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Event-related potential correlates of phasic and tonic measures of the orienting reflex

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Abstract

We examined putative central nervous system (CNS) indices of tonic and phasic aspects of the orienting reflex (OR) in a passive event-related potential (ERP) dishabituation paradigm. Pre-stimulus skin conductance level (SCL) and the subsequent skin conductance response (SCR) were used as tonic and phasic OR "yard-sticks", respectively. Their stimulus—response patterns were used to assess two ERP components: the tonic pre-stimulus contingent negative variation (CNV) and the subsequent phasic late positive complex (LPC). SCLs and SCRs derived from each trial of the first train presented were compatible with traditional OR studies. Across-train means were also derived for each of the four measures examined. Arousal changes, as indexed by the SCL, were weak in the CNV which showed an additional expectancy effect. The LPC showed a stimulus—response pattern across trials identical to that of the SCR. This study clarifies links between the traditional autonomic measures of the indifferent OR and its CNS correlates, and encourages an OR perspective and/or interpretation of ERP effects.

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1. Introduction

Sokolov (1960, 1963) proposed that a cortical representation (neuronal model) develops with repeated presentation of a given stimulus, and that new stimuli failing to match the model elicit an orienting reflex (OR), the magnitude of which is proportional to the extent of the mismatch. Sokolov distinguished between ORs based on their duration: "phasic" refers to the rapid, short-lasting response, while "tonic" refers to the slower, longer-lasting state changes commonly associated with levels of arousal/activation (Barham and Boersma, 1975; Barry, 2004; Barry et al., 2004). Sokolov (1963) hypothesised that the tonic reflex has an important role in OR elicitation through its association with general arousal, which amplifies the phasic reflex produced in the stimulus-comparator mechanism.

Skin conductance level has had a long history of use as an index of CNS arousal (e.g., Lykken and Venables, 1971; Raskin, 1973). For example, in the developmental study of psychopathology, high levels of electrodermal arousal have been found to predict later schizotypal behaviours (Raine et al., 2002), while

low levels predict antisocial outcomes (Raine et al., 1990, 1995, 2000). Lawrence et al. (2005) examined the effects of methylphenidate stimulant medication on behavioural, autonomic nervous system (ANS) and CNS measures in children with attention deficit/hyperactivity disorder (AD/HD). They found that SCL was lower in children with AD/HD than controls, and that this difference was ameliorated after medication, supporting the hypoarousal model of AD/HD (Satterfield and Cantwell, 1974). In an examination with normal children, Barry et al. (2004) showed that resting SCL was inversely related to alpha power in the simultaneous eyes-open EEG, and directly related to alpha frequency. Studies using functional imaging techniques (e.g., Critchley et al., 2001, 2002; Nagai et al., 2004) have related the generation and level of electrodermal activity to specific brain areas. These specific regions are the ventromedial prefrontal cortex, orbitofrontal cortex, left primary motor cortex, and the anterior and posterior cingulate, which have been shown to be associated with emotional and motivational behaviours (Critchley, 2002; Damasio, 1994; Fredrikson et al., 1998; Nagai et al., 2004). Such findings indicate the close association of peripheral and central measures of arousal, re-emphasise the close connections between electrodermal activity, arousal, attention, cognition and emotion, and encourage the clarification of these linkages.

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Current ANS research examining the OR typically relies on variants of the dishabituation paradigm, in which a repetitive stimulus (S1) is presented for a series of trials, during which a different stimulus (S2) is interpolated. OR theory predicts response decrement to repetitions of S1, response recovery of the habituated OR to the novel S2, and enhanced responding (dishabituation) to a subsequent representation of S1. These three properties define the decremental process as habituation, ruling out alternative explanations such as receptor fatigue. The skin conductance response (SCR) is the most consistent autonomic measure that conforms to these predictions (Barry and James, 1981; Connolly and Frith, 1978; Groves and Thompson, 1970; Webster et al., 1965).

Although Sokolov noted that the tonic reflex would also be expected to habituate, there has been very little examination of trials effects in tonic measures. Barry and Sokolov (1993) examined the role of the tonic OR in modulating the phasic OR during a simple habituation paradigm. Subjects were presented with a series of repetitive stimuli which had no task requirements associated with them (termed indifferent in traditional OR terms). Pre-stimulus SCLs were taken as measures of arousal existing at each stimulus presentation, and post-stimulus SCRs were taken as indices of the phasic OR. SCL showed evidence of an initial increase in arousal (sensitisation) after the first stimulus in the series, followed by a systematic decline with stimulus repetition. Response decrement was shown for the SCR, and this pattern remained after the arousal effects were removed by linear regression, suggesting that the process was independent of arousal changes. This was noted as "consonant with the conceptualisation of arousal as an amplifying factor in response evocation, serving only to modulate the stimulus-response reflex" (p. 42). In a follow-up study, these data were replicated by Barry (2004), who also showed that the initial sensitisation was not a result of the phasic OR to the initial stimulus, but represents an independent tonic effect of the initial stimulus.

Sensitisation effects shown after the initial novel stimulus (Barry, 2004; Barry and Sokolov, 1993) suggest that sensitisation will also occur after a novel change trial. To explore this, we examined phasic and tonic aspects of the OR in a dishabituation paradigm. In addition, the sensitivity of the tonic and phasic OR components to stimulus intensity was also examined. A consistent relationship has been shown between stimulus intensity and SCR magnitude, but intensity effects upon the tonic OR has rarely been examined. Iacono and Lykken (1983) examined intensity effects in SCL over trials and found sensitisation was more sustained at 110 dB, but this has not been examined within the innocuous OR intensity range, as used in the present study.

The major aim of this study was to examine putative CNS correlates of the phasic and tonic OR. Both central measures of brain function (e.g., EEG and ERPs) and peripheral measures (e.g., electrodermal activity or heart rate changes) reflect processing of stimulus material and have been found useful in exploring the mechanisms of perceptual and cognitive functioning. However, the types of experimental procedures used by researchers in the separate areas to investigate

essentially the same phenomena are very different. ERP paradigms commonly present stimuli for a duration in the tens of milliseconds with very short interstimulus intervals (ISIs) often of the order of 1 s. Because of poor signal to noise ratio, ERPs are normally derived from the averages of many responses to the same stimulus. This contrasts with traditional autonomic OR studies, in which habituation is studied with repeated presentation of a single stimulus (duration in the s range) with long ISIs (typically >10 s). Although a large number of ERP components have been suggested as possible CNS correlates of the OR (e.g., N1: Kenemans et al., 1989; N2: Näätänen and Gaillard, 1983; O-wave: Loveless, 1979; Rohrbaugh, 1984; slow wave: Zimmer, 2002; P300: Donchin et al., 1984; P3a: Squires et al., 1975 and novelty P3: Courchesne et al., 1975), differences in methodology have hindered our understanding of the relationship between peripheral and central measures.

Barry et al. (1992, 1993) and Budd et al. (1998) used an ERP style of averaging approach for examining novelty effects in ERP components. Subjects were presented with a stimulus sequence similar to those used in ANS dishabituation studies, but the stimulus train was repeated 21 times. The data were then averaged over trains, according to stimulus position in the train (i.e. trial number), to obtain ERPs. Using the SCR as the OR yardstick, Barry et al. (1992) examined the extent to which response decrement for the N1 component was due to a genuine habituation process. They found no evidence of dishabituation, demonstrating that response decrements were primarily due to the refractory period of the neural elements underlying the N1 response, and suggested that this effect is inherent in paradigms with short interstimulus intervals (ISIs). Barry et al. (1993) was able to show that habituation, response recovery and dishabituation did occur with SCRs in a similar short-ISI paradigm. The authors noted that response decrements can only be described as habituation when all other possible explanations, such as refractoriness, diminished arousal, sensory adaptation and receptor fatigue have been ruled out. Evidence of response recovery and dishabituation exclude such explanations. Hence, we did not include examination of the N1 in this study.

It has not gone unnoticed by leading researchers in both the ERP and ANS fields that the antecedent conditions that lead to the SCR-OR are not dissimilar to those found to elicit the late positive complex (LPC or P300) of the ERP (e.g., Barry, 1996; Donchin et al., 1984; Polich and Criado, 2006; Simons et al., 1987). Early studies showed that elicitation of the LPC was associated with the processing of novel and task-relevant stimuli and that this information was incorporated into the schema or neuronal model of the stimulus in a process that Donchin termed context-updating (Duncan-Johnson and Donchin, 1977; Johnson and Donchin, 1978). The contextupdating hypothesis has its roots in Sokolov's concept of the orienting reflex (OR) (Donchin et al., 1984; Polich and Criado, 2006), and although the LPC has been the most commonly examined ERP correlate of the OR (e.g. Becker and Shapiro, 1980; Donchin et al., 1984; Kenemans et al., 1989; Polich, 1989; Polich and McIsaac, 1994; Roth et al., 1984; Verbaten, 1983; Wetter et al., 2004; Woestenburg et al., 1983), no studies

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