from 1 – not scary at all to 7 – very scary (Fear) and (2) objective dangerousness assessment from 1 – not dangerous at all to 7 – very dangerous (Danger). They were also asked how easy each picture was to recognise, both in terms of its quality and typicality from 1 – very difficult to recognise to 7 – very easy to recognise. The rankings confirmed that pictures pre-classified as threatening (M = 5.1, SD = 0.7) were rated as significantly more fearsome than non-threatening pictures (M = 1.37, SD = 0.24), $t(71) = 39.4$, $p < 0.001$. Threatening pictures (M = 4.8, SD = 1.5) were also rated higher on dangerousness scale than non-threatening pictures (M = 1.6, SD = 0.3), $t(71) = 17{,}5$, $p < 0.001$. Finally, there was no significant difference between threatening pictures (M = 6.21, SD = 0.31) and non-threatening pictures (M = 6.29, SD = 0.25) in how easy they were to recognise, $t(71) = –1.6$, $p = 0.11$.

Procedure

Participants were seated approximately 70 cm. from the computer screen, so that the stimuli subtended ca. 19 degree visual angle.

Participant were randomly assigned to one of three experiment versions. In each version, each picture was presented only once at only one level of distortion, to avoid the effect of familiarity (caused by multiple exposures to the same image) on recognition. At the same time, between-participants, each picture was presented at each level of distortion equal number of times, to prevent the effect of interaction between specific picture characteristics and distortion level (e.g. some pictures may be easier or harder to recognize at higher levels of distortion).

In total, each participant saw 72 images, each at one of the three possible levels of distortion, half of these were threats and the other half were neutral.

For each trial, a fixation cross was displayed for 200 ms, followed by 300 ms blank screen and then target picture was displayed for 500 ms. Participants were asked whether they recognised the object on the picture and how confident they were about their decision on a scale from 1 (completely unsure) to 5 (very sure). They were asked to indicate which object they saw, choosing from three alternatives displayed on the left, right and in the middle of the screen, i.e. the target picture – e.g. ‘spider’, its counterpart – ‘flower’ or ‘none of these’. The reason for adding the third option (i.e. “none of these”) was to distinguish between cases of misperceptions, i.e. cases where a threatening image was mistaken for a neutral image or vice versa (i.e. a flower is mistaken for a spider, or a spider for a flower), from cases of lack of recognition (i.e. participant does not identify any object in the image) or instances where participant saw something else entirely in the image (for example sun, instead of flower or spider). The position in which the alternatives appeared on the screen and picture order were randomised from trial to trial, and for every participant.

Data analysis

The proportion of positive recognitions was calculated as the proportion of ‘Yes’ responses to the question ‘Did you recognise the object on the picture?’ to all responses, and served as a measure of propensity to accept the visual evidence as sufficient for recognition, considering the content of the image and noise level. Secondly, confidence levels served as a measure of internal assessment of the reliability of visual evidence, which may not be entirely dependent on the decision to positively identify an object, as in some circumstances we may require less evidence to commit to recognition (for example when a potential threat is involved).

Thirdly, proportion of hits was calculated as the proportion of correct responses to the second question, where participants were asked to indicate what they saw and represented accuracy in the task. All “none of these” responses (i.e. 16.9% of all responses) were discarded from the data. The reaction times related to these responses were significantly longer than both correct responses and false alarms, and their confidence levels were significantly lower. This suggests that they were predominantly related to lack of recognition, and for this reason they were excluded from the analysis, as the purpose of the study was to analyse only genuine misperceptions, i.e. cases where one object is mistaken for another.

Finally, reaction times longer than the mean plus two standard deviations were winsorised, i.e. replaced by the value of mean added to two standard deviations. This was equal to 3276 ms. and 3.5% of the collected reaction times were replaced. A comparison analysis of both winsorised and trimmed data showed that the results were not significantly impacted by the choice of either of these standard procedures.

Alpha level of .05 was used for all statistical tests. When the Mauchly's test revealed that the assumption of sphericity was violated, the degrees of freedom were corrected using Greenhouse-Geiser estimates of sphericity. The measure of effect size reported here is eta squared (η^2), that is a proportion of variance explained by the manipulation of the independent variable to total variance in the data.

Criterion (c) was calculated as half of a standardised sum of proportion of hits and false alarms, while sensitivity (d') was calculated as a standardised difference between the proportion of hits and false alarms, separately for every participant.

Results

Effect of stimulus threat -content

A 2 (threat content: threatening vs. neutral stimuli) × 3 (level of distortion) repeated- measures ANOVA revealed that threatening stimuli were recognised more often ($F(1, 29) = 36.1$, $p < 0.001$, $\eta^2 = 0.13$) and more accurately ($F(1, 29) = 21.3$, $p < 0.001$, $\eta^2 = 0.18$) than neutral stimuli (Figure 1). Threatening stimuli were also related to higher levels of confidence ($F(1, 29) = 64.9$, $p < 0.001$, $\eta^2 = 0.29$) and shorter reaction times ($F(1, 29) = 25.1$, $p < 0.001$, $\eta^2 = 0.19$) than neutral stimuli.

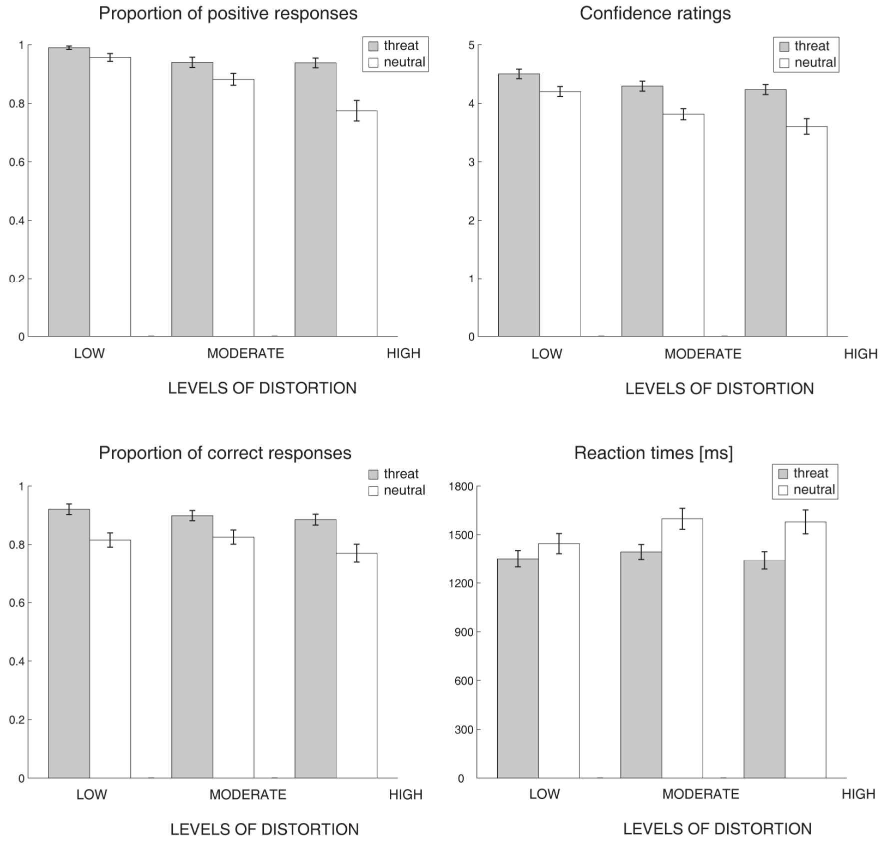
Effect of distortion level

There was a significant main effect of level of distortion on proportion of positive recognitions ($F(2, 58) = 16.9$, $p < 0.001$, $\eta^2 = 0.17$), confidence levels ($F(2, 58) = 21.1$, $p < 0.001$, $\eta^2 = 0.17$) and reaction times ($F(2, 58) = 4.46$, $p = 0.02$, $\eta^2 = 0.04$), but not on the proportion of hits ($F(2, 58) = 2.47$, $p = 0.09$).

The interaction between the level of distortion and threat-content in the stimuli was significant for the proportion of positively recognised pictures ($F(1.4, 40.3) = 7.11$, $p = 0.01$, $\eta^2 = 0.06$) and confidence levels ($F(1.5, 44.3) = 5.01$, $p = 0.02$, $\eta^2 = 0.02$), but not for reaction times ($F(2, 58) = 2.55$, $p = 0.87$) or proportion of hits ($F(2, 58) = 0.6$, $p = 0.55$).

Significant interactions were followed by a repeated-measures ANOVA with distortion as the factor, performed on the proportion of positively recognised pictures and confidence levels threatening and neutral, separately for threatening and neutral images. The effect of distortion was significant for all analyses, i.e. in case of positive recognition for threatening images ($F(2, 58) = 5.06$, $p = 0.01$, $\eta^2 = 0.15$) and neutral images ($F(2,58) = 14.73$, $p < .001$, $\eta^2 = 0.34$), and in case of confidence levels

Figure 1. Recognition of evolutionary threats. Proportion of positive responses, confidence ratings, proportion of hits and reaction times for evolutionary threats and their neutral counterparts at different levels of distortion. As level of the noise increases, recognition of the neutral images becomes harder, while threatening images remain resistant to the degradation in image quality.



for both threatening images ($F(2, 58) = 8.56$, $p = 0.001$, $\eta^2 = 0.23$) and neutral images ($F(2, 58) = 18.27$, $p < .001$, $\eta^2 = .39$). However, given that the interaction between threat and distortion in the omnibus ANOVA was significant, we can conclude that the effect of distortion was smaller on the threatening images, compared to neutral images, as evidenced by smaller effect sizes.

Signal Detection

Criterion was significantly different from the optimal criterion with value of 0 and biased towards threats, $t(29) = 3.73$, $p = 0.001$.

A one-way ANOVA performed on the sensitivity and criterion values, with the level of distortion as the factor, revealed a significant main effect of level of distortion on sensitivity, $F(2, 58) = 8.3$, $p = 0.001$, $\eta^2 = 0.08$, but not the criterion, $F(2, 58) = 1.6$, $p = 0.22$. Contrasts revealed that sensitivity for level 2 of distortion (moderate) was significantly higher than for level 3 of distortion (high), $F(1, 29) = 6.5$, $p = 0.02$, but there was no significant difference in sensitivity between level 1 (mild) and level 2 of distortion, $F(1, 29) = 2.5$, $p = 0.13$.

Correlations

Fear and danger ratings as well as animal/non-animal and threat/non-threat categories for every picture were correlated with all dependent variables. These correlations are presented in Table 1.

Discussion

Problem of sufficient stimulus control

In experiments investigating reactions to natural (i.e. not experiment- induced) threats, confounds occluding or distorting the results are inevitable. Choice of controls is very much limited by the target stimuli, which are entirely determined by the subject of the study. In our study, we have focused on matching the stimuli in terms of visual similarity, i.e. we wanted to ensure that threatening stimuli and their neutral counterparts were sufficiently alike to be occasionally mistaken for another. To ensure that one threatening stimuli were not simply easier to recognise on purely visual level, we asked an independent group of participants to rate all pictures in terms of easiness of recognition. We found that there was no significant difference between the two picture sets, with non-threatening pictures even slightly easier to recognise. Another possible confound could be the animal superiority effect, i.e. easier and faster detection of animals compared to non-animals (Tipples, Young, Quinlan, Broks, & Ellis, 2002) since threatening stimuli usually represent animals and are matched to non-animate counterparts. We did find a positive correlation between the dependent variables and animal/non-animal category (Table 1). However, the correlations for all threat-related factors, i.e. threat/non-threat category, fear and danger ratings were stronger. For all four dependent variables, fear ratings were the strongest correlate, followed by threat/non-threat category, which supports the general threat superiority hypothesis.

Is recognition of threats special?

Similar to previous studies (Becker & Rinck, 2004; Windmann & Krüger, 1998), we found a liberal response bias for threats. Additionally, accuracy was higher for the threatening stimuli, which means that participants mistook neutral stimuli for threatening stimuli more readily than the other way round (given that "none of these" responses were excluded from the analysis). This suggests that the perceptual threshold for detection of threats is lower than threshold for other stimuli, i.e. less information is needed to confirm detection of a threatening stimulus than neutral stimulus.

This is also supported by the effect of level of distortion on recognition of threatening and neutral stimuli. Increasing the degree of noise in the pictures from mild to high had barely any effect on recognition of threatening pictures, but caused substantial deterioration in performance for neutral stimuli. For most dependent variables, the difference between neutral and threatening stimuli was larger for high levels of noise compared to mild or moderate noise. In other words, recognition of threatening stimuli was resistant to noise and deteriorated at much lower rate than recognition of neutral stimuli. What is important, although confidence levels, reaction times and proportion of positive recognitions for threatening stimuli declined only slightly, sensitivity significantly decreased for higher levels of distortion. Therefore, lack of effect of noise on reaction times or confidence levels was coupled

Table 1. Correlations (one-tailed) between the dependent variables (proportion of positive responses, reaction times, confidence ratings, proportion of false alarms) and fear ratings (1–7), danger ratings (1–7), threat category (threatening/non-threatening) and animal category (animal/non-animal) based on all pictures in the set (N = 72).

	Fear		Danger		Threat		Animal	
	r(72)	p	r(72)	p	r(72)	p	r(72)	p
Proportion of Positive Responses	**–.37**	.001	–.26	.013	.34	0.002	–0.23	0.027
Reaction Times	**–.44**	< .001	–.28	.008	.43	< 0.001	–0.35	0.001
Confidence Ratings	**.50**	< .001	.38	< .001	–.41	< 0.001	0.34	0.002
Proportion of False Alarms	**–.31**	.004	–.25	.016	.22	0.031	–0.19	0.055

Note. Bold font indicates the highest correlation for the dependent variable.

with decrease in accuracy, which means that recognition of threats is related to strategic preservation of characteristics that are crucial to optimise this task.

This could suggest that the purpose of threat recognition is slightly different to the purpose of 'ordinary' recognition. Normally, the aim is to obtain as accurate representation of the sensory input as possible. For this reason, loss of input quality inevitably leads to more cautious recognition and is also echoed in indirect measures of recognition success such as confidence levels or reaction times. In other words, poorer stimulus quality leads to less confident, slower and more cautious recognition, reflecting the uncertainty related to the input, which is an important gauge of recognition accuracy (Król & El-Deredy, 2011a, 2011b). In contrast, in case of threat recognition the priorities are to avoid misses and to decide quickly, while accuracy can be sacrificed. For this reason, threat recognition will not be sensitive to changes in stimulus quality, but will retain two crucial characteristics- high speed and avoidance of false negatives, reflected in a liberal response bias.

The outcome of threat detection is an 'all or nothing' decision (Curio, 1993; Lima & Dill, 1990) – either the fear response is activated or not. Therefore, all is needed is a binary, 'all or nothing' information whether the threat is present or not. Any additional information, like for example the level of accuracy or confidence in the sensory input is in this case superfluous and adds unnecessary computational load when speed and efficiency of processing is of utmost importance. For this reason, although accuracy as measured by sensitivity dropped at higher levels of distortion, perceivers were still confident and quick in their decisions. Similar results have been obtained by Norberg, Peira and Wiens (2010) Gao and Jia (2017) and Soares, Lindström, Esteves and Öhman (2014), who found that threatening stimuli were more often detected than neutral stimuli, even under high perceptual and attentional load conditions.

Conclusion

We have found a threat superiority effect for recognition of threats. Threats were also related to a liberal criterion and participants were more likely to mistake neutral stimuli for threatening stimuli than the other way round. Moreover, recognition of threatening stimuli was resistant to noise and did not deteriorate as a result of increasing the level of distortion in the pictures to the same extent as recognition of neutral stimuli.

We conclude that recognition of threats is special in a sense that its primary aim is not necessarily maximising accuracy, but minimising processing time and avoiding false negatives, which can be very costly for the organism. To serve this purpose all is needed is an 'all or nothing' information confirming or negating presence of the threat.

For this reason, threat recognition does not reflect changes in stimulus-related uncertainty, i.e. inevitable loss of accuracy is not accompanied by deterioration in proportion of positive recognitions, confidence levels and reaction times.

References

Balcetis, E., & Dunning, D. (2006). See What You Want to See: Motivational Influences on Visual Perception. *Journal of Personality & Social Psychology*, *91*(4), 612–625.

Becker, E. S., & Rinck, M. (2001). Sensitivity and response bias in fear of spiders. *Cognition & Emotion*, *18*(7), 961–976.

Bruner, J. S., & Goodman, C. C. (1947). Value and need as organizing factors in perception. *Journal of Abnormal and Social Psychology*, *42*, 33–44.

Curio, E. (1993). Proximate and developmental aspects of antipredator behavior. *Advances in the Study of Behavior*, *22*, 135–238.

Dougal, S., & Rotello, C. M. (2007). 'Remembering' emotional words is based on response bias, not recollection. *Psychonomic Bulletin & Review*, *14*(3), 423–429.

Gao, H., & Jia, Z. (2017). Detection of Threats under Inattentional Blindness and Perceptual Load. *Current Psychology*, *36*(4), 733–739.

Geisler, W. S., & Diehl, R. L. (2003). A Bayesian approach to the evolution of perceptual and cognitive systems. *Cognitive Science*, *27*(3), 379–402.

Gray, J. A. (1982). Précis of the neuropsychology of anxiety: An enquiry into the functions of the septo-hippocampal system. *Behavioral and Brain Sciences*, *5*, 469–543.

Green, D. M., & Swets, J. A. (1966). *Signal Detection Theory and Psychophysics*. New York: Wiley & Sons.

Haselton, M. G., & Buss, D. M. (2000). Error Management Theory: A New Perspective on Biases in Cross-Sex Mind Reading. *Journal of Personality & Social Psychology*, *78*(1), 81–91.

Isbell, L. (2009). *The Fruit, the Tree, and the Serpent*. Harvard University Press.

Król, M. E., & El-Deredy, W. (2011a). Misperceptions are the price for facilitation in object recognition. *Journal of Cognitive Psychology*, *23*(5), 641–649.

Król, M. E., & El-Deredy, W. (2011b). When believing is seeing: The role of predictions in shaping visual perception. *The Quarterly Journal of Experimental Psychology*, *64*(9), 1743–1771.

LeDoux, J. E. (1986). Sensory systems and emotion: A model of affective processing. *Integrative Psychiatry*, *4*, 237–248.

LeDoux, J. E. (1996). *The Emotional Brain*. New York: Simon & Schuster.

Lennie, P. (2003). The cost of cortical computation. *Current Biology*, *13*, 493–497.

Lima, S., & Dill, L. (1990). Behavioral decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology*, *68*, 619–640.

LoBue, V. (2010). And along came a spider: An attentional bias for the detection of spiders in young children and adults. *Journal of Experimental Child Psychology*, *107*(1), 59–66.

LoBue, V. (2014). Deconstructing the Snake: The Relative Roles of Perception, Cognition, and Emotion on Threat Detection. *Emotion*, *14*(4), 701–711.

LoBue, V., & DeLoache, J. S. (2010). Superior detection of threat-relevant stimuli in infancy. *Developmental Science*, *13*(1), 221–228.

LoBue, V., & Matthews, K. (2014). The snake in the grass revisited: An experimental comparison of threat detection paradigms. *Cognition and Emotion*, *28*(1), 22–35.

LoBue, V., Matthews, K., Harvey, T., & Stark, S. L. (2014). What accounts for the rapid detection of threat? Evidence for an advantage in perceptual and behavioral responding from eye movements. *Emotion*, *14*(4), 816–823.

Macmillan, N. A., & Creelman, C. D. (2005). *Detection Theory: A User's Guide*. Cambridge: Cambridge University Press.

March, D. S., Gaertner, L., & Olson, M. A. (2017). In: Harm's Way: On Preferential Response to Threatening Stimuli. *Personality and Social Psychology Bulletin*, *43*(11), 1519–1529.

Nesse, R. M. (2001). The Smoke Detector Principle. *Annals of the New York Academy of Sciences*, *935*, 75–85.

Neuberg, S. L., Kenrick, D. T., & Schaller, M. (2011). Human threat management systems: Self-protection and disease avoidance. *Neuroscience & Biobehavioral Reviews*, *35*(4), 1042–1051.

New, J. J., & German, T. C. (2015). Spiders at the cocktail party: an ancestral threat that surmounts inattentional blindness. *Evolution and Human Behavior*, *36*(3), 165–173.

Norberg, J., Peira, N., & Wiens, S. (2010). Never mind the spider: Late positive potentials to phobic threat at fixation are unaffected by perceptual load. *Psychophysiology*, *47*(6), 1151–1158.

Öhman, A., & Mineka, S. (2001). Fears, Phobias, and Preparedness: Toward an Evolved Module of Fear and Fear Learning. *Psychological Review*, *108*(3), 483–522.

Öhman, A., & Soares, J. J. F. (1993). On the Automatic Nature of Phobic Fear: Conditioned Electrodermal Responses to Masked Fear-Relevant Stimuli. *Journal of Abnormal Psychology*, *102*(1), 121–132.

Öhman, A., Soares, S. C., Juth, P., Lindström, B., & Esteves, F. (2012). Evolutionary derived modulations of attention to two common fear stimuli: Serpents and hostile humans. *Journal of Cognitive Psychology*, *24*(1), 17–32.

Proffitt, D. R. (2006). Embodied Perception and the Economy of Action. *Perspectives on Psychological Science*, *1*(2), 110–122.

Rosa, P. J., Gamito, P., Oliveira, J., Morais, D., & Saraiva, T. (2011). Attentional orienting to biologically fear-relevant stimuli: data from eye tracking using the continual alternation flicker paradigm. *Journal of Eyetracking, Visual Cognition and Emotion*, *1*(1), 1647–7677.

Sakaki, M., Niki, K., & Mather, M. (2012). Beyond arousal and valence: The importance of the biological versus social relevance of emotional stimuli. *Cognitive, Affective, & Behavioral Neuroscience*, *12*(1), 115–139.

Soares, S. C., Lindström, B., Esteves, F., & Öhman, A. (2014). The Hidden Snake in the Grass: Superior Detection of Snakes in Challenging Attentional Conditions. *PLoS ONE*, *9*(12), e114724.

Stein, D. J., & Nesse, R. M. (2011). Threat detection, precautionary responses, and anxiety disorders. *Neuroscience & Biobehavioral Reviews*, *35*(4), 1075–1079.

Tipples, J., Young, A. W., Quinlan, P., Broks, P., & Ellis, A. W. (2002). Searching for threat. 55(3), 1007–1026. *Quarterly Journal of Experimental Psychology*, *55*(3), 1007–1026.

Van Le, Q., Isbell, L. A., Matsumoto, J., Le, V. Q., Nishimaru, H., Hori, E., … Nishijo, H. (2016). Snakes elicit earlier, and monkey faces, later, gamma oscillations in macaque pulvinar neurons. *Scientific Reports*, *6*(1), 20595.

Van Le, Q., Isbell, L. A., Matsumoto, J., Nguyen, M., Hori, E., Maior, R. S., … Nishijo, H. (2013). Pulvinar neurons reveal neurobiological evidence of past selection for rapid detection of snakes. *Proceedings of the National Academy of Sciences*, *110*(47), 19000–19005.

Wiens, S., Peira, N., Golkar, A., & Öhman, A. (2008). Recognizing Masked Threat: Fear Betrays, But Disgust You Can Trust. *Emotion*, *8*(6), 810–819.

Wilson, M. (2002). Six views of embodied cognition. *Psychonomic Bulletin & Review*, *9*, 625–636.

Windmann, S., & Krüger, T. (1998). Subconscious Detection of Threat as Reflected by an Enhanced Response Bias. *Consciousness and Cognition*, *7*(4), 603–633.

Windmann, S., & Kutas, M. (2001). Electrophysiological Correlates of Emotion-Induced Recognition Bias. *Journal of Cognitive Neuroscience*, *13*(5), 577–592.