Biological Psychology 126 (2017) 19–29

Contents lists available at ScienceDirect

Biological Psychology

journal homepage: www.elsevier.com/locate/biopsycho

Feedback from the heart: Emotional learning and memory is controlled by cardiac cycle, interoceptive accuracy and personality

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ARTICLE INFO

Keywords:
Emotional memory
Associative memory
Attentional narrowing
Cardiac timing
Interoception
Baroreceptors
Personality
Extraversion
Neuroticism

ABSTRACT

Feedback processing is critical to trial-and-error learning. Here, we examined whether interoceptive signals concerning the state of cardiovascular arousal influence the processing of reinforcing feedback during the learning of 'emotional' face-name pairs, with subsequent effects on retrieval. Participants (N = 29) engaged in a learning task of face-name pairs (fearful, neutral, happy faces). Correct and incorrect learning decisions were reinforced by auditory feedback, which was delivered either at cardiac systole (on the heartbeat, when baroreceptors signal the contraction of the heart to the brain), or at diastole (between heartbeats during baroreceptor quiescence). We discovered a cardiac influence on feedback processing that enhanced the learning of fearful faces in people with heightened interoceptive ability. Individuals with enhanced accuracy on a heartbeat counting task learned fearful face-name pairs better when feedback was given at systole than at diastole. This effect was not present for neutral and happy faces. At retrieval, we also observed related effects of personality: First, individuals scoring higher for extraversion showed poorer retrieval accuracy. These individuals additionally manifested lower resting heart rate and lower state anxiety, suggesting that attenuated levels of cardiovascular arousal in extraverts underlies poorer performance. Second, higher extraversion scores predicted higher emotional intensity ratings of fearful faces reinforced at systole. Third, individuals scoring higher for neuroticism showed higher retrieval confidence for fearful faces reinforced at diastole. Our results show that cardiac signals shape feedback processing to influence learning of fearful faces, an effect underpinned by personality differences linked to psychophysiological arousal.

1. Introduction

Peripheral theories of emotion (James, 1884, 1894; Lange, 1885/1912) postulate that the subjective experience of an emotion is caused by changes in bodily state evoked by the encounter with an emotive stimulus. Often implicit is the notion that distinct emotional experiences are linked to different bodily states, notably specific patterns of autonomic arousal (Ekman, Levenson, & Friesen, 1983; Friedman, 2010; Harrison, Kreibig, & Critchley, 2013; Janig & Habler, 2000; Kreibig, 2010). Other mental processes, including perception, decision-making and memory, may be influenced directly by bodily physiology, or secondarily by changes in subjective emotional feelings. The integration of viscerosomatic signals with central brain representations is acknowledged by theoretical models of emotion such as the somatic marker hypothesis (Damasio, 1996, 2004), proposing that preconscious effects of bodily arousal bias behaviour and underpin emotion. However, such arousal signals are subject to appraisal and interpretation of an individual's psychological and social situation, which further shape and contextualize emotional feeling states (Barrett, 2006, 2011; Russell, 2003; Schachter & Singer, 1962).

1.1. Fear effects on arousal and associative memory

We typically remember emotional information better than neutral information. The enhancement of emotional memories is linked to states of psychophysiological arousal (Cahill & McGaugh, 1998) and mediated by dedicated neural (amygdalar monoaminergic) mechanisms within the brain (Kensinger & Corkin, 2004; McGaugh, Cahill, & Roozendaal, 1996; Yonelinas & Ritchey, 2015). Thus, emotionally arousing stimuli are better encoded into long-term memory than neutral events. Fear stimuli are particularly salient, since they convey the presence of danger and threat, engendering rapid, automatic

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http://dx.doi.org/10.1016/j.biopsycho.2017.04.001
Received 24 August 2016; Received in revised form 30 March 2017; Accepted 1 April 2017
Available online 03 April 2017

encoding, even prior to conscious awareness (Critchley, Mathias, & Dolan, 2002; LeDoux, 2014; Öhman, 2005). Passive processing of threat-related stimuli elicits central and autonomic reactivity, evidenced by enhanced amygdala responses (Hariri, Tessitore, Mattay, Fera, & Weinberger, 2002; Mattavelli et al., 2014), heightened cortical arousal (Wieser & Keil, 2014), and increased electrodermal (Hariri et al., 2002; Hedger, Adams, & Garner, 2015), cardiovascular (Kreibig, 2010), and pupillary responses (Sterpenich et al., 2006; Tamietto et al., 2009).

However, associative memory paradigms challenge the notion that memory is always enhanced by fear and threat (Yonelinas & Ritchey, 2015). In fact, the retrieval of neutral items is frequently observed to be impaired by negative emotional contexts (Erk et al., 2003; Mather, 2007; Mather & Knight, 2008; Smith, Henson, Dolan, & Rugg, 2004); but see (Sterpenich et al., 2006). An 'attentional narrowing effect' is proposed to account for a retrieval disadvantage of neutral items associated with negative emotional stimuli (Easterbrook, 1959). According to this model, emotionally-valenced stimuli attract a focusing of attention at the expense of related or nearby neutral stimuli. This effect benefits the learning and subsequent memory of the emotional stimulus (Bisby & Burgess, 2014; Kensinger & Schacter, 2006; Pierce & Kensinger, 2011; Rimmele, Davachi, Petrov, Dougal, & Phelps, 2011; Touryan, Marian, & Shimamura, 2007), but impairs associative binding to surrounding neutral stimuli, hence yielding an associative retrieval deficit.

1.2. Cardiovascular arousal and stimulus processing

Cardiac timing paradigms permit targeted investigation of the impact of internal bodily arousal signals on perception and behaviour (Critchley & Garfinkel, 2015). The brain receives phasic signals concerning states of cardiovascular arousal (stronger, faster heartbeats). Arterial baroreceptors (pressure sensors) in the great vessels leaving the heart fire when the heart contracts to eject blood (at systole). These neural signals inform the brain of the strength and timing of that heartbeat. Baroreceptors are quiet between heartbeats (at diastole), so the signalling of cardiovascular arousal occurs in bursts within the cardiac cycle. By presenting brief stimuli at systole or diastole, one can compare how central processing is specifically affected by the presence or absence of signals concerning the state of cardiovascular arousal (without more general confounding effects of psychophysiological arousal).

Cardiac signals inhibit processing of some types of stimuli and enhance processing of others, consistent with a cardiac-controlled specificity of emotional experience and behaviour (Garfinkel & Critchley, 2016). In healthy individuals, the effect of cardiac signals on the processing of brief pain stimuli is largely inhibitory: Cardiac systole attenuates pain-evoked event related potentials (Gray, Minati, Paoletti, & Critchley, 2010), pain motor reflexes (Edwards, McIntyre, Carroll, Ring, & Martin, 2002), and evoked autonomic responses through differential modulation of amygdala, cortical and brainstem centres (Gray, Rylander, Harrison, Wallin, & Critchley, 2009). In contrast to these inhibitory effects, cardiac systole can enhance the detection of rapidly presented visual stimuli (Garfinkel et al., 2013; Park, Correia, Ducorps, & Tallon-Baudry, 2014; Pramme, Larra, Schächinger, & Frings, 2016) and increase the perceived intensity of facial expressions of fear (Garfinkel, Minati et al., 2014) and disgust (Gray et al., 2012). In studies of memory for faces, a shift in response bias is observed during face recognition, wherein cardiac systole evokes increased false feelings of familiarity for novel faces (Fiacconi, Peter, Owais, & Köhler, 2016). During memory for words, systole enhances confidence at encoding to predict better memory at retrieval (Garfinkel et al., 2013).

1.3. Interoceptive sensitivity to cardiac signals and the effects on stimulus processing

Many of the effects observed at cardiac systole occur pre-consciously. However, heartbeats can be perceived consciously, particularly in states of heightened arousal, and individuals vary in their sensitivity to such internal 'interoceptive' sensations. Heartbeat detection tasks are used as objective behavioural tests to quantify individual differences in interoceptive sensitivity (Garfinkel, Seth, Barrett, Suzuki, & Critchley, 2015; Schandry, 1981). The impact of bodily states of arousal on cognitive and emotional processing is influenced both by the strength of the afferent heartbeat signal and by an individual's sensitivity to, and appraisal of, changes in the signal (Critchley, Wiens, Rotshtein, Ohman, & Dolan, 2004; Garfinkel et al., 2013). Critically, these individual differences in interoceptive sensitivity may moderate the impact of cardiac afferent signals on stimulus processing. Thus, heightened interoceptive accuracy is associated with improved implicit memory (Werner, Peres, Duschek, & Schandry, 2010) and enhanced explicit verbal recall, mitigating the deleterious effect of cardiac systole on later memory for words (Garfinkel et al., 2013). Together, studies of cardiac timing and interoceptive sensitivity demonstrate how learning and memory are shaped by internal states of bodily arousal and their mental representation.

However there is still a paucity of studies using cardiac timing to characterise how physiological arousal impacts fear learning and memory (Garfinkel et al., 2013; Fiacconi et al., 2016). Notably, both studies reported no fear memory enhancement; an issue likely attributable to study design. Garfinkel et al. (2013) used words, thus reducing the salience typically elicited with pictorial fear stimuli. Fiacconi et al. (2016) presented fearful and neutral stimuli in a block design. This approach diminishes emotional enhancement of memory, an effect dubbed the list composition effect (Barnacle, Montaldi, Talmi, & Sommer, 2016). In the present study, we investigated the selectivity with which fear stimuli affect learning and memory following their reinforcement at cardiac systole (e.g. Garfinkel, Minati et al., 2014). Specifically, our approach allows us to address whether cardiac signals contribute additively to psychological salience linked specifically to fear processing (Garfinkel & Critchley, 2016).

1.4. Personality, arousal and performance

Of further interest in the present study were the effects of personality differences on learning and memory, motivated by previous findings showing the influence of personality differences on fear perception at specific cardiac timings (Garfinkel, Minati et al., 2014). Differences in physiological reactivity and interoceptive sensitivity may underpin personality traits. In Eysenck's arousal theory of personality (Eysenck, 1967), extraverts are proposed to be characterised by lower levels of cortical activity compared to introverts (Fink, Grabner, Neuper, & Neubauer, 2005; Kumari, ffytche, Williams, & Gray, 2004). Extraverts also show reduced autonomic arousal, including lower heart rate and attenuated sympathetic skin responses during perceptual and cognitive tasks, when compared to introverts, (Geen, 1984; Harvey & Hirschmann, 1980). Within the same framework, neuroticism is linked to heightened autonomic reactivity to emotional stimuli (Harvey & Hirschmann, 1980; Norris, Larsen, & Cacioppo, 2007), an effect arguably mediated through heightened reactivity of 'visceral brain' centres [amygdala, anterior cingulate cortex (ACC), insula, and vmPFC (Ormel et al., 2013)].

1.5. The present study

We implemented a trial-and-error learning task of face-name pairs (associative learning), in which auditory feedback was presented at specific cardiac timings. Critically, feedback was essential for learning to occur. Our aim was to test how cardiovascular arousal affects