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Separation of the components of the late positive complex in an ERP dishabituation paradigm

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Abstract

Objective: A substantial body of evidence shows that several separate components underlie the late positive complex (LPC) of the ERP. Each of these has been proposed as a possible neural index of the orienting reflex (OR), but none has clearly met the criteria required for identification as an OR. The skin conductance response (SCR) is the most extensively examined index of the OR, and was used here as an OR 'yard-stick'. The primary aim of this study was to determine if any of the components of the LPC show stimulus–response relationships analogous to those of the SCR.

Methods: ERPs and SCRs were simultaneously recorded from 72 subjects during an ERP dishabituation paradigm, in which a habituation stimulus (S1) was presented for a series of trials, during which a different stimulus (S2) was interpolated. This sequence was presented in a series of trains, allowing across-train LPC and SCR exploration as a function of trial. The sensitivity of these components to stimulus intensity and significance, other stimulus dimensions important in defining the OR, was also examined. We utilised a PCA with varimax rotation to separate the ERP components underlying the LPC.

Results: Four factors extracted appeared to correspond to the classic Slow Wave, the P3b, the Novelty P3 and the P3a. While the LPC exhibited a stimulus–response relationship analogous to the SCR, each of the separate components was differentially sensitive to aspects of the stimulus manipulations examined here.

Conclusions: This study has demonstrated that the LPC is an adequate EEG index of the OR. However, the underlying components of the LPC examined here—which we consider to be the classic slow wave, P3b, Novelty P3 and P3a—cannot be used interchangeably as OR indices.

Significance: This study clarifies links between the autonomic OR and its CNS correlates.

Keywords: Orienting response; Skin conductance response; Late positive complex; P3a; P3b; Novelty P3; Slow Wave; Habituation

1. Introduction

The concept of the orienting response (OR) was introduced by Pavlov (1927) to describe the reflex that brings about an immediate response (both behavioural and physiological) to the slightest change in the environment. Sokolov (1963) proposed that a cortical representation (neuronal model) develops with repeated presentations of a given stimulus, and that new stimuli failing to match the model elicit an OR, with magnitude proportional to the extent of the mismatch. Sokolov (1963) focused on 3 of the determinants of the OR—the novelty or newness of the stimulus, its intensity, and its significance. Novelty of a stimulus is operationalised in terms of its decrease with stimulus repetition, and, as novelty decreases, so also does the magnitude of the OR elicited. Current ANS research examining the OR typically relies on variants of the dishabituation paradigm, in which a habituation 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 representation of S1. The skin

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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). In the moderate range of innocuous stimulus intensities, the magnitude of the SCR–OR has been shown to be directly related to stimulus intensity (Barry, 1975; Barry and Furedy, 1993; Barry and James, 1981; Jackson, 1974). Additionally, stimulus significance effects are evident when a stimulus has outcomes beyond those associated with the physical characteristics of the stimulus. For example, stimuli become significant to the subject when asked to count or respond to them (Barry, 1982a,b, 2004; Germana, 1968), and result in a larger OR.

The late positive component of the event-related potential (ERP), first described by Sutton et al. (1965), is a large centro-parietal deflection, peaking approximately 300 ms after stimulus onset. Sutton et al. (1965) showed that the amplitude of this component increased as the subject's degree of certainty concerning stimulus probability decreased. A number of studies investigating this component quickly followed. Initial reports emphasised the need for attention as a necessary condition for elicitation (Picton and Hillyard, 1974; Ritter and Vaughan, 1969; Squires et al., 1973). However, evidence of a late positive wave to unpredictable but irrelevant stimuli (Ritter et al., 1968; Roth, 1973), that differed in both latency and topographic distribution from the component originally described by Sutton et al. (Courchesne et al., 1975; Snyder and Hillyard, 1976; Squires et al., 1975a,b), suggested that, rather than a single entity, this component represented a complex response that differed with experimental design. Vaughan and Ritter (1970) proposed an early change in nomenclature, introducing the more appropriate 'late positive complex' (LPC). The LPC[1] is elicited by stimuli of any modality, and has been associated with orienting, attention, stimulus evaluation and memory (Courchesne et al., 1975; Donchin et al., 1986; Hillyard and Picton, 1987; Knight, 1996; Squires et al., 1975). The amplitude of the LPC has been shown to be augmented by increased stimulus intensity (Covington and Polich, 1996; Picton and Hillyard, 1974; Polich et al., 1996; Ritter and Vaughan, 1969; Roth et al., 1982; Rushby et al., 2004) and stimulus significance (Donchin and Coles, 1988; Picton and Stuss, 1980; Squires et al., 1975a,b, 1977). Such similarities between measures encouraged an international panel of researchers to propose examination of the LPC as an index of the OR (Donchin et al., 1984).

A number of studies examining *habituation* of the LPC have reported evidence of response decrement over stimulus repetitions (Becker and Shapiro, 1980; Kenemans et al., 1989; Verbaten, 1983; Woestenburg et al., 1983). This effect is not observed with active discrimination tasks (Polich, 1989; Roth et al., 1984) or when the stimulus is made relevant in some way to the subject (Wetter et al., 2004); although response decrement and response recovery have been shown after several blocks of trials (Polich and McIsaac, 1994). No studies, however, have formally shown whether these effects are due to a genuine habituation process—in CNS research, there has been a tendency to simply apply the term 'habituation' to any rapid response decrement with repetition of a stimulus. This common failure to adequately define habituation has led to substantial confusion in interpreting ERP response decrements. Barry et al. (1992) and Budd et al. (1998) examined the extent to which such an amplitude decrement in the N100 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 N100 response, and 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 the same 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. Our current research attempts to integrate these two traditions, in order to understand the relationship between peripheral and central measures during elicitation of the OR.

A large majority of studies examining the LPC have employed variants of the 'oddball' paradigm, in which subjects may be asked to attend (e.g. count or button press) or ignore deviant stimuli randomly presented within a series of homogeneous stimuli. In 1975, two papers confirmed elicitation of other late positive components in no-response or ignore conditions (Courchesne et al., 1975; Squires et al., 1975a,b). These components had an earlier, more fronto-central distribution, than the traditional parietal maximal component elicited by attend-deviants. Squires et al. (1975a, b) reported elicitation of an early (250–280 ms) fronto-central positive component by both attend and ignore deviants, labelled the P3a, and a later (340 ms) parietal positivity enhanced for attended deviants, labelled the P3b. They further showed that a broadly distributed slow wave (SW) component 'was in part contemporaneous with the P3a and P3b peaks' (p. 398). Courchesne et al. (1975) reported another component, the Novelty P3, that was also more frontally distributed, but showed a longer peak latency (360–450 ms) and was elicited by complex rare non-target pictures interspersed randomly in an attended oddball series. Later work (Courchesne, 1983; Courchesne et al., 1984) examined complex novel sounds in attend oddball tasks, and

[1] The LPC is often referred to in the literature as the P3, P300 or P3b component. For the sake of clarity throughout this paper, we use the LPC label for the global response peak and P3b to refer to the dominant principal components analyses (PCA)-extracted parietal component.