NeuroImage 59 (2012) 883–884

Contents lists available at SciVerse ScienceDirect

NeuroImage

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

Comments and Controversies

No evidence for a negative prediction error signal in peripheral indicators of sympathetic arousal

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ARTICLE INFO

Article history:
Received 14 May 2011
Revised 20 August 2011
Accepted 22 August 2011
Available online 2 September 2011

ABSTRACT

Recently, the existence of a prediction error signal to the omission of expected punishment in skin conductance recordings has been posited. Here, we re-analyse an existing dataset on aversive delay conditioning and find no evidence for such a signal. We discuss methodical reasons for this discrepancy and technical implications for estimation of central processes from skin conductance data.

Skin conductance responses (SCR) can be harvested to infer sympathetic nerve activity (SNA), and hence brain processes, by using inversion of generative models. We have recently proposed a novel method of quantifying conditioned fear by estimating anticipatory SNA from measured SCR using a dynamic causal model (Bach et al., 2010a). We have shown that this approach has much higher sensitivity than previous methods.

In Bach et al. (2010a), conditioned or anticipatory (aSCR), and unconditioned or US-evoked (eSCR) responses were estimated separately (Fig. 1). We reported only responses to a conditioned stimulus CS+ not followed by an unconditioned stimulus US (CS+/US−), to avoid the confounding effects of an eSCR on aSCR estimates. This approach assumes that the absence of a US does not itself elicit a (potentially confounding) eSCR.

Challenging this assumption, Spoormaker et al. (2011) recently posited a positive SCR to the unexpected omission of a US (or negative prediction error). Because the presence of a US (or positive prediction error) always elicits a positive SCR, such responses would conform to unsigned prediction error (or surprise) signals: signals that are similar for the unexpected presence or unexpected absence of a US. Reinforcement learning theories built on behavioural data (Pearce and Hall, 1980) assume that unsigned prediction error increases associability, and recently such signals have been demonstrated in anterior cingulate cortex (Hayden et al., 2011). Note that because there is also a response to the omission of the US in CS− trials, where this omission is entirely expected, the shock omission response in CS+/US− trials has to be larger than in CS−/US− trials to fulfil the definition of a negative prediction error response.

Surprisingly, Spoormaker et al. did not find a learning effect in the early CS onset response, that is, a different CS onset response in CS−/US− vs. CS+/US− trials, as would be expected from the fear conditioning literature (Boucsein, 1992). Instead, they report a significantly different late CS response in the last 3 trials of each type, which they attribute to shock omission and thus qualify it as prediction error signal. However, the time window for defining this response (1.4–4.4 s after shock omission) only narrowly includes the average peak latency of evoked skin conductance responses at 4.3 s (Bach et al., 2010b). Further, from the example shown in the supplemental material, it appears that SCR onset latency of the late response (about 1.6 s after shock omission) is shorter than SCR onset latency of the early response (about 2.2 s after CS presentation), and that the peak of late responses in non-reinforced trials occurs earlier (about 2.9 s after shock omission) than the peak of late responses to electric shock in reinforced trials (about 3.8 s after electric shock). Hence, this late response in non-reinforced trials might be too early to qualify as response to the CS offset, and could conceivably constitute a late response to CS onset. Note that biphasic responses to a CS+ are often reported as first and second interval responses (Boucsein, 1992); so Spoormaker et al. might simply report a second interval response to CS+ onset, rather than a prediction error signal.

Here, we re-analyse our own data, using the second dataset and the methods reported in our previous paper (Bach et al., 2010a), together with the freely available software *SCRalyze b2.1.4* (http://scralyze.sourceforge.net) to answer the following questions: is there an eSCR to omission of the US? And could such a signal bias estimates of the aSCR (i.e. the conditioned response)?

To answer the first question, we contrasted the estimated eSCR in CS+/US− and CS−/US− trials (Fig. 1). Across the whole experiment, the difference was not significant ($t_{19} = 0.7$; two-tailed $p = .48$). To replicate Spoormaker's analysis, we contrasted only the last 3 trials without US of the first 15 trials for each CS+ and CS−, a difference that was again not significant ($t_{19} = 1.7$; $p = .11$). Further, we investigated systematic time-dependent differences between CS−/US− and CS+/US− trials. Because the stimulus order was randomised per individual, we linearly interpolated responses for each participant,

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doi:10.1016/j.neuroimage.2011.08.091

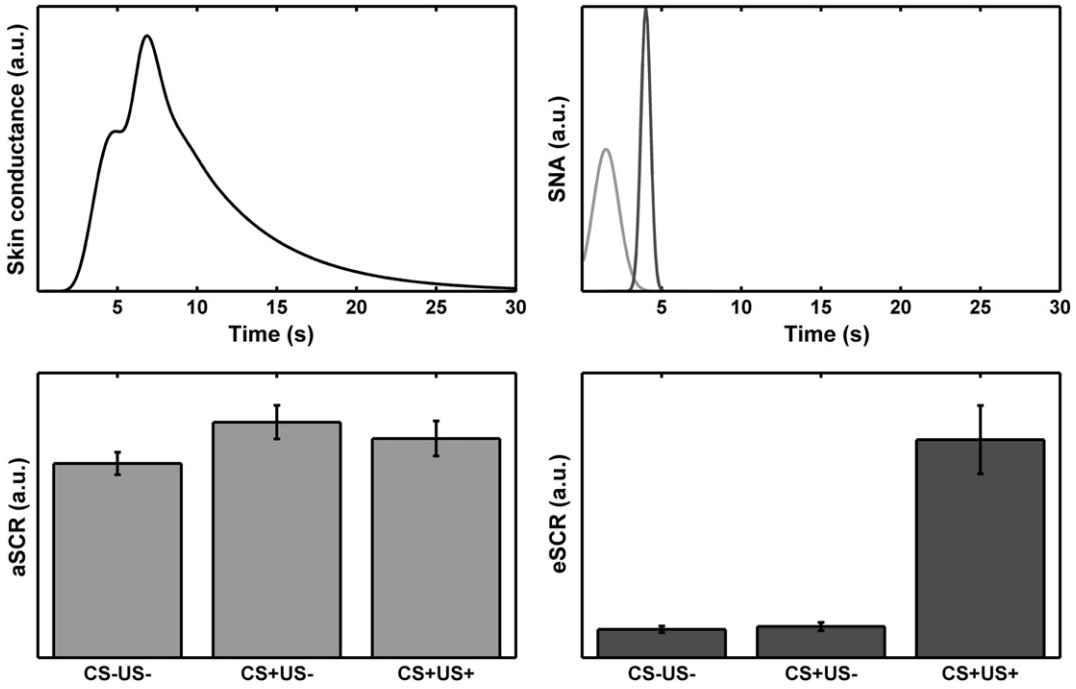

Fig. 1. *Top left*: Anticipatory (conditioned) and evoked (unconditioned) skin conductance responses overlap. *Top right:* The underlying sudomotor nerve activity components are estimated separately. *Bottom:* aSCR and eSCR from a previous dataset, shown as mean ± standard error of the mean. Note that aSCR and eSCR are depicted at different scale (both arbitrary units).

and then computed a repeated-measures two-way (time, CS type) ANOVA using Greenhouse–Geisser correction. There was no effect of CS and no interaction with time. Hence, from our data we conclude (i) that the offset response does not differ between CS− and CS+ trials; (ii) that it is therefore not related to US expectancy, and (iii) that it cannot bias the difference in anticipatory responses between CS− and CS+ trials. At the same time, in contrast to Spoormaker et al. but in keeping with the majority of fear conditioning literature, we find a significantly stronger anticipatory SCR in CS+/US− trials than in CS−/US− trials (Fig. 1), both across the whole experiment ($t_{19} = 3.9$; $p = .0009$) and in the 3 selected trials chosen by Spoormaker et al. ($t_{19} = 3.7$; $p = .002$).

Although we could not find evidence for a negative prediction error signal, we were interested in whether such a signal – if it existed – could potentially bias the contrast aSCR+/aSCR−. A US is clearly followed by a much larger eSCR than the omission of a US. Hence, the contrast between CS+/US+ and CS+/US− trials can help determine whether an eSCR can bias the estimation of the aSCR. As expected, eSCRs in CS+/US+ trials were markedly larger than in CS+/US− trials ($t_{19} = 6.1$; $p = .000008$). In these trials, the aSCR (that theoretically cannot differ between these trial types because the occurrence of the US is not yet known) was slightly underestimated ($t_{19} = -1.9$; $p = .07$).

To summarise, neither Spoormaker et al. (2011) nor our own data provide clear evidence for a negative prediction error signal in skin conductance responses. Should such a signal exist under certain circumstances, it may possibly lead to underestimation of the conditioned response. This would be conservative when contrasted with aSCR in CS− trials, but it might be best to test for such a signal (as described above) before comparing conditioned responses.

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