Affective modulation of conditioned eyeblinks

Suvi Karla a, Timo Ruusuvirta b,c,d, Jan Wikgren a,*

a Department of Psychology, University of Jyväskylä, P.O. Box 35, FIN-40014 Jyväskylä, Finland
b Turku Institute for Advanced Studies, Centre for Cognitive Neuroscience, Department of Psychology, University of Turku/Turku School of Economics, Assistentinkatu 7, FIN-20014 Turku, Finland
c Department of Psychology, University of Tampere, Kalevan tie 5, FIN-33014 Tampere, Finland
d Cognitive Brain Research Unit, Department of Psychology, University of Jyväskylä, FIN-00014, Helsinki, Finland

1. Introduction

The motivational priming hypothesis (for details see, e.g. Lang et al., 1990) states that reflexive actions are augmented when they are congruent with the ongoing motivational state. In practice, the hypothesis states that negative emotions activate the brain’s aversive motivational system and prime defensive reflexes.

Experimentally, motivational states (and emotions) are typically induced by presenting images varying in content from unpleasant to pleasant. Indeed, the motivational priming hypothesis has withstood a plethora of tests combining picture viewing with an acoustic startle probe. Additionally, other types of emotional background stimuli have been utilized; for example, movies (Jansen and Frijda, 1994; Kaviani et al., 1999), words (Aitken et al., 1999), odours (Miltner et al., 1994; Ehrlichman et al., 1995; Prehn et al., 2006), imagery (Vrana and Lang, 1990) or stimuli previously paired with negative consequences (Grillon, 2002; Asli and Flaten, 2007; Mallan and Lipp, 2007). Likewise, tactile eyelblink reflexes, evoked by mild airpuffs (Hawk and Cook, 1997) have been shown to be modulated by emotional background stimuli. Only reflexes of a neutral, non-defensive nature, such as the tendon reflex, seem to be unaffected by such modulation (Bonnet et al., 1995).

The motivational priming hypothesis (Lang et al., 1990) implies that any defensively motivated behaviour, not only innate reflexes, should be modulated by emotional state. However, it is unclear whether a probe for emotional priming could be based on associative plasticity. The present study aimed at investigating whether conditioned eyelblinks in response to initially neutral auditory stimuli could provide such a probe. The adult human participants were first subjected to classical eyelblink conditioning while they viewed emotionally neutral images. Next, the conditioned eyelblink responses (CRs) of the participants were tested during the viewing of unpleasant, neutral, or pleasant images. The most vigorous CRs were found during the unpleasant images, although they did not differ between neutral and pleasant images. The results add to the motivational priming hypothesis by demonstrating its partial applicability to associatively learned defensive behaviour.
2.3. Procedure

The participants were informed that their task was to sit in a comfortable chair in a dimly lit room and to watch images presented on a 17 in. computer monitor approximately 1 m in front of them, while occasional tones and airpuffs to the corner of the eye were administered.

Eyeblinks were recorded as EMG activity of the orbicularis oculi muscle beneath the right eye. The ground electrode was attached to the forehead. The raw EMG signal was fed into custom-built amplifier, digitized (sampling rate 1000 Hz), rectified, and digitally off-line filtered with low-pass (<20 Hz) filter.

The experiment consisted of two phases. In the acquisition phase, 80 CS–US pairs were presented during viewing of pictures, presented in a random order and selected from among 40 neutral Images.1 In the test phase, 30 CS–US pairs were presented during presentation of pictures varying in emotional content (10 pleasant, 10 neutral, and 10 unpleasant pictures in presented pseudorandom order). During both phases, the pictures were visible for 6 s and CS–US pairs were presented within that time-frame so that the onset of the CS varied randomly between 1 and 5 s from the image onset. The CS and US were presented in a delayed fashion with an inter-stimulus interval (onset-to-onset) of 400 ms. The inter-trial intervals varied between 15 and 24 s, during which the monitor was black. E-Prime software was used to control the experiment.

2.4. Data analysis

To minimize the between-subject variability in the EMG magnitude, the signal was standardized for each participant by expressing each data point as a percentage of the average response magnitude across the first five unconditioned responses. All off-line signal processing was carried out using Matlab with the Signal Processing Toolbox.

Three periods were determined for the purpose of the analyses: baseline (200 ms before the onset of the CS), CR (200 ms before the onset of the US) and UR (200 ms after the onset of the US). For each trial, the maximum CR and UR magnitudes were determined from corresponding 200 ms periods using the standardized EMG signals and then averaged for eight conditioning blocks (10 trials each) in the acquisition phase, and for each image content in the test phase.

Variation in spontaneous EMG activity was determined from the baseline activity. An eyeblink was considered to have occurred when the maximum EMG activity in a given period exceeded the spontaneous activity by more than 5 standard deviations. Blink probability was thus determined in each trial for baseline and CR periods. The CR probability was then calculated by subtracting the blink probability in the baseline period from that of the CR period in each trial block.

Analysis of variance for repeated measures and subsequent paired samples t-tests with Bonferroni-correction were used to analyse the effects of conditioning and image content. Greenhouse–Geisser corrected degrees of freedom were used if the sphericity assumption was violated.

3. Results

3.1. Development of the CR

As a function of training, average CR magnitude increased from 12.59 (SEM = 1.54) to 19.02 (2.34) standardized units and CR probability from 40.0 (7.64) to 74.0 (4.43). There was a significant main effect of conditioning for both CR magnitude [F(7,168) = 6.52, p < 0.001], CR partial = 0.214] and probability [F(7,168) = 10.96, p < 0.05, CR partial = 0.313]. Subsequent paired comparisons verified that both CR magnitude and CR probability in blocks 2–8 were significantly higher than in the first block [CR magnitude: t(24) = 3.39–4.47, p < 0.01; CR probability: t(24) = 2.92–4.47, p < 0.01]. Comparison of CR magnitude and probability in blocks 3–8 with that in block 2 only yielded a statistically significant difference for CR probability [block 2 vs. block 8: t(24) = 2.17, p < 0.05], suggesting that the level of conditioned responding was relatively stable from the block 2 onwards.

3.2. Effect of image content on CR and UR magnitudes

Fig. 1 shows the CR and UR magnitudes as a function of picture content in the test phase. The picture content had a significant main effect on CR magnitude [F(2,48) = 6.76, p < 0.01, CR partial = 0.220], but not on CR probability [F(2,48) = 0.63, p < 0.54, CR partial = 0.026] or UR magnitude [F(2,48) = 1.80, p < 0.178, UR partial = 0.069]. Subsequent paired comparisons showed higher CR magnitudes during unpleasant relative to pleasant pictures [t(24) = 2.68, p < 0.05] and relative to neutral pictures [t(24) = 2.82, p < 0.01]. No difference was observed between neutral and pleasant pictures [t(24) = 0.15, p = 0.879].

4. Discussion

We investigated the applicability of the motivational priming hypothesis (Lang et al., 1990) to associatively learned, defensive eyeblinks. We found that defensive eyeblink CRs were augmented during unpleasant pictures. This augmentation is analogous to that of startle responses in similar contexts (Lang et al., 1990). Our finding, therefore, suggests that emotional state also affects associatively learned, motivationally driven, yet emotionally relatively neutral, behavioural acts. This adds to the general validity of the motivational priming hypothesis (Lang et al., 1990).

However, the lack of observable CR diminution for pleasant relative to neutral pictures was in contrast to the previous findings of such diminution in startle eyeblinks (Lang et al., 1990). The cause of this discrepancy remains unclear. Nevertheless, we must acknowledge that CRs and URs recruit partially distinct neural networks and mechanisms. In other words, whereas eyeblink reflexes are driven by simple brain-stem pathways, conditioned

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1 IAPS-slide numbers:

Neutral: 2190, 2200, 2210, 2239, 2514, 2600, 5130, 5500, 5510, 5740, 7550, 7900, 7002, 7004, 7009, 7010, 7020, 7030, 7031, 7050, 7060, 7080, 7900, 7100, 7110, 7130, 7150, 7160, 7170, 7180, 7182, 7184, 7217, 7217, 7233, 7350, 7550, 7700, 7705.


Unpleasant: 1070, 1090, 1110, 1114, 1120, 1205, 1274, 1280, 1300, 2053, 2095, 2120, 2141, 2205, 2276, 2683, 2710, 2800, 3000, 3010, 3030, 3100, 3120, 3130, 3140, 3150, 3530, 6020, 6190, 6200, 6230, 6370, 6415, 6555, 7380, 9001, 9040, 9041, 9050, 9340, 9342, 9490.

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1 International Affective Picture System (IAPS; The Center for Research in Psychophysiology, 2001). The mean normative valence ratings for the pictures used were 7.53, 5.00 and 2.67, respectively (1–9 scale, low values representing unpleasantness) and arousal ratings were 4.85, 2.97, and 5.91 (1–9 scale) for the pleasant, neutral, and unpleasant categories, respectively.
eyeblinks also depend on a distinct cerebellar learning circuit (e.g. Steinmetz, 2000), which might be differently affected by experienced valence, specifically concerning pleasant states.

Unexpectedly, however, the emotional state did not modulate the magnitude of airpuff URs. The reason for this was most likely methodological. The high US intensity used to assure robust learning was very likely the cause of a ceiling effect for UR magnitude, even with pleasant pictures. In line with this, emotional state has been shown to modulate airpuff-induced eyeblinks in the case of milder airpuffs (Hawk and Cook, 1997).

To conclude, our findings add to the motivational priming hypothesis (Lang et al., 1990) by showing that unpleasant affective states also augment associatively learned defensive responses. Future studies should address the lack of their diminution by pleasant affective states.

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References
