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

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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.

Acknowledgements

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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).

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 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.

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).

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 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).

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)].

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 feedback processing, and its impact on learning and retrieval of emotional face-name stimuli (portraying fearful, happy and neutral expressions). The attentional narrowing hypothesis (Easterbrook, 1959), proposes that emotional stimuli capture and focus attention during learning, thereby compromising the attention-dependent processing and associative binding of, circumstantial information (in this case names). We therefore predicted that associative learning would be impaired, especially for fearful face-name pairs, consistent with the salience of fear stimuli (Critchley et al., 2002; LeDoux, 2014; Öhman, 2005) that might interfere with the binding of peripheral names.

We further predicted that the presentation of reinforcing feedback at cardiac systole (i.e. during afferent cardiovascular arousal signalling) would selectively enhance associative learning of fearful face-name pairs. This hypothesis is predicated on peripheral theories of emotion, proposing that autonomic activity (e.g. cardiovascular arousal) enhances the experience of emotions, and on the observation that systole enhances stimulus processing as a whole (Fiacconi et al., 2016; Garfinkel et al., 2013; Garfinkel, Minati, et al., 2014), thus reinforcing encoding of fearful face-name pairs.

Our investigation of cardiac-timed feedback effects on the learning and retrieval of happy face-name pairs was more exploratory: Cardiovascular arousal during the experience of happiness, or when viewing happy faces, is more nuanced, with both evoked increases and decreases in heart rate reported (Critchley et al., 2005; Dimberg & Thunberg, 2007; Gehricke & Fridlund, 2002; Joansson & Sonny-Borgstroem, 2003; Kreibig, 2010). Nevertheless, we predicted that feedback during cardiac afferent signalling of arousal would amplify attentional narrowing related to happy faces with enhanced associative learning effects and poorer retrieval.

Concerning associative retrieval, we sought to reveal binding deficits for emotional face-name pairs. We predicted that such deficits from attentional narrowing would be most prominent for fearful face-name pairs (Critchley et al., 2002; LeDoux, 2014; Öhman, 2005). Moreover, we reasoned that feedback at systole might amplify the processing of fearful faces during learning (cf. (Garfinkel, Minati, et al., 2014)), hence enhance the detrimental effect of attentional narrowing on subsequent recollection of fear faces from name prompts. We

therefore hypothesized a selective deficit in the retrieval of fearful faces that were initially reinforced at systole relative to diastole.

Accurate perception of afferent cardiac signals can enhance the perception of and/or memory for emotional stimuli (Garfinkel et al., 2013; Werner et al., 2010). We therefore predicted that individual differences in cardiac interoceptive accuracy (heartbeat detection task performance) would be linked to better learning of fearful face-name pairs when reinforced at cardiac systole. Similarly, interoception was hypothesised to correlate negatively with the later retrieval of fearful faces for which feedback was initially presented at systole, as a result of greater attentional narrowing toward salient fear stimuli reinforced at higher levels of cardiac arousal.

Lastly, we predicted a modulatory influence of personality on emotion-related associative learning and memory reinforced at specific cardiac timings. Extraverts reportedly perform better in stimulating ('high arousal') environments, evidenced by better performance, relative to introverts, on fast-paced change detection tasks (Hahn, Buttaccio, Hahn, & Lee, 2015) and on associative learning tasks in acoustically noisy contexts (Geen, 1984). We therefore predicted that extraverts would show improved learning and/or retrieval of face-name pairs reinforced at systole as a result of enhanced cardiovascular arousal. We further predicted that extraverts would show a particular encoding advantage of fearful face-name pairs reinforced at systole, and/or a retrieval deficit (increased attentional narrowing).

Neuroticism is linked to heightened autonomic reactivity (Eysenck, 1967) and is a trait predictor for anxiety (Zinbarg et al., 2016). Individuals scoring high on state anxiety show greater intensity ratings to fearful faces presented at diastole, consistent with a sustained fear response, even at lower levels of cardiovascular arousal and in the absence of afferent physiological arousal signals (Garfinkel, Minati, et al., 2014). We therefore predicted that individuals scoring high for neuroticism would show a learning advantage of fearful face-name pairs when feedback was presented at diastole. Similarly, at retrieval, individuals scoring high in neuroticism were expected to show a selective fear deficit for faces initially reinforced at diastole.

Method

Participants

Thirty-two volunteers (19 female; mean age 23.8 yrs; range 18–35 yrs) took part in the experiment. Participants were recruited via advertisements placed around the University of Sussex and Brighton and Sussex Medical School. All participants were healthy individuals with no history of psychiatric or neurological diseases. The participants' resting heart rate was in the normal range between 53 – 90 beats per minute ($M = 70.91$; $SE = 1.89$). The average number of years of education was $M = 16.88$ ($SD = 3.08$). All participants gave their written informed consent and were compensated £15 for their time. The study was reviewed and approved by the BSMS Research Governance and Ethics committee (BSMSRGEC13/122/CRI). Data of three participants was rejected as outliers (below-chance performance), leaving twenty-nine participants for the analysis.

Stimuli

Twelve face-name pairs (six male, six female) served as our experimental stimuli. The face images were taken from the Karolinska Directed Emotional Faces database (Lundqvist, Flykt, & Öhman, 1998). Male and female faces encompassed two neutral, two fearful and two happy facial expressions. Names were selected from the Social Security Administration's records list of the top 200 names of the 2000s (available on <http://www.ssa.gov/oact/babynames/decades/names2000s.html>). All names consisted of four letters and were matched in name frequency. An emotion by gender (3x2) mixed ANOVA showed that the chosen name frequency did not significantly differ between emotional facial expressions ($F[2,3] = 0.138$, $p = 0.876$), or between gender ($F[1,3] = 0.513$, $p = 0.526$), and there was no emotion by gender interaction ($F[2,3] = 0.786$, $p = 0.531$). Two auditory tones (representing confirmatory and negative feedback) were delivered through IXOS dj1003 headphones and served as feedback in the associative learning task. The confirmatory tone was selected from the website <http://www.mediacollege.com/downloads/sound-effects/beep/>. The tone was chosen from the beep sound effects list (Beep 6) and was played for 100ms. The negative tone was created using a signal generator available on <http://www.wavtones.com/functiongenerator.php>. This tone consisted of a continuous sine

sweep tone played between two frequencies (Start Frequency 20 Hz, Stop Frequency 20000), at a level of -3 dBFS for 100ms duration. Both, the confirmatory and aversive tones were delivered at a volume of 85 dB_{SPL} (decibels sound pressure level) and sound checks were performed to ensure the tones were reliably perceived.

Design

The experiment consisted of a 3 x 2 repeated measures design, with 3 levels of emotion (neutral, fearful, happy face-name pairs) and 2 levels of cardiac timing (systole, diastole) at which an auditory feedback tone was delivered. Specifically, the factorial combination ensured that each emotion of a face was reinforced at fixed cardiac timings (i.e. of the four fearful faces, two faces were consistently reinforced at systole, while the other two faces were consistently reinforced at diastole). The ordering of feedback timings and the assignment of names to different faces were fully counterbalanced. A repeated-measures design accounted for differences in heart rate, personality, stimulus and feedback effects during learning, retrieval and emotional intensity rating.

Equipment

Participants were tested on an 18 inch CRT monitor at an approximate distance of 50cm. The monitor had a screen resolution of 1280 x 1024 pixels and a refresh rate of 85Hz. Stimuli were delivered using Cogent2000 v1.32 running under MATLAB R2013a (The MathWorks, Inc., Natick, MA). During the associative learning task, participants were fitted with a three lead electrocardiograph (ECG) with bandlimits set between 10 and 100 Hz. The ECG (Ag-AgCl Electrodes, Einthoven's triangle, standard lead I configuration) was acquired via an isolated preamplifier (Model 1902, CED Ltd., Cambridge, U.K.). Physiological waveforms were digitised and monitored on PC (power 1401, Spike2 v7 software, CED Ltd.).

Procedure

Associative learning

Each participant was informed that she/he was required to learn and memorise the correct combination of twelve face-name pairs by trial-and-error for a later memory retrieval test.

Each trial began with a fixation cross, presented for a jittered time-period of 1-2s. This was followed by a face image presented at the top of the screen and four possible matching names below (Figure 1). The names were a sub-selection of the stimulus-set and one name was always a match. The participant was required to indicate (within 3s), which of the four names belonged to the face using different keyboard responses for each name. Immediately following a response the selected name turned bold and italic. Next, a confirmatory or aversive auditory feedback tone was delivered for 100ms to reinforce correct and incorrect responses, respectively. The tones either coincided with late cardiac diastole (indexed by the ECG R-wave) when baroreceptors are largely silent, or during mid/late systole (approximately at the ECG T-wave) when baroreceptor impulses are processed centrally (Garfinkel et al., 2013; Garfinkel, Minati, et al., 2014; Gray et al., 2012). The timing of feedback presentation was predicted from the median duration of three consecutive RR-intervals. RR-intervals were measured periodically, either following participants' behavioural responses or at the end of the 3 second face-name display (in case no response was provided). Feedback was then presented relative to the immediately preceding heartbeat, either at diastole (on the R-wave) or at systole (300ms after the R-wave). If the participant failed to give a response within 3 seconds, none of the names turned bold and italic, and the aversive tone was played at its respective cardiac timing. The entire learning task consisted of 20 Runs, with each run containing 12 trials.

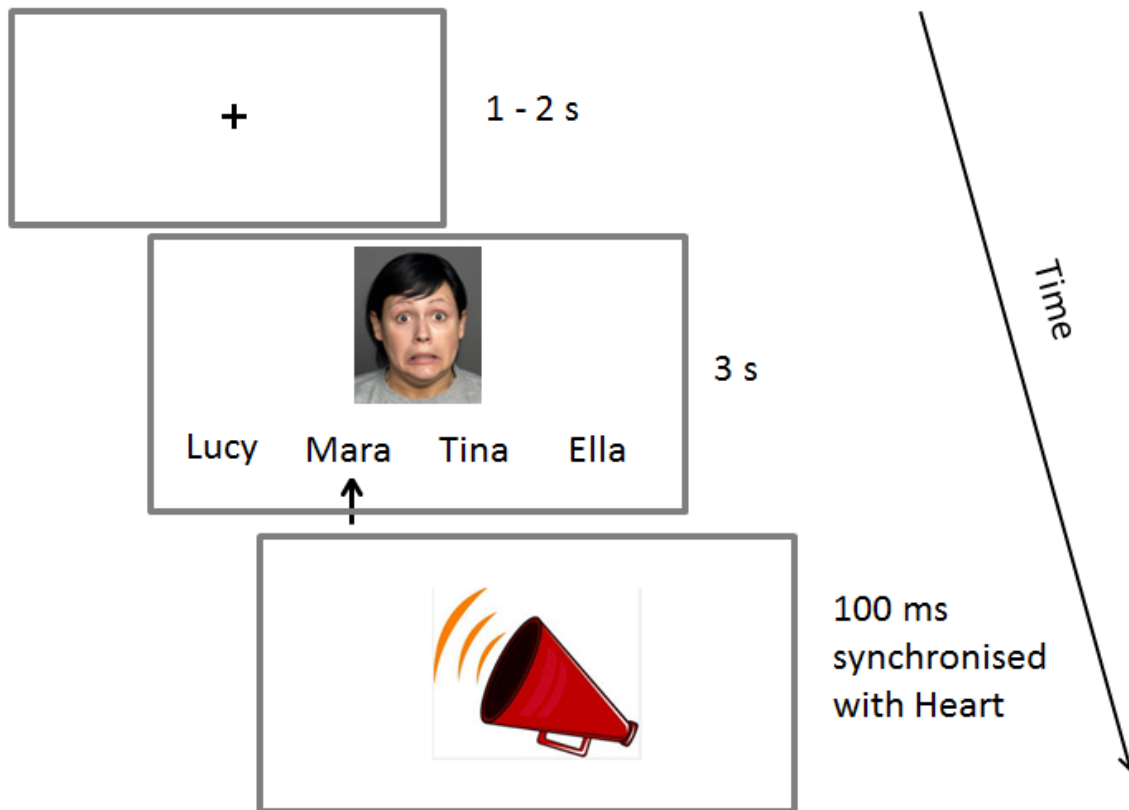


Figure 1. Example of an associative learning trial.

Interoceptive accuracy

Following performance of the associative learning task, we assessed interoceptive accuracy using the heartbeat counting task (Schandry, 1981). Each participant was given verbal instructions: “*Without manually checking, can you silently count each heartbeat you feel in your body from the time you hear ‘start’ to when you hear ‘stop’*”. The task was repeated six times, using randomly presented time-windows of 25, 30, 35, 40, 45, and 50 s. During each time window, the participant’s heart beats were recorded using a pulse oximeter and the participant reported the number of perceived beats counted at the end of the time-window. Accuracy scores were computed for each trial: $1 - (|nbeats_{real} - nbeats_{reported}|) / ((nbeats_{real} + nbeats_{reported}) / 2)$. These scores were averaged over the six presentations, yielding an average interoceptive accuracy score for each participant. The pulse oximeter recordings constituted our participants’ resting heart rate and were used for subsequent correlation analysis with extraversion scores.

Associative retrieval

Associative retrieval was assessed after the heartbeat counting task. Each participant was informed that they would be tested on the twelve pair-associates acquired during the learning phase. Each trial began with a fixation cross (1s), followed by a name presented at the centre of the screen (2s). The participant was asked to use the name to recall the matching face, including its emotion. In a subsequent response window (3s), three emotion words were presented (fear, neutral, happy), and the participant was asked to select the emotion that was associated with the face they had recalled from memory. Next, a fixation cross appeared for 1 second, after which participants were asked to provide confidence ratings on a scale of 0 (not at all confident) to 100 (very confident) (see Figure 2) using a visual analogue scale (VAS). Associative retrieval was assessed in two runs containing 12 trials each.

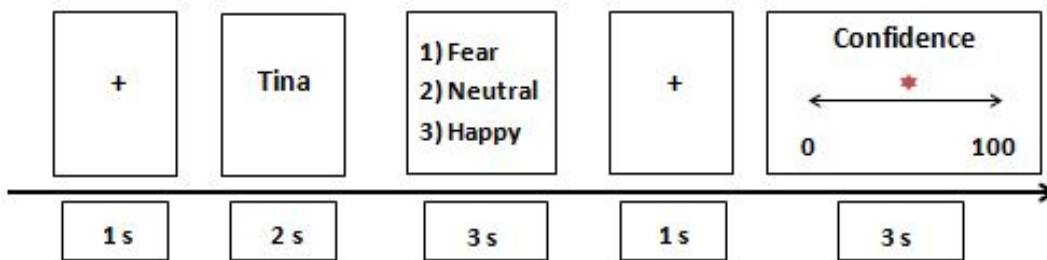


Figure 2. Example of a retrieval trial.

Emotional intensity ratings

Emotional intensity ratings were collected to verify participants' perceptual appraisal of the emotions, and to examine the influence of the point in the cardiac cycle at which the faces were initially reinforced. Each of the twelve faces was presented in a random order, accompanied by the question "How intense is the emotion of the face?" A rating scale was presented below on which participants could move a cursor along ten increments, ranging from "Not at all" (far left), to "Average" (centre), to "Very intense" (far right). Each of the twelve trials stayed on screen for 8 seconds, allowing sufficient time to provide the ratings.

Questionnaires

At the end of the experiment, we administered two questionnaires: the State Trait Anxiety Inventory (Spielberger, Gorsuch, Lushene, Vagg, & Jacobs, 1983) and the Eysenck Personality Inventory (H.J. Eysenck & Eysenck, 1964). The State Trait Anxiety Inventory (STAI) examines state and trait anxiety using two separate subscales with twenty items each. In the state anxiety subscale, participants are asked to rank emotional states according to how they feel right now, while in the trait anxiety subscale, participants rank emotional states according to how they feel generally.

The Eysenck Personality Inventory (EPI) is a fifty-seven item personality questionnaire measuring the two orthogonal factors extraversion and neuroticism and requires ‘yes’ or ‘no’ responses. Extraversion and neuroticism are assessed upon twenty-four items each; additional nine items constitute a lie scale that can be analysed to predict response biases. Items considered in the current study were restricted to extraversion and neuroticism.

Data analysis

Associative learning

For the associative learning task, we examined accuracy (proportion correct responses) and response times (RTs) in two separate (3 x 2) repeated measures ANOVAs with emotion (fear, neutral, happy) and cardiac cycle (systole, diastole) as independent variables. For accuracy, participants’ trial-by-trial responses were averaged across runs 2–16 and entered as the dependent variable. Run 2 was the first run where mean proportion correct responses exceeded chance performance ($N=29$, average accuracy = 26%). Likewise, run 16 was the first run where mean proportion correct responses started to exceed 75% accuracy ($N=29$; 76.14%). We have therefore included runs 2 – 16 to cut off the approximate lower and upper 25% of performance accuracy to avoid floor and ceiling effects. For RTs, participants’ average RTs across runs 2–16 were entered in the second ANOVA as the dependent variable. Only accurate trials were considered for this analysis. To explore individual differences in interoception, two (3 x 2) repeated measures ANOVA were computed for proportion correct responses and RT respectively, with participants’ interoceptive accuracy scores for the heartbeat counting task entered as a covariate. Initial analyses demonstrated that the linear

regression of fearful face-name pairs reinforced at systole-diastole (proportion correct responses) on interoceptive accuracy violated the assumptions of homoscedasticity (Breusch-Pagan test: $X^2 = 4.698$; $p = 0.03$). To mitigate this problem, we transformed the interoception scores using the rank-based inverse normal distribution method available in SPSS (Solomon & Sawilowsky, 2009). Using this transformation, our data no longer showed significant heteroscedasticity (Breusch-Pagan test: $X^2 = 0.106$; $p = 0.745$). Analyses of the proportion correct responses in associative learning were therefore performed with the transformed measures of interoceptive accuracy. All correlation results are reported as one-tailed p-values. A threshold significance of $p < 0.05$ was applied throughout.

Associative retrieval and emotional intensity ratings

For the associative retrieval task, we conducted a (3 x 2) repeated measures ANOVAs with emotion (fear, neutral, happy) and cardiac cycle (systole, diastole) as independent variables and proportion correct responses as the dependent variable. RTs for the retrieval task could not be analysed since there were not enough accurate responses, which resulted in too many missing cases. Another (3 x 2) repeated measures ANOVA was computed for the emotional intensity ratings, from mean percent ratings of fearful, neutral and happy faces. One participant's data for emotional intensity ratings was lost, hence our results are presented for the remaining participants (N = 28).

Interoceptive accuracy and extraversion

We tested for effects of interoceptive accuracy and extraversion on associative learning, retrieval and intensity ratings, conducting (3 x 2) repeated measures ANOVAs with emotion (fear, neutral, happy) and cardiac cycle (systole, diastole) as independent variables and participants' interoceptive and extraversion scores entered as covariates. We further correlated extraversion scores with participants resting heart rate, the results of which are reported as one-tailed p-values.

Results

Associative learning: Cardiac influence of feedback processing as a function of interoceptive accuracy

We observed no suprathresholded main effect on associative learning of emotion or cardiac timings, and no interaction between emotion and cardiac timings, as determined by the proportion correct responses on the averaged runs 2–16 (Figure 3; Table 1). However, when individual differences in interoception were included as a covariate, we observed a significant three-way interaction between emotion, cardiac cycle and interoceptive accuracy ($F[2,54] = 3.735, p = 0.030, \eta p^2 = 0.122$) (Figure 4). Tests of within-subject contrasts showed that, as interoceptive accuracy increased, fearful faces were learned significantly better than happy faces when feedback was presented at systole versus diastole ($F[1,27] = 5.556, p = 0.026, \eta p^2 = 1.171$). Similarly, there was a learning advantage of neutral versus happy faces reinforced at systole versus diastole ($F[1,27] = 5.125, p = 0.032, \eta p^2 = 1.160$) for participants with higher interoceptive accuracy scores, while interoceptive accuracy had no significant effect on fearful versus neutral faces reinforced at systole versus diastole ($F[1,27] = 0.290, p = 0.595, \eta p^2 = 0.011$). We correlated interoceptive accuracy with the difference scores of proportion correct responses at systole minus diastole for each emotion to examine further the relationship between emotion, cardiac cycle and interoceptive accuracy. Fear, modulated by cardiac timings, was the only emotion that showed a significant positive correlation with interoceptive accuracy ($r = 0.316; p = 0.047$). This confirmed that participants with high interoceptive accuracy showed enhanced encoding of fear stimuli at systole. No significant relationship was found between interoceptive accuracy and cardiac modulation of happy faces ($r = -0.279; p = 0.072$), or between interoceptive accuracy and cardiac modulation of neutral faces ($r = 0.221; p = 0.125$).

There was no significant main effect of emotion and cardiac timings on RTs, and no interaction between emotion and cardiac timings on RTs during associative learning. Similarly, interoceptive accuracy did not modulate the main effect of emotion and cardiac timings on RTs, or yield an interaction between emotion and cardiac timings on RTs during associative learning (all p -values > 0.05).

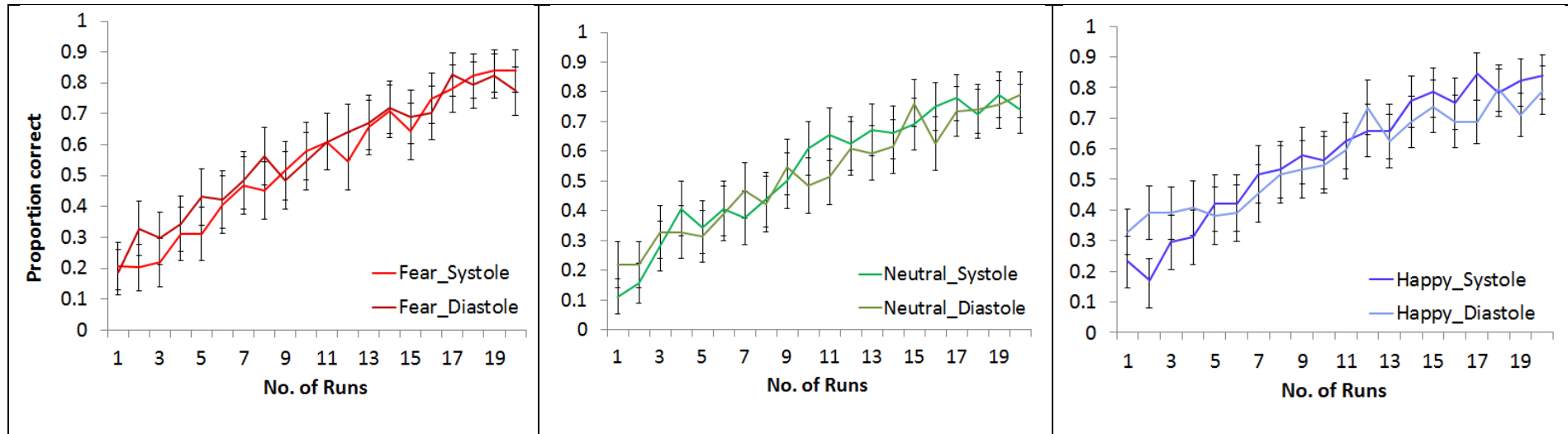


Figure 3. Learning curves. The y-axes present mean proportion correct responses for each emotion reinforced at systole and diastole. A steady learning-increase was found across emotion and cardiac timing throughout the numbers of runs (x-axis). Error bars represent the standard error of the mean.

Table 1. Mean response times (in seconds) and standard errors during the trial-and-error learning task.

Condition	Mean response time in seconds (<i>SE</i>)
Fear, Systole	1576.40 (52.74)
Fear, Diastole	1600.85 (76.55)
Neutral, Systole	1675.00 (55.71)
Neutral, Diastole	1663.58 (61.72)
Happy, Systole	1606.51 (69.86)
Happy, Diastole	1667.25 (77.65)

Interoceptive accuracy enhances fear-learning at systole

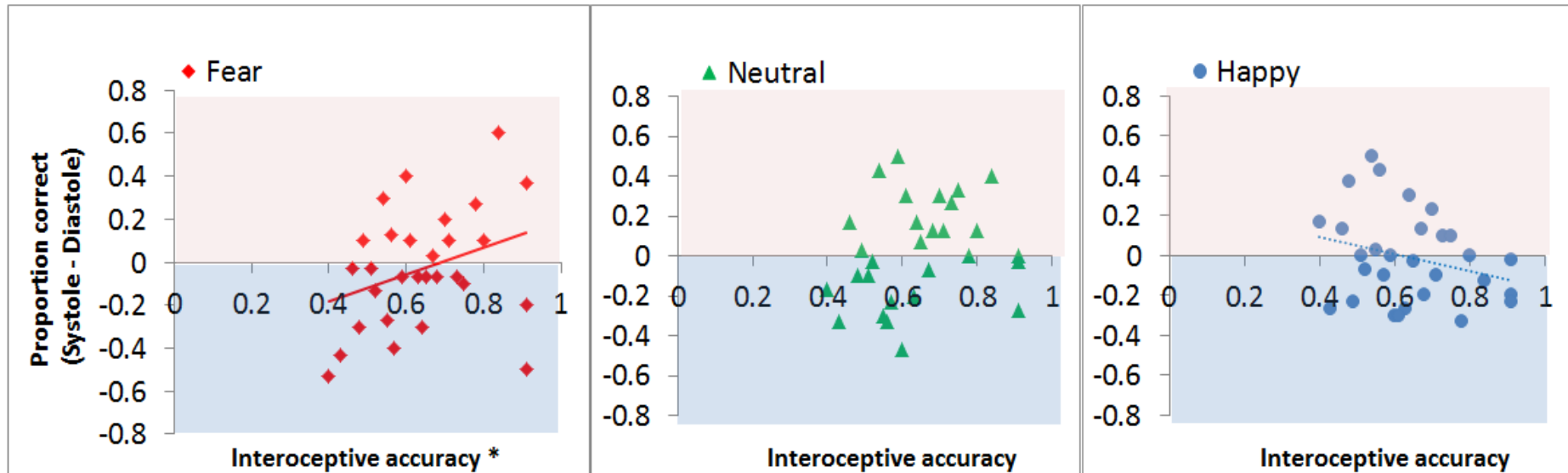


Figure 4. Scatterplots depicting correlations between interoceptive accuracy and proportion correct responses (systole – diastole) for each emotion. The y-axes show proportion correct responses at systole relative to diastole. Associative learning of fearful faces correlated significantly with interoceptive accuracy (solid trend line) when feedback was provided at systole versus diastole ($r = 0.316$; $p = 0.047$). Neutral faces initially reinforced at systole versus diastole showed no significant, or trending, correlation with interoceptive accuracy ($r = 0.221$; $p = 0.125$). A trend relationship was found between interoceptive accuracy and happy faces initially reinforced at systole versus diastole ($r = -0.279$; $p = 0.072$), as signified by the dashed trend line. The interaction between emotion, heart and interoceptive accuracy was significant: Higher interoceptive accuracy was associated with better learning of fearful versus happy faces, neutral versus happy faces, but not fearful versus neutral faces, when feedback was provided at systole versus diastole. *Scatterplot depicting transformed interoception scores of the rank-based inverse normal distribution method to meet the assumptions of homoscedasticity.

Associative retrieval: effects of emotional stimulus content and extraversion

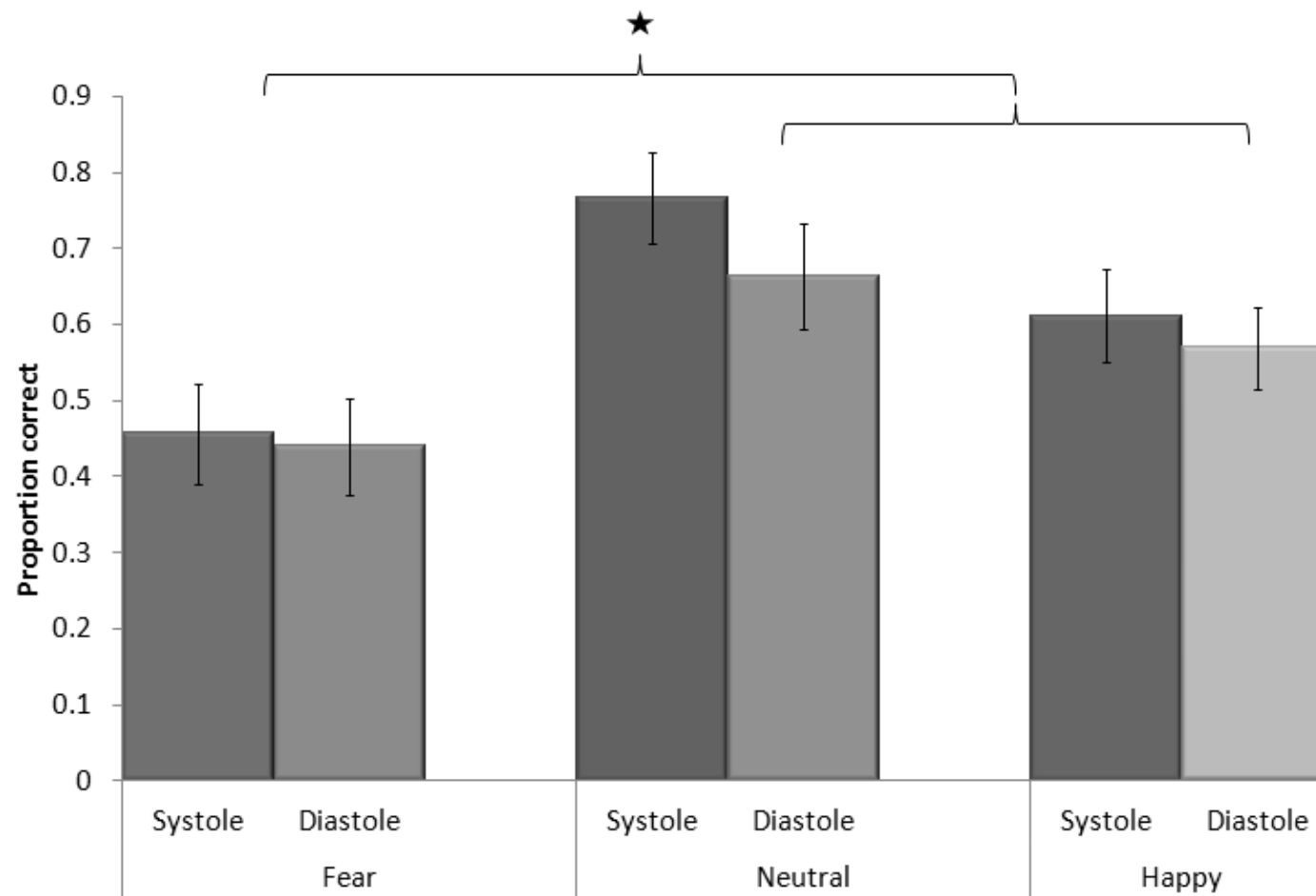
We observed a significant main effect of emotion on proportion correct responses ($F[1.63,45.52] = 9.40, p = 0.001, \eta p2 = 0.251$) but no main effect of cardiac cycle ($F[1,28] = 1.37, p = 0.252, \eta p2 = 0.047$) and no interaction between emotion and cardiac cycle ($F[2,56] = 0.379, p = 0.686, \eta p2 = 0.013$) (Figure 5A). Within-participant tests of the effects of emotion revealed a retrieval advantage for neutral versus fearful faces ($F[1,27] = 34.52, p < 0.001, \eta p2 = 0.552$) and for happy versus fearful faces ($F[1,27] = 4.83, p = 0.036, \eta p2 = 0.147$), yet no significant difference was found between the retrieval of neutral versus happy faces ($F[1,27] = 3.03, p = 0.093, \eta p2 = 0.089$), thus demonstrating significantly reduced associative memory for fearful faces.

Retrieval was further influenced by personality. There was a significant main effect of extraversion on retrieval ($F[1,27] = 5.319, p = 0.029, \eta p2 = 0.165$). In a subsequent correlational analysis, higher extraversion was associated with poorer retrieval accuracy ($r = -0.406; p = 0.015$) (Figure 5B).

Extraversion showed a significant negative correlation with resting heart rate ($r = -0.316, p = 0.047$) (Figure 5C) and with state anxiety ($r = -0.384; p = 0.020$). Thus, in line with our prediction, we demonstrated that extraversion was associated with low arousal and correlated with poorer retrieval performance.

Associative Retrieval

A)



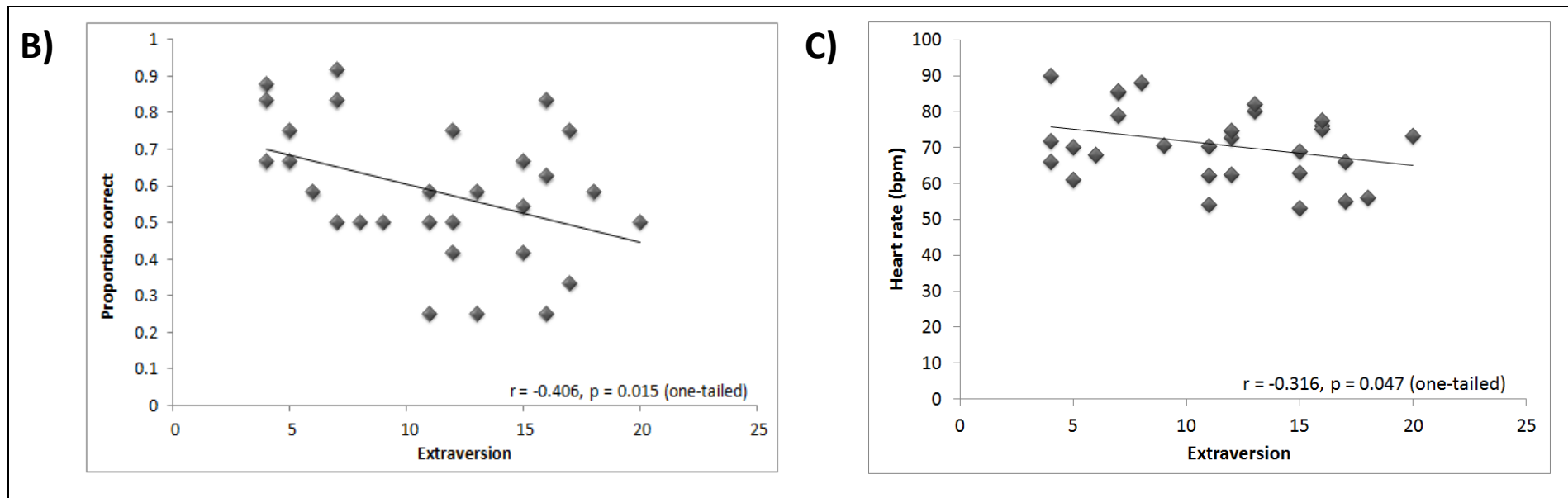


Figure 5. Associative retrieval. A) Bar chart illustrating the mean proportion correct responses for the retrieval of fearful, neutral and happy faces that were initially reinforced at systole and diastole. There was a main effect of emotion, driven by enhanced recall of neutral relative to fearful faces and happy relative to fearful faces, while the difference in recall between neutral and happy faces was non-significant. Error-bars represent the standard error of the mean. B) Scatterplot showing that higher extraversion (x-axis) was associated with poorer retrieval accuracy (y-axis). Retrieval scores were averaged across emotions and cardiac cycle. C) Scatterplot depicting the significant negative relationship between heart rate (y-axis) and extraversion (x-axis), showing that higher extraversion was associated with lower bodily states of arousal.

Retrieval confidence as a function of cardiac cycle, emotion and neuroticism

Confidence ratings (Table 2) showed no overall main effect of emotion ($F[2,46.52] = 1.14$, $p = 0.327$, $\eta p2 = 0.039$), no main effect of cardiac cycle ($F[1,28] = 0.768$, $p = 0.401$, $\eta p2 = 0.025$), and no emotion by cardiac cycle interaction ($F[2,56] = 0.265$, $p = 0.768$, $\eta p2 = 0.009$). Personality influenced confidence judgements: There was a three-way interaction between emotion, cardiac cycle and neuroticism ($F[2,54] = 4.301$, $p = 0.018$, $\eta p2 = 0.137$). Within-participant tests showed that individuals with higher neuroticism scores retrieved fearful faces with greater confidence than neutral faces when feedback was initially presented at diastole versus systole ($F[1,27] = 8.603$, $p = 0.007$, $\eta p2 = 0.242$). Next, we correlated neuroticism with the difference scores of the confidence ratings at systole minus diastole for each emotion. Fear was the only emotion that showed a significant negative correlation with neuroticism ($r = -0.500$; $p = 0.003$), confirming that higher neuroticism was associated with higher confidence for fearful faces initially reinforced at diastole. No significant relationship was found between neuroticism and happy faces ($r = -0.013$; $p = 0.474$), and between neuroticism and neutral faces ($r = 0.161$; $p = 0.202$). We also correlated neuroticism with state anxiety scores and demonstrated that higher neuroticism was associated with greater state anxiety ($r = 0.584$, $p < 0.001$).

Table 2. Mean confidence ratings (in percent) and standard errors during associative retrieval of fearful, neutral and happy faces that were initially reinforced at systole and diastole during learning.

Condition	Mean confidence ratings in percent (SE)
Fear, Systole	65.09 (3.80)
Fear, Diastole	62.00 (4.33)
Neutral, Systole	67.52 (3.85)
Neutral, Diastole	67.96 (3.51)
Happy, Systole	69.07 (3.88)
Happy, Diastole	65.20 (3.76)

Emotional intensity ratings: effects of emotional stimulus content and extraversion

Participants provided the highest emotional intensity ratings for fearful faces (fear rating, $M \pm SE$; systole: 75.16 ± 2.64 , diastole: 76.45 ± 2.88). This was followed by slightly lower intensity ratings provided for happy faces (happy rating, systole: 67.04 ± 2.03 ; diastole: 66.32 ± 2.12). Lowest emotional intensity ratings were provided for neutral faces (neutral, systole: 33.13 ± 3.57 and diastole: 34.09 ± 3.45). These differences reached significance, as reflected by a significant main effect of emotion on intensity ratings ($F[2,31.76] = 71.99$, $p < 0.001$, $\eta p^2 = 0.727$). Post hoc tests confirmed significant differences between intensity ratings for fear and neutral faces ($F[1,27] = 72.094$, $p < 0.001$, $\eta p^2 = 0.728$), fear and happy faces ($F[1,27] = 16.47$, $p < 0.001$, $\eta p^2 = 0.379$), and happy and neutral faces ($F[1,27] = 96.54$, $p < 0.001$, $\eta p^2 = 0.781$).

Our main motivation for including intensity ratings was to ensure active perceptual appraisal of the emotional aspects of the face stimuli. However, we also tested whether emotional intensity was influenced by the timing of feedback presentation in relation to the cardiac cycle during the initial learning phase. We found no main effect of cardiac cycle ($F[1,27] = 0.169$, $p = 0.684$, $\eta p^2 = 0.006$) and no interaction between emotion and cardiac cycle ($F[2,54] = 0.181$, $p = 0.835$, $\eta p^2 = 0.007$). However, we observed a nuanced effect of personality on judgements of emotional intensity: There was a significant three-way interaction between emotion, cardiac cycle and extraversion ($F[2,54] = 3.504$, $p = 0.037$, $\eta p^2 = 0.119$) (Figure 6). Individuals scoring higher for extraversion judged the intensity of fearful faces to be greater at systole when compared to happy faces ($F[1,27] = 5.154$, $p = 0.032$, $\eta p^2 = 0.165$), or to neutral faces ($F[1,27] = 4.401$, $p = 0.046$, $\eta p^2 = 0.145$). Extraversion did not affect the expression of cardiac influence on intensity ratings of happy versus neutral faces ($F[1,27] = 0.369$, $p = 0.549$, $\eta p^2 = 0.014$).

We further examined the relationship between emotion, cardiac timings and extraversion by correlating extraversion with the difference scores of the intensity ratings at systole minus diastole for each emotion. Fear was the only emotion showing a significant positive correlation with extraversion ($r = 0.470$; $p = 0.006$), indicating that the initial reinforcement of fear stimuli at systole resulted in stronger post fear-perception in extraverts. No significant relationship was found between extraversion and happy faces ($r = 0.076$; $p = 0.701$), and between extraversion and neutral faces ($r = -0.099$; $p = 0.618$).

Extraversion correlates with enhanced intensity ratings for fearful faces initially reinforced at systole

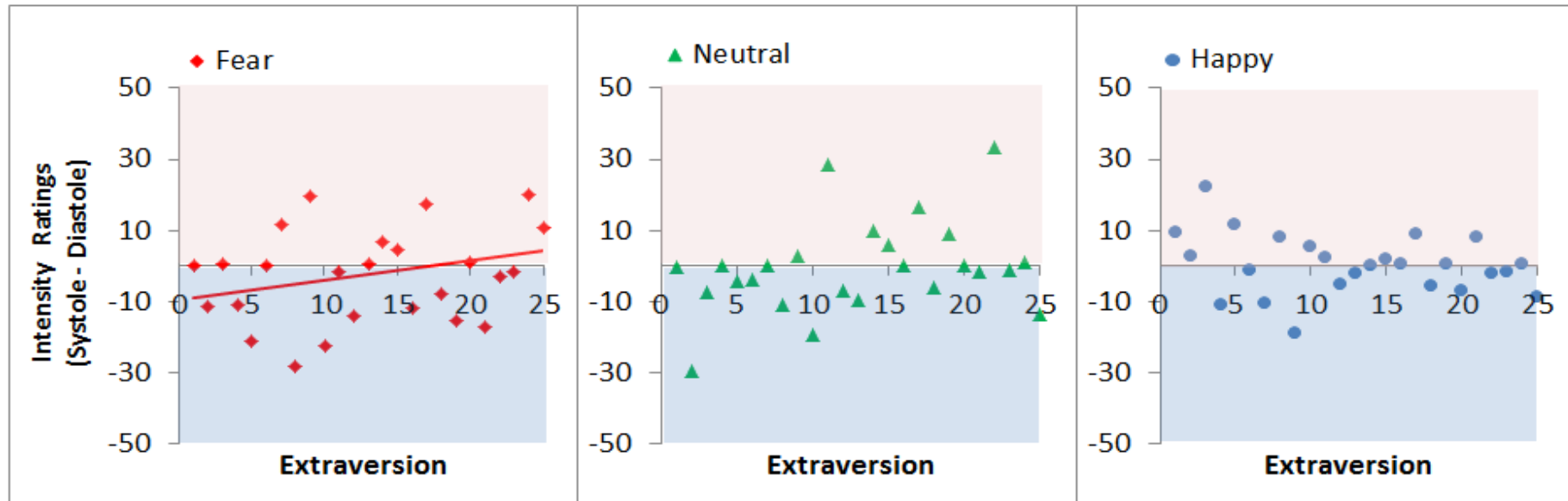


Figure 6. Scatterplots depicting correlations between extraversion and intensity ratings (systole – diastole) for each emotion. The y-axis shows intensity ratings at systole relative to diastole. Intensity ratings of fearful faces correlated significantly with extraversion (solid trend line) when feedback was initially provided at systole versus diastole ($r = 0.470$; $p = 0.006$). The relationship between extraversion and neutral and happy faces for which feedback was provided at systole versus diastole, was non-significant ($p > 0.05$). There was a significant three-way interaction between emotion, cardiac timing and extraversion on emotional intensity ratings, showing that higher extraversion was associated with higher intensity ratings for fearful versus happy faces, fear versus neutral faces, but not neutral versus happy faces, when feedback was provided at systole versus diastole. Results suggest that the reinforcement of fear stimuli at systole during learning resulted in stronger post fear-perception in

extraverts.

Discussion

The present study was guided by peripheral theories of emotion, investigating the contributions of internal bodily states to emotional learning and memory. Specifically, we sought to examine how timing of feedback to coincide with cardiac afferent signals (the interoceptive basis to central representation of internal cardiovascular arousal states) modulates the learning of affective stimuli, with subsequent effects on retrieval. Our study revealed an influence of heart signals on the processing of feedback during learning in some but not all individuals, engendering better learning and memory of face-name combinations depicting fearful emotional expressions. This memory effect therefore highlighted an interaction between bodily arousal signals and stimulus content, consistent with previous research (Garfinkel, Minati, et al., 2014). Importantly, however, these effects were only manifest as a function of interoceptive accuracy and personality (extraversion, neuroticism). People who were more accurate in perceiving interoceptive heart signals showed enhanced learning when fearful faces were reinforced by feedback at systole. More extraverted individuals perceived a greater intensity of fearful faces reinforced by feedback at systole, while less neurotic individuals reported higher confidence ratings for memory judgements of fearful faces reinforced by feedback at systole. Our study extends previous reports of cardiac control on fear perception, learning and memory (Fiacconi et al., 2016; Garfinkel et al., 2013; Garfinkel, Minati, et al., 2014), showing that interoception and personality are important factors that mediate the impact of afferent cardiac signals on perception and cognition.

Interoceptive accuracy and fear-learning

Individuals with enhanced interoceptive ability were more sensitive to threat stimuli reinforced by feedback at afferent cardiovascular arousal signals. Better interoceptive ability enhances the retrieval of confidently encoded words during cardiac systole (Garfinkel et al., 2013). In our paradigm, interoceptive accuracy was uniquely correlated with greater learning of fearful faces reinforced at systole. This suggests that feedback processing during afferent cardiac signals, coupled with accurate perception of these cardiac signals, contribute additively to the psychological salience associated with threat (Critchley et al., 2002; Öhman, 2005), yielding a fear-encoding advantage. The fear-enhancing interoceptive mechanism is underpinned by baroreceptor-evoked activation of neurons in the solitary tract nucleus

(Mifflin & Felder, 1990). These neurons project to locus coeruleus (Van Bockstaele, Peoples, & Telegan, 1999), gating the disseminated release of noradrenaline across the brain (Murase, Inui, & Nosaka, 1994; Svensson & Thoren, 1979). The locus coeruleus contributes to both peripheral and central arousal through innervation of the amygdala and hippocampus (Samuels & Szabadi, 2008), and hence can contribute to enhanced fear perception (Garfinkel, Minati, et al., 2014; Redmond & Huang, 1979) and memory (Sterpenich et al., 2006). The fact that people with heightened interoceptive accuracy also showed a significant learning advantage of neutral over happy faces (but not between fearful and neutral faces) that were initially reinforced at systole versus diastole, may be explained by distinct low-level perceptual features in happy faces, such as the end lip-raise, which distinguishes happy facial expressions from all other emotions (Maher, Ekstrom, & Chen, 2014). Thus, in an experimental design that combines happy, fearful and neutral faces, fearful and neutral faces can appear more similar to each other and result in comparable encoding and recognition accuracy relative to happy faces (Calvo & Beltran, 2013; Righi et al., 2012).

Interestingly, we found a trend relationship between higher interoceptive accuracy and improved learning of happy face-name pairs for which feedback was presented at cardiac diastole. Thus, contrary to our prediction, reinforcing feedback did not amplify attentional narrowing to happy faces during afferent cardiac signalling, but in the absence of physiological arousal signals, in individuals with higher interoceptive accuracy. This observation converges with the notion of autonomic specificity for emotions, suggesting that specific cardiovascular arousal patterns shape the experience of an emotion (Ekman et al., 1983; Friedman, 2010; Harrison et al., 2013; Janig & Habler, 2000; Kreibig, 2010) and influence learning and memory (Abercrombie, Chambers, Greischar, & Monticelli, 2008). Individuals with heightened interoceptive accuracy, who demonstrate enhanced sensitivity of the visceral channel (Vaitl, 1996), may therefore show particular sensitivity to specific autonomic arousal signals, as expressed by opposing encoding preferences for fear when feedback was presented at systole, and for happiness when feedback was presented at diastole.

Effects of emotional valence and cardiac timing on associative retrieval

Associative retrieval was modulated by the emotionality of the face-name pairs, and was unaffected by reinforcing feedback presented at specific cardiac timings during the learning phase. Cued retrieval of fearful faces resulted in a memory deficit relative to cued retrieval of happy and neutral faces. Our result adds to previous associative memory studies showing a retrieval deficit for negative emotions that were cued with an associated neutral stimulus (in our case names) (Bisby & Burgess, 2014; Kensinger & Schacter, 2006; Mather & Knight, 2008; Pierce & Kensinger, 2011; Rimmele et al., 2011). Our finding is consistent with the attentional narrowing hypothesis (Easterbrook, 1959), which proposes that emotionally valenced stimuli receive focused attention at the expense of peripheral information. Attentional narrowing to emotive stimuli compromises binding to peripheral stimuli and results in an associative retrieval deficit of peripheral stimuli (Burke, Heuer, & Reisberg, 1992; Christianson & Loftus, 1991; Christianson, Loftus, Hoffman, & Loftus, 1991). It is conceivable that the presentation of fearful faces in our learning paradigm attracted more focal attention than neutral and happy faces, at the cost of attention paid to the names presented in the periphery. The detrimental effects of attention paid to the fear emotion were not observed during learning (when both the face and the names were displayed on screen), but emerged at retrieval. Specifically, the name cues that we used at retrieval represented the putative peripheral stimuli for which the associative memory of fearful faces was weakened.

Cardiac timing did not affect retrieval, although previous studies have identified baroreceptor-mediated influences on memory (Fiacconi et al., 2016; Garfinkel et al., 2013). One explanation is that our trial-and-error learning paradigm did not synchronise the face presentation, but the feedback following participants' name selection, with afferent cardiac signals. Hence, stimulus-response mappings between face-name pairs and auditory tone, formed during online encoding, may have been lost at retrieval where the critical contextual response (i.e. the cardiac-invoked feedback) was missing (Armony & Dolan, 2001; Maren, Phan, & Liberzon, 2013). Fluctuations in bodily physiology can be considered as context for memory details: Patients with post-traumatic stress disorder showed reduced skin conductance and lower amygdala reactivity following danger-evoking contextual changes, and these effects were expressed as impaired fear memory renewal (Garfinkel, Abelson, et al., 2014). A second explanation for the lack of cardiac influences on memory is that our

retrieval paradigm eliminated the emotional salience of the facial expressions by presenting name cues. The effect of salience in detecting emotional stimuli has been demonstrated by the attentional blink paradigm, in which fearful faces presented at systole received a selective breakthrough to perceptual awareness within a masked rapid serial visual presentation procedure (Garfinkel, Minati, et al., 2014). By contrast, when the salience of the emotional stimulus was reduced, by presenting verbal rather than visual emotive stimuli, there was no perceptual breakthrough at systole (Garfinkel et al., 2013), similar to our retrieval paradigm.

Cardiac influences on associative retrieval as a function of personality

Our experiment revealed that personality mediated the impact of internal states of bodily arousal on feedback-driven emotional memory. First, we found that higher extraversion was related to poorer retrieval performance, irrespective of emotional content and cardiac-invoked feedback presentation during learning. Extraversion is often associated with lower baseline cortical and autonomic arousal (Fink et al., 2005; Geen, 1984; Harvey & Hirschmann, 1980; Kumari et al., 2004). This dovetails with the Yerkes & Dodson law of arousal and performance (Yerkes & Dodson, 1908), wherein low levels of arousal can be detrimental for task performance. This view is supported by our finding that higher extraversion was associated with lower heart rate, such that lower autonomic arousal might have underpinned poorer retrieval performance (Geen, 1984; Harvey & Hirschmann, 1980). Notably, the relationship between arousal and performance determines how different levels of arousal match optimal task environments: Overall, extraverts may not generally perform worse than introverts on cognitive tasks, but are more likely to outperform introverts in fast-paced (Hahn et al., 2015), sensory stimulating environments (Geen, 1984), arguably since higher task demand increases extraverts' cortical (Fink et al., 2005; Kumari et al., 2004) and autonomic arousal (Geen, 1984; Harvey & Hirschmann, 1980) to drive optimal performance. The fact that our retrieval task was slow-paced (three second responses) and carried out in a quiet lab environment could have contributed to extraversion-related retrieval deficits.

If low-arousal extraversion correlates with poorer retrieval performance, it follows that experimentally induced increases in arousal should stimulate extraverts' performance. This is what the results of our emotional intensity rating task seem to suggest: Higher extraversion scores were positively correlated with intensity ratings of fearful, but not neutral and happy, faces that were initially reinforced at systole. Importantly, unlike in a previous emotional

intensity paradigm (Garfinkel, Minati, et al., 2014), the stimuli in our task were not triggered at different phases of the cardiac cycle during the time of rating. Cardiac timing was only used during the trial-and-error learning task to synchronise auditory feedback to participants' responses. This means that, in extraverts, the reported increase in fear intensity reflects an implicit memory of mappings between face-name pairs and cardiac-invoked feedback established during learning. Our finding converges with the notion that extraversion is associated with enhanced sensitivity to feedback/reward (Lucas, Diener, Grob, Suh, & Shao, 2000). Moreover, (Hutcherson, Goldin, Ramel, McRae, & Gross, 2008) showed a relationship between extraversion and heightened experience of, specifically negative emotions (as in our rating paradigm), following active attention paid to the emotion, concomitant with activation-decrease in reward sensitive brain regions (ventral striatum, amygdala). Speculatively, the intrinsic enhancement of psychophysiological arousal during feedback presentation at cardiac systole, coupled with a trace representation of an emotionally salient stimulus (i.e. fear), drives exaggerated, implicit fear sensitivity, as manifest in our extraverts' intensity ratings. Future experiments would benefit from incorporating methods that allow the precise measurements of increased bodily arousal responses in extraverts to fear-evoking stimuli and/or systole-induced feedback presentation. This could incorporate the use of signal detection measures as a useful method to assess individual differences in response times and accuracy (Pfeifer, Rothen, Ward, Chan, & Sigala, 2014; Snodgrass & Corwin, 1988), as well as physiological measures such as galvanic skin conductance responses and event-related potentials.

Beyond extraversion, our results add to recent evidence for enhanced (Fiacconi et al., 2016; Garfinkel, Minati, et al., 2014; Gray et al., 2012; Park et al., 2014; Pramme et al., 2016) rather than reduced, processing of stimuli presented at cardiac systole. This was further apparent in people with low levels of neuroticism in whom retrieval confidence was enhanced for fearful faces initially reinforced at systole. Our finding extends previous reports of cardiac signalling at systole leading to enhanced decision confidence (Fiacconi et al., 2016; Garfinkel et al., 2013), by showing that personality differences influence retrieval confidence for fear stimuli. Neuroticism is closely associated with anxiety (H. J. Eysenck, 1967), and characterised by biased orientation towards aversive emotional events (Norris et al., 2007) and threat (Cremers et al., 2010; Ormel et al., 2013). Our data (showing that neuroticism was associated with higher confidence ratings for fearful faces that were initially reinforced by feedback at *diastole*) implies that anxiety-prone individuals show a subjective

memory bias for fear stimuli that were initially learned through reinforcement at *lower* levels of cardiovascular arousal. This observation relates to earlier findings of a correlation between anxiety scores and enhanced fear perception at diastole, suggesting chronic fear responses in anxious individuals, even at lower levels of cardiovascular arousal (Garfinkel, Minati, et al., 2014). Interestingly, our finding of heightened confidence in the retrieval of fearful faces goes against the predictions of the attentional narrowing hypothesis. If, during trial-and-error learning, people scoring high for neuroticism had paid greater attention to fearful faces reinforced at diastole relative to neutral and happy faces reinforced at diastole, then the retrieval of fearful faces from name prompts should have been more difficult, and consequently should have received lower confidence judgements. The fact that we did not observe an objective retrieval deficit of fearful faces initially reinforced at diastole, and that fearful faces were judged more confidently in people scoring high for neuroticism, suggests an implicit mapping between fearful face-name pairs and reinforcing feedback presented at diastole, which manifested as excitatory metacognitive judgements in people scoring higher for neuroticism. Cumulatively, our results indicate altered fear perception and memory in anxious individuals, underpinned by a failure to suppress threat and inhibit responses at lower levels of autonomic arousal, resulting in sustained fear orientation. Ongoing investigations of clinical populations with anxiety are characterising the influence of cardiac signals on threat perception, to clarify the hypothesized clinical relevance of our findings. There is, moreover, a need for neuroimaging and related investigations to define mechanisms through which fear memory is influenced by physiological arousal in clinical and non-clinical populations. Further behavioural research with increased sample sizes will help establish the broader relevance of personality differences in emotional learning and memory, as these will have implications for treatment of anxiety disorder. Moreover, future fMRI studies should target cardiac-mediated activity in the locus coeruleus during fear encoding to gain further insight into interaction between personality and fear memory.

Conclusion

Together, our results contextualize the explanatory validity of peripheral theories of emotion (Ekman et al., 1983; Friedman, 2010; Harrison et al., 2013; James, 1884, 1894; Janig & Habler, 2000; Kreibig, 2010; Lange, 1885/1912) by showing effects of autonomic arousal states on emotional learning and memory, that are shaped by individual characterological

traits. Using the cardiac timing paradigm, we observed effects that predict a fear learning advantage at higher levels of autonomic arousal in individuals most sensitive to physiological changes. This was demonstrated by enhanced stimulus-response mappings between fearful face-name pairs and systole-invoked feedback presentation during trial-and-error learning. Specifically, the fear learning advantage was mediated by interoceptive accuracy, linking heightened bodily sensitivity and greater susceptibility to threat-evoking information. Internal bodily states of arousal were further mediated by personality, with differential effects on emotional memory: low-arousal extraversion and high-arousal neuroticism were both associated with enhanced implicit fear memory and fear confidence, respectively. However, these personality traits showed divergent effects of cardiac arousal signals: Fear sensitivity was conveyed by reinforcing feedback presented at systole in extraversion and by reinforcing feedback presented at diastole in neuroticism. Overall our results demonstrate that emotional memory is mediated by interoceptive sensitivity and personality factors associated with constitutional states of arousal and reactivity.

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