



Testing the S–R link hypothesis of P3b: The oddball effect on S1-evoked P3 gets reduced by increased task relevance of S2

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ABSTRACT

We had previously reported that the oddball effect on the P3b EEG potential evoked by infrequent vs. frequent S1 presented in a sequence of two stimuli, S1 and S2, gets reduced in a “combination task”. In this task, responses were determined by the combinations of S1 and S2 rather than by S1 only. We had attributed this reduction of the oddball effect to increased task difficulty. The present study investigated possible reasons for this reduction of S1-evoked P3b in more detail, by making the combination task easier in several respects: allowing for forming associations from S1 to responses (Experiment 1), reducing the complexity of stimulus–response (S–R) mappings (Experiment 2), and decreasing S2 relevance in defining responses (Experiment 3). The results showed that only S2 relevance affected the oddball effect on S1-evoked P3b. Namely, when S2 attained some relevance by inducing a go/no-go decision for S1-defined responses, the oddball effect on S1-evoked P3b was intermediate between the large effect in the simple oddball task and the small effect in the combination task. The results may be explained in terms of the S–R link hypothesis of P3b which interprets P3b as reflecting reactivation of well-established S–R links.

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1. Introduction

Several lines of evidence have converged to show that the P3b component of the human event-related EEG potential lies at the interface between stimulus (S) processing and response (R) preparation (Gerson, Parra, & Sajda, 2005; Kelly & O’Connell, 2013; Connell, Dockree, & Kelly, 2012; Ouyang, Herzmann, Zhou, & Sommer, 2011; Poli, Cini, Citi, & Sepulveda, 2010; Saville et al., 2011; Verleger, Jaśkowski, & Wascher, 2005; Verleger, Schroll, & Hamker, 2013). In this context, Verleger, Metzner, Ouyang, Śmigasiewicz, and Zhou (2014) have recently specified what might be P3b’s function, referring to the well-established “oddball” effect. The oddball effect is the massive increase of P3b amplitudes with infrequent stimuli when two stimuli, one rare and one frequent, are presented in unpredictable random series and require different responses (Duncan-Johnson & Donchin, 1977; Johnson & Donchin, 1980; Ritter & Vaughan, 1969; Squires, Squires, & Hillyard, 1975). Verleger, Metzner, et al. (2014) suggested that P3b in general, and the oddball P3 in particular, reflects reactivation of some already

well-established S–R link that is currently not in an activated state. They argued that in most standard laboratory task (typically consisting of long series of trials) there is no particular selection of new responses in each successive trial. Rather, a few fixed S–R links are established by instruction and practice, most frequently only two (e.g., “frequent S → left key”, “rare S → right key”). If during some consecutive trials only one of these S–R links is used, the other one, not having been used for some time, will have to be reactivated when the corresponding stimulus is perceived. This process of reactivating well-established S–R-links is assumed to be reflected in P3b amplitude.

This hypothesis was put to test by Verleger, Baur, Metzner, and Śmigasiewicz (2014). In their modification of the oddball task, two stimuli were presented (S1 and S2) and responses were defined either by only one of these stimuli or by their combination. S1 was the letter X or U, one frequent and one rare (80% vs. 20%). The letter was accompanied or followed (as will be the case in the present study) by a blue or yellow frame (S2) that surrounded letter position. In the standard oddball condition, key selection depended on the S1 letter only and S2 served just as “go” signal for pressing that key, S2 color being irrelevant. In this easy task, a large oddball effect was obtained on the S1-evoked P3 amplitudes. In contrast, in the “combination task”, S2 color determined the key to be pressed depending on the letter, e.g., blue frame meant “left”

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and yellow frame “right” after frequent X, but blue meant “right” and yellow “left” after infrequent U. In this task, the oddball-P3 evoked by S1 (in this example by infrequent Us) was massively reduced. When conceiving of P3b being independent of response processing (“stimulus evaluation hypothesis”, e.g., Callaway, 1983; Duncan et al., 2009) difficulty of response selection is not expected to modify the oddball effect because in any case the S1 letters are easily identified and are task-relevant. When, on the other hand, P3b is assumed to reflect decision processes (O’Connell, Dockree, & Kelly, 2012; Kelly & O’Connell, 2013) then, if anything, P3b is expected to increase when difficult decisions have to be made. In contrast, Verleger, Metzner, et al.’s (2014) conception of P3b as reflecting reactivation of readily available S–R links may account for this reduction of P3b by assuming that such links were not readily available with the infrequent stimuli in the combination task.

The question still remains what actually are the factors responsible for unavailability of S–R links in this combination task. Several possibilities will be tested in the present study. One factor may be the absence of any association between S1 and responses: when seeing X or U in the combination task, participants did not know whether left or right key-presses would be required. If this factor is critical, then making S2 predictable based on S1 may allow for creating such associations and for activating the appropriate response already by perceiving S1, thereby for undoing the reduction of the oddball effect. This account will be tested in Experiment 1. Another factor may be complexity of S–R mappings. This complexity may result from the overlap of the same two responses with four different S1–S2 combinations (4:2 mapping): Perhaps, response mapping for the infrequent U (e.g., left with yellow, right with blue) cannot be held in readiness because the responses “left” and “right” are continuously required for the frequent X. Moreover, this overlap may lead to conflicts between mapping of responses to S2 after rare S1 with such mappings after frequent S1. E.g., blue means left and yellow right for the frequent X, but blue means right and yellow left for the infrequent U. This account in terms of complexity will be tested in Experiment 2: By gradually decreasing the S–R overlap between frequent and rare S1 and the interdependency of S1 and S2 in defining the responses, the oddball effect is expected to become gradually restored. Alternatively, the critical factor may not be difficulty of response selection but rather the increased relevance of S2 for determining the responses. This account will be tested in Experiment 3 by comparing the oddball and combination tasks to go/no-go tasks where S2 color will indicate whether the selected response should or should not be executed: With S2 being more relevant in the go/no-go tasks than in the oddball task and less relevant than in the combination task, the oddball effect on P3b is expected to be smaller in the go/no-go task than in the oddball task and larger than in the combination task.

A large negative potential appeared in the ERPs evoked by infrequent stimuli in Verleger, Baur, et al.’s (2014) combination task. So it could be suspected that P3b proper had remained unchanged and was only apparently reduced by overlap with this negative potential. But this negativity could be spatially and temporally dissociated from P3b, because of its fronto-central focus, which was distinct from P3b’s parietal focus, and by its being time-locked to onset of the S2 color frames following the infrequent S1, rather than to S1 onset. P3b remained reduced in that study even when, with lengthened intervals between S1 and S2, the increased negativity occurred much later than S1-evoked P3b. So the reduction of P3b was genuine. The negative potential was interpreted as a correlate of difficult response selection (cf. Hanslmayr et al., 2008; Johnson, Henkell, Simon, & Zhou, 2008; Lang, Obig, Lindinger, Cheyne, & Deecke, 1990) and is expected to occur in the present study as well, whenever responses are difficult to select.

stimuli		tasks			
S1	S2	S2 irrelevant		S2 relevant	
letters	colors	oddball (S1 80/20, S2 80/20)		combination 50% (S1 80/20, S2 50/50)	combination 80% (S1 80/20, S2 80/20)
X		left 64%		left 40%	left 64%
X		left 16%		right 40%	right 16%
U		right 16%		right 10%	right 16%
U		right 4%		left 10%	left 4%

Fig. 1. Outline of tasks in Experiment 1. Entered are percentages of occurrence of each stimulus in each task. Each task was performed twice, once with frequent Xs and once with frequent Us (in the first and second half of the experiment). Only the version with frequent Xs is depicted, for simplicity. See text for further description of the tasks.

2. Experiment 1

2.1. Introduction

In Experiment 1, we aimed at replicating the reduction of the oddball effect on S1-evoked P3b in the combination task (Verleger, Baur, et al., 2014) and at studying whether the reason for this reduction is the absence of associations between S1 and responses. The combination task was presented in two versions that differed from each other by the absence versus presence of associations between S1 and S2, thereby between S1 and responses. Making responses predictable might activate the S–R links with S1 already, which might restore the oddball effect on P3b. The stimuli consisted of the letters X and U (S1) and following blue or yellow color frames (S2), separated by onset asynchronies of 500 ms. One of the two letters was frequently presented, the other rarely (80/20%). Fig. 1 displays the stimuli and the assignments to left or right key-press responses in the three tasks.

One task was a simple oddball task with delayed responses. The letter X required a left response, U a right response, and S2 served as go-signal, independently of its color. The second task was the combination task used by Verleger, Baur, et al. (2014), except that stimulus onset asynchronies (SOAs) between S1 and S2 had been 0 ms, 100 ms, 400 ms, or 800 ms in that study, while 500 ms SOA was used here. This is a “combination task” because information from S1 and S2 has to be combined to determine the response. Here, it will be termed “combination 50%” to denote that blue and yellow S2s, and thereby left and right responses, were equally probable. The third task was “combination 80%” because, while response assignments were identical to combination 50%, blue and yellow S2 were presented with probabilities of 4/1, rather than 1/1, such that a given letter as S1 predicted the response with 80% probability (cf. Fig. 1). Thereby, combination 80% might be considered midway between oddball, where a given S1 predicted the response with 100%, and combination 50%, where a given S1 predicted the response with 50% only. Therefore, if reduction of the oddball effect on P3b in the combination task (Verleger, Baur, et al., 2014) was due to different predictive validities of S1 on responses, then probabilities of 80% might still produce a smaller oddball effect than the 100% S1-response probabilities in the oddball task but a larger one than with the 50% chance probabilities in combination 50%.

We also expected to replicate the large S2-evoked negativity that accompanied the difficult response selections following infrequent S1 in Verleger, Baur, et al.’s (2014) combination task. Since response selection will be easier in combination 80% when S1 allowed for predicting the probable response, this S2-evoked negativity may be reduced in this task.

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