International Society of Polygraph Examiners

1704 Locust Street, 2d Floor, Philadelphia, PA 19103, United States.
Tel: +1-215-307-5600. Fax: +1-215-545-1773
Website: http://www.isope.net

Research Digest

James Allan Matte, Editor

Volume 3 **2016** **Number 2**

The following excerpts of a study by Andreas Low, Mathias Weymar and Alfons O. Hamm, Department of Biological and Clinical Psychology, University of Greifswald; Department of Humanities and Social Sciences, Helmut-Schmidt-University/ University of the Federal Armed Forces, Hamburg, Germany, published in *Psychological Science*, online before print October 6, 2015, doi: 10.1177/0956797615597332, is reprinted by permission of SAGE Publications in this issue of *Research Digest* with its Editor's Comment at the end of the cited study.

When Threat Is Near, Get Out of Here
Dynamics of Defensive Behavior During Freezing and Active Avoidance

Abstract

When detecting a threat, humans and other animals engage in defensive behaviors and supporting physiological adjustments that vary with threat imminence and potential response options. In the present study, we shed light on the dynamics of defensive behaviors and associated physiological adjustments in humans using multiple psychophysiological and brain measures. When participants were exposed to a dynamically approaching, uncontrollable threat, attentive freezing was augmented, as indicated by an increase in skin conductance, fear bradycardia, and potentiation of the startle reflex. In contrast, when participants had the opportunity to actively avoid the approaching threat, attention switched to response preparation, as indicated by an inhibition of the startle magnitude and by a sharp drop of the probe-elicited P3 component of the evoked brain potentials. These new findings on the dynamics of defensive behaviors form an important intersection between animal and human research and have important implications for understanding fear and anxiety-related disorders.

Discussion

Our data provide direct evidence for a dynamic organization of defensive behavior in humans supporting the threat-imminence model derived from animal research. First, autonomic, somatic, and brain responses varied systematically with the increasing imminence of a potential threat and the behavioral options available. Second, at the imminent circa-strike stage, startle responses were potentiated during passive anticipation of the threat but were inhibited when active coping was possible. This provides a direct measure for the switch from attentive freezing to active avoidance. These behavioral changes were associated with appropriate physiological adjustments to support effective action. Third, **the cognitive system also supports effective defensive responding by sensitizing sensory encoding and reducing selective attention to irrelevant stimuli.**

Inevitable threat and passive freezing

When there is no possibility to actively avoid the aversive stimulus, humans—as rodents do—show defensive behavior that can be described as attentive freezing. With approaching imminence of the potential threat, sympathetic activation increases linearly, which suggests increased orienting and autonomic arousal to the approaching threat. Heart rate decreased more quickly during the threat than during the safe condition, starting by the last picture of the approaching-threat sequence. Heart rate deceleration has been reliably observed during increased orienting toward external stimuli (Bradley, 2009) and has been associated with facilitated sensory intake (Graham & Clifton, 1966) coupled with somatic inhibition (Obrist, 1981). Heart rate deceleration can become fear bradycardia as attention is focused on the predator, and immobility is a means to avoid discovery (Campbell et al., 1997). Strong heart rate deceleration was observed when the painful stimulus was inevitably approaching.

The cortical data support this pattern of defensive reactivity. The increase in the sensory N1 component of the evoked brain potential to the acoustic probe would also support this interpretation. Again, the N1 component was larger during the threat condition than during the safe condition, which suggests that the general alertness to external stimuli (in this case, the acoustic probe) increased with increasing proximity of the threat. Supporting previous research (for a review, see Hamm & Weike, 2005), our results showed that startle-eyeblink responses were significantly potentiated when elicited during a sequence of cues predicting the occurrence of an aversive event relative to when those cues did not predict an aversive event. Fear-potentiated startle increased linearly with increasing size of the aversive stimulus. These data are in line with findings showing temporal specificity of startle potentiation, with strongest potentiation when the electric shock was expected (Grillon, Ameli, Merikangas, Woods, & Davis, 1993).

Threat and active avoidance

The pattern of defensive reactivity changed substantially when the aversive stimulus was avoidable: a sharp increase in skin conductance, a direct measure of sympathetic arousal, immediately prior to the initiation of the motor response as well as a strong heart rate acceleration when active avoidance was possible. According to the cardiac-somatic-coupling hypothesis (Obrist, 1981), cardiac acceleration is associated with somatic activation in the behavioral context of defense. Notably, a drastic reversal of the fear-potentiated-startle reflex became evident when individuals could actively avoid the electrical stimulus. This pattern of the fear-potentiated startle is remarkably consistent with findings from animal experimentation relating the switch from startle potentiation to startle inhibition to different patterns of defensive behaviors in rodents that are modulated by different subregions of the PAG (Benarroch, 2012; Fanselow, 1991; Walker et al., 1997). The current data suggest that different subregions of the PAG might also regulate adjustments of defensive reflexes in humans, probably actively inhibiting postencounter attentive freezing defense by the dorsolateral PAG during preparation for active avoidance. Data from neuroimaging studies by Mobbs and coworkers support these interpretations. Mobbs et al. (2007, 2009, 2010) found increased activation of the midbrain PAG area and an increased coupling between the midbrain and the mid dorsal anterior cingulate when a threat became imminent, although no further discrimination between different subregions of the PAG depending on different defensive response patterns was possible in these functional MRI studies. Preliminary evidence from our own lab suggests that PAG activation under threat is more pronounced during preparation for active avoidance compared with attentive freezing in humans (Wendt et al., 2014).

Selective attention and defensive action

The P3 component to probes presented during the last picture of the approaching-threat sequence was significantly reduced when active avoidance was possible. In other words, the inhibition of the startle reflex was associated with a reduced P3 amplitude elicited by the same probe stimulus. The P3 amplitudes to secondary acoustic startle probes are also significantly reduced when individuals view emotionally arousing visual stimuli (Bradley et al., 2006; Schupp et al., 1997) or experience unpleasant interoceptive cues (Alius, Pané-Farré, Löw, & Hamm, 2015; Ceunen, Vlaeyen, & Van Diest, 2013), which suggests that more attentional resources are allocated to the visual or interoceptive foreground stimuli that predict the occurrence of the threat and set the stage for effective active avoidance. As a consequence, elaborated processing of the secondary acoustic probe is reduced. This reduction of the P3 component was specific for the active condition, which suggests that the blocking of irrelevant stimuli is relevant only when effective action is required.

Conclusions

In a recent article, LeDoux (2014) argues very convincingly that terms such as “fear conditioning” and “fear system” blur the distinction between processes that give rise to feelings that we call fear and processes that control perception and defensive responses to threat. The current data support this view that defensive behavior is not an entity but is rather dynamically organized depending on the imminence of the threat and the behavioral repertoire at hand. When the threat is inevitable—as in a typical Pavlovian fear-conditioning procedure—the conditioned stimulus elicits defensive attentive freezing characterized by a robust potentiation of the startle reflex that increases with progressive proximity of the approaching threat. Studies that have investigated fear learning have mainly focused on this form of defensive freezing. If the organism, however, has the opportunity to actively avoid the progressing threat, startle responses are inhibited in preparation of active avoidance. These findings are in line with animal data from Moscarello and LeDoux (2013) showing that active avoidance directly opposes the expression of conditioned freezing. Training animals for active avoidance recruits infralimbic prefrontal cortex (ilPFC) to inhibit central-amygdala-mediated expression of conditioned freezing. Pretraining lesions of the ilPFC increased conditioned freezing while causing a corresponding decrease in active avoidance.

Our findings are not only theoretically important for understanding the dynamic organization of defensive systems and circuits but also have substantial clinical implications. In a clinical study, Richter and coworkers (2012) found a strong potentiation of the startle reflex in a high proportion of patients with panic disorder and agoraphobia while being trapped in a small dark room. Notably, for patients who left the small room prematurely (thus showing active avoidance), heart rate increased before escape and startle responses were inhibited, which shows the same blockade of attentive freezing during active avoidance. Indeed, by blocking active avoidance during exposure therapy, we would expect to increase defensive freezing again. A better understanding of these interactions between defensive behaviors and their underlying neural circuits might prove important for improving behavioral treatments of anxiety disorders.

RESEARCH DIGEST EDITOR'S COMMENT:

The above study reflects human and animal defensive behavior and supporting physiological adjustments "that vary with threat imminence and potential response options" which were categorized as *Attentive Freezing* and *Active Avoidance.* During Attentive Freezing, the heart rate decreases, but during Active Avoidance the heart rate increases. This phenomenon was elucidated in *Guiding Principles and Benchmarks for the Conduct of Validity Studies in Psychophysiological Veracity Examinations Using the Polygraph* (Matte 2010). A field study using a large sample of confirmed Deceptive and Non-Deceptive polygraph examinations is currently being conducted by two members of ISOPE to determine the pulse rate in the Reaction Tracing Segment and the Relief Tracing Segment for DI and NDI cases, for comparison with its related Average Tracing Segment. The collected data should provide answers to the diagnostic accuracy of each of the two defensive behaviors and their value in the decision making process.

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