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Sequential P3 effects in a Posner's spatial cueing paradigm: Trial-by-trial learning of the predictive value of the cue

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The neurocognitive consequences of correct or incorrect spatial prediction in a sequential S1–S2 paradigm were assessed. Sequential dependence on previous trial outcome (valid or invalid) was assessed by late Event-Related Potentials (ERPs) and behavioural responses. Two different experiments were performed, situating the target in the vertical (Experiment 1) or in the horizontal (Experiment 2) meridian. RTs and late positivities (P3a and P3b) were recorded. ERPs showed that posterior positivity (probably a P3b) was greater in invalid–valid trials than in valid–valid trials but lower than in valid–invalid trials. However, at the frontal electrodes, late positivity (probably a P3a) only appeared in valid–invalid trials, indicating that invalid trials are analyzed as novel-like stimuli. The P3b results suggest trial-by-trial learning of the predictive value of the cue, which needs to be updated as indicated by the pattern of P3b amplitudes: valid–invalid > invalid–valid > valid–valid.

Key words: sequential effects, predictive value, trial-by-trial learning, P3a, P3b

INTRODUCTION

In daily life, humans continuously monitor their actions to ensure that they are appropriate for the environment. In a broader perspective, the "perception-action cycle" concept was introduced by Fuster (2003, 2004) to highlight the continuous interplay and evaluation of outcomes between perceptual and executive networks. In this neurocognitive model, the sensory and executive networks interact continuously at different levels of the processing hierarchy. One major consequence of such interaction would be the ability to monitor appropriateness between perception and action. Recently, the feedback that the neural system may generate as a result of a trial outcome has been demonstrated through the Error-Related Negativity component (Gehring et al. 1993, Falkenstein et al. 1995, Holroyd and Coles 2002). Another hypothesis linking frontomedial negativities to the evaluation of outcome has been proposed by Vidal and coauthors (2003). These authors sought to explain the frontomedial negativities that may occur after responses to correct trials (Vidal et al. 2003, Burle et al. 2005); they proposed that post-response negativities could be related to the response evaluation process. Therefore, there are clear neurophysiological signs of trial assessment as a function of trial outcome.

The perception of a target stimulus is often preceded by a cue that creates expectations about the features and relevance of the target, and this leads to a more complex view of the perception–action cycle: there is a continuous expectancy bias for certain stimuli and actions, converting the former perception-action cycle

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into a preparation-perception-action cycle. A neural signature indicating adequacy of preparation, perception and action might help to validate the hypothesis of a complete preparation–perception–action cycle. One type of stimulus sequence that seems particularly well suited to testing congruency between the expected and the current stimulus is the central cue Posner paradigm. In this paradigm, the central cue may validly (VC trials) or invalidly (IC trials) indicate the spatial position of the upcoming target. If the cue is a valid predictor of the target, there is a benefit in the RT with respect to neutral cues. However, if the target is incorrectly cued, a cost occurs in the RT with respect to neutral cues (Posner 1980). Part of this effect is due to the preparation of the incorrect response for invalidly cued target stimuli (Eimer 1993, Gómez et al. 2004).

From neurophysiological recordings, the preparation phase of the proposed cycle is explained by the Contingent Negative Variation (CNV). During the late period of the CNV in central cue Posner paradigms, it is possible to observe task-specific preparatory activation of the motor and sensory areas which are potentially needed to complete the task upon the information conveyed by the S1 (Gómez et al. 2003, 2004). Activation of fronto-medial and fronto-parietal areas can also be observed, probably sustaining endogenous attentional effort during the CNV period (Hopfinger et al. 2000, Brunia and Van Boxtel 2001, Gómez et al. 2003, 2004, 2007, Fan et al. 2007). A consequence of the task-specific preparation indicated by the CNV is that the prepared neural set may be correct or incorrect, depending on whether S1 represents the characteristics of S2 validly or invalidly.

The spatial cueing effects on the early ERP components reflecting attentional sensory processing have previously been evaluated by analyzing the modulation of early ERPs to target stimuli that are preceded by valid and invalid cues (Mangun and Hillyard 1991, Eimer 1993, Anllo-Vento 1995, Perchet and García-Larrea 2000, Perchet et al. 2001). The posterior positive components under IC conditions are also larger than those under VC conditions at the time latency of the P3 component (Mangun and Hillyard 1991, Eimer 1993). Recently (Gómez et al. 2008a,b, Digiacomo et al. 2008), the P3b effects were replicated and an increased P3a was also found when IC and VC targets were compared.

The latter results suggest that invalidly cued targets are processed in a similar manner to low frequency targets in oddball paradigms, as indicated by the greater P3a and P3b in IC trials. The P3a component is generated as a brain response to stimuli that are novel in comparison to more frequent stimulation. In fact, completely novel stimuli generate a higher-amplitude P3a component than deviant but often-repeated stimuli (Escera et al. 1998, Friedman et al. 2001, Wronka et al. 2008). The larger P3a (Friedman et al. 2001, Dien et al. 2003) indicates that the invalidly cued target is processed as a novel stimulus. In contrast, the P3b is a late positive component with a parietal distribution and typically appears in oddball paradigms. It is well known that the amplitude of P3 is inversely related to the probability of stimulus appearance (Duncan-Johnson and Donchin 1977). According to Donchin and Coles (1988), the higher P3b in invalid trials represents the context-updating operation and subsequent memory storage (Polich 2007). An alternative explanation of the cognitive meaning of P3 was suggested by Verleger and others (2005), who proposed that P3 is related to the neural linkage between stimulus perception and the response to that stimulus. A recent proposal relates the P3b component to the neuroinhibition needed to focus attention on the relevant task, facilitating the interference-free action of memory systems (Polich 2007). For the central cue Posner´s paradigm, the greater P3 in IC than VC trials represents assessment of the adequacy of sensory-motor preparation, sensory perception and action. It has been suggested that the most important component of this assessment is revision of the S1–S2 (cue–target) contingency value (Gómez et al. 2008a). In this approach, it is important to separate anterior and early P3 components of ERPs (P3a) from posterior and late ones (P3b), since source localization studies and scalp current source analysis have allowed early anterior and late posterior sources to be separated under IC and VC conditions (Gómez et al. 2008a,b).

An important issue that has scarcely been studied in central cue Posner paradigms is how correct or incorrect prediction in a given trial can induce changes in the processing of the next trial, i.e. sequential effects. A recent behavioral report on the central cue Posner paradigm addresses this point (Jongen and Smulders 2007). These authors found an inter-trial validity effect: the benefit in RTs when compared to neutral cues is higher if a valid trial is preceded by a valid trial than if it is preceded by an invalid one. On the other hand, the cost of an invalid trial is greater if it is preceded by a valid trial than by an invalid one. To our

knowledge, there have been no ERP studies analyzing the sequential effects of inter-trial validity using Event Related Potentials (ERPs). ERP studies could elucidate the timing and neurocognitive effects of inter-trial validity in cueing paradigms. Other effects related to neutral and catch trials, to the effects of alternate or repeated responses and to the inhibition of return are also reported by Jongen and Smulders (2007).

The aim of the present report is to analyze the sequential effects of valid S1–S2 trials preceded by other S1–S2s. We expect the outcome of the current trial to affect the behavior and ERPs of the next one. To achieve this objective, two experiments were conducted using the central cue Posner paradigm. One experiment presented central cues orientated vertically and targets situated in the vertical meridian, while the other presented central cues orientated horizontally and targets situated in the horizontal meridian (see Figures 1 and 2). Behavioral activity and EEG were recorded simultaneously. More specifically, the sequential effects on the behavioral responses and the P3a and P3b components were analyzed. Two different types of effects on the processing of a target are expected: (i) effects due to the implicit meanings of spatial cues and to the global predictive values of cues during the experiment (the so-called validity–invalidity effect); and (ii) local effects due to the spatial validity or invalidity of the previous trial. The late positive components allow us to analyze how novel the stimuli are considered (*via* P3a) and how much the internal model of the current predictive value associated with the cue presented (S1–S2 contingency value) needs to be revised (*via* P3b). Consistency of the results between the two experiments, in which the shapes and positions of targets (vertical vs. horizontal) and the S1–S2 interval (random vs. fixed duration) differed, would indicate robustness. As we are interested only in robust outcomes, we will discuss the results of both experiments together.

METHODS

Experiment 1

Subjects

Fourteen subjects (9 female and 5 male, 10 right-handed) between 21 and 36 years old (mean 24.5) took part in the experiment. The experiments were conducted with the informed and written consent of each subject following the rules of the Helsinki Convention. The Ethics Committee of the University of Seville approved the study.

Stimuli and behavioral paradigm

The stimulus presentation was computer-controlled (EEVOKE, ANT). Participants were seated 60 cm in front of a computer screen. They were instructed to fix their eyes on a white square in the centre of the screen, which remained visible throughout the experiment in order to sustain central fixation. The complete trial period included a central directional cue that was on for 200 ms, then an attentive waiting period lasting randomly between 1 800 and 2 000 ms (Fig. 1). Finally, a peripheral target appeared, subtending a visual angle of 0.91º and situated 8.3º eccentrically in the vertical meridian. Since the central directional cue could indicate the direction of appearance of the target correctly or incorrectly, two different conditions arose: validly cued targets (VC) (82.13% of trials) and invalidly cued targets (IC) (17.87% of trials).

In the present report, we will focus on the behavioral and ERP effects of valid and invalid trials that were preceded by validly or invalidly cued trials. We will

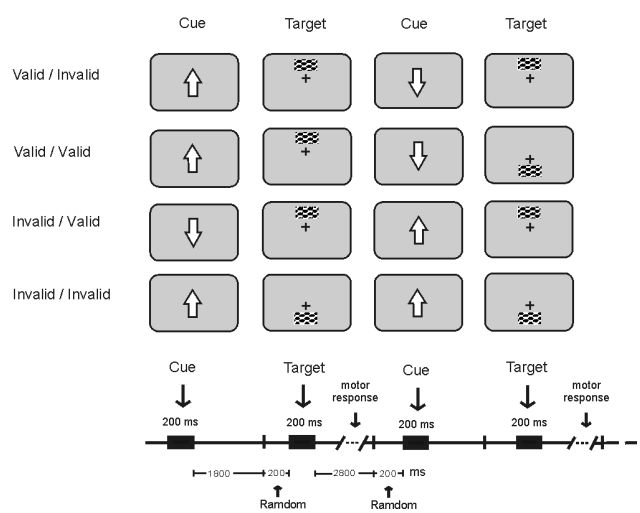

Fig. 1. Paradigm for Experiment 1. The different types of sequence trials considered in the experiment are shown. The temporal sequence of stimulus presentation appears in the lower part of the figure. Notice that the RTs and ERPs were obtained from the S2 stimulus in the second trial. This corresponds to the stimulus right side of the figure in each stimulus sequence.

therefore consider four types: S1–S2 valid trials preceded by a valid one (VV) (159 trials, 67.66% of the total); valid trials preceded by an invalid one (IV) (34 trials, 14.47% of the total); invalid trials preceded by a valid one (VI) (34 trials, 14.47% of the total); and invalid trials preceded by an invalid one (II) (8 trials, 3.40% of the total). The most relevant comparison in the present report is between IV and VV: there were too few II trials for reliable results, and comparisons between invalidly-cued trials and validly-cued trials have already been described (Mangun and Hillyard 1991, Eimer 1993, Perchet and García-Larrea 2000, Perchet et al. 2001, Gómez et al. 2008a,b, Digiacomo et al. 2008).

The participants used their right hands to respond to the targets by pressing a joystick button. They used the index finger to respond to targets presented in the upper visual hemifield and the thumb to respond to targets presented in the lower one. The inter-trial intervals were randomly selected between 2 800 and 3 000 ms. Subjects were presented with a total of 235 trials. There were no training trials.

Behavioral statistical analysis

The RTs were measured for VV, IV, VI and II trials and analyzed by a one-factor ANOVA with four levels. The Bonferroni test was used for planned *a priori* comparisons.

As an indicator of the subjects' general performances, the errors in individual trials were computed regardless of the type of the previous trial. Responses to S1, omissions to S2 and response errors to S2 were computed independently for validly and invalidly cued trials. The total numbers of errors in the two trial types were compared statistically by repeated measures ANOVA

EEG recording, processing and analysis

The EEG was recorded from 64 scalp sites in an extended version of the International 10–20 system, using tin electrodes mounted in an electrode cap (electrocap). All the electrodes were referred to the left mastoid. Impedance was maintained below 5 000 Ohms. Data were recorded in DC and no filtering was applied to them. The amplification gain was 20 000 (ANT amplifiers). The data were acquired at a sampling rate of 512 Hz, using a commercial AD acquisition and analysis board (ANT). Recordings were averaged off-line using an artifact-rejection protocol based on voltage amplitude. All the epochs for which the EEG exceeded 100 microvolts in any channel were automatically discarded for ERP analysis; 56.51% of VV trials, 56.72% of IV trials, 64.29% of II trials and 59.87% of VI trials were accepted for analysis. Rejections resulted not only from blinks and eye movements, but also from behavioral errors in the sequences of the two trials, since correct responses were needed in both the actual and the preceding trial. Moreover, not only should the double trial be behaviorally correct, it should not present artifacts in either trial sequence. Also, the first trial in each block (the experiment had five blocks) had to be rejected because there was no preceding trial. ERPs were obtained for each subject by averaging the EEG, using the switching-on of the target as a trigger. The baseline was the interval 200–0 ms before target stimulus. The algebraically linked mastoids were computed off-line and used as reference for analysis purposes. Eye movements and blinks were monitored using the electrodes installed in the 64-channel cap, after the sensitivity of the AF7–AF8 in monitoring horizontal eye movements and of the prefrontal electrodes (Fp1, Fpz and Fp2) in monitoring vertical eye movements and blinks had been checked.

Statistical analysis of ERPs

Repeated measures ANOVA was performed on the voltage data from selected electrodes. The mean voltage in selected time windows was analyzed independently for P3a and P3b under VV, IV and VI conditions. The II condition was not included in the analysis because there were so few II trials after the artifact rejection protocol had been implemented. The *P* values were calculated using the Greenhouse-Geisser correction. The Bonferroni method was used as *post-hoc* test when necessary.

Early positivity (P3a)

A two factor repeated measures ANOVA was performed on the voltage data with selected midline electrodes (Fz, Fcz, Cz). The mean voltage in the P3a time window (280–340 ms) was computed for each of the three conditions previously described. The factors considered were the type of trial (3 levels: VV, IV and VI) and the electrodes.

Late positivity (P3b)

A three factor repeated measures ANOVA was performed on the voltage data with selected electrodes (O1, O2, P3, P4, P5 and P6). The mean voltage in the P3b time window (300–400 ms) was analyzed independently for each of the three conditions considered. The factors considered were the type of trial (3 levels: VV, IV and VI), the hemisphere (left or right) and the electrodes.

Experiment 2

The main methodological differences between experiments 1 and 2 were the number of subjects, the location of the stimuli, the response hand, the S1–S2 period and the number of electrodes. In Experiment 2, the stimuli were in the horizontal meridian and the time between S1 and S2 was fixed. Moreover, responses were produced with both hands.

Subjects

Sixteen subjects (9 female and 7 male, all 16 right-handed) between 19 and 23 years old (mean 21) took part in the experiment. All experiments were conducted with the informed and written consent of each subject following the rules of the Helsinki Convention. The Ethics Committee of the University of Seville approved the experiment.

Stimuli and behavioral paradigm

The stimulus presentation was computer-controlled (EEVOKE, ANT). Participants were seated 50 cm in front of a computer screen. They were instructed to fix their eyes on a white square in the centre of the screen, which remained visible throughout the experiment in order to sustain central fixation. The complete trial period included a central directional cue that was on for 300 ms, then an attentive waiting period lasting 1 360 ms (Fig. 2). Finally, a peripheral target appeared, subtending a visual angle of 4.56º and situated 3.66º eccentrically in the horizontal meridian. The targets were cartoon figures that were constant in each block of trials. There were five blocks of trials. Five different figures were used in the whole experiment. Since the central directional cue could indicate the direction of appearance of the target correctly or incorrectly, two possibilities arose: validly cued targets (VC) (82.13% of trials) and invalidly cued targets (IC) (17.87% of trials). The numbers and percentages of VV, IV, VI and II trials were identical to those in Experiment 1. The subjects used the right index finger to respond to targets on the right of the screen by pressing a joystick button, and the left index finger to respond to targets on the left. The inter-trial intervals were 1 860 ms. Subjects were presented with a total of 235 trials. There were ten training trials. Behavioral statistical analysis was identical to that used in Experiment 1.

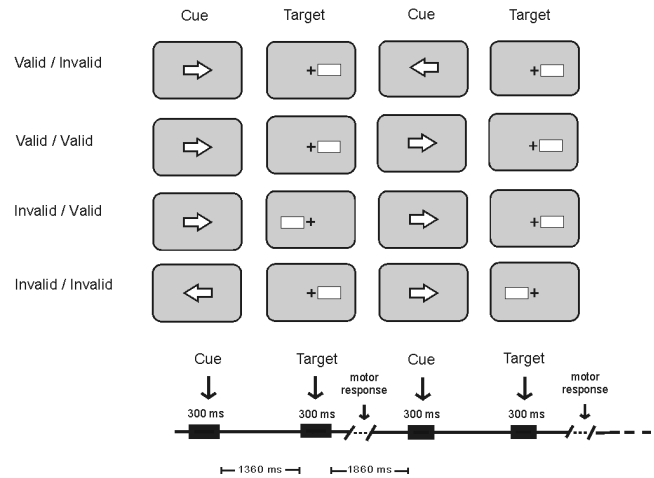

Fig. 2. Paradigm for Experiment 2. The different types of sequence trials considered in the experiment are shown. The temporal sequence of stimulus presentation appears in the lower part of the figure. Notice that the RTs and ERPs were obtained from the S2 stimulus in the second trial. This corresponds to the stimulus on the right side of the figure in each stimulus sequence.

EEG recording, processing and analysis

The EEG was recorded from 20 scalp sites in an extended version of the International 10–20 system, using tin electrodes mounted in an electrode cap (easy cap). The EEG processing was identical to that in Experiment 1; 62.54% VV, 58.82% IV, 57.81% II and 59.38% VI trials were accepted for ERP analysis. ERPs were obtained for each subject by averaging the EEG, using the switching-on of the target as trigger. The II condition was not included in the statistical analysis because it involved very few trials. Statistical analysis of ERPs was identical to that in Experiment 1.

Table I

Reaction times of the four experimental stimulus sequences analyzed in Experiment 1

Condition	Reaction Times	SD
Valid–Valid (VV)	372.89	106.67
Invalid–Valid (IV)	379.69	98.04
Invalid–Invalid (II)	413.48	92.95
Valid–Invalid (VI)	430.03	116.78

Table III

Post-hoc results for the component P3a in the Experiment 1

	Fz	Fcz	Cz
VV vs. VI		0.001	0.006
IV vs. VI	0.008	<0.001	<0.001
VV vs. IV			

In all cases the Bonferroni correction was applied. The cells with no values were not statistically significant

RESULTS

Experiment 1

Behavioral results

The RTs in the different sequences of trials appear in Table I. ANOVA showed an effect of the type of trial sequence ($F_{3,39}$=17.828, P<0.001). The fastest condition was VV, followed by IV, II and finally VI. Bonferroni analysis showed that the attentional cueing manipulation was effective, as indicated by the statistically significant differences between conditions II and VV (P<0.015), II and IV (P<0.033), and VI and both VV (P<0.001) and IV (P<0.001).

Table II shows the percentages of the different types of error in the valid and invalid trials. Comparisons showed a significant difference between the percentages of response errors in valid and invalid trials; there were more errors in the invalid trials (P<0.039). No other comparisons (responses to S1 and omissions to S2) were statistically significant.

Event-Related Potentials

P3a

Figure 3 shows higher positivity for the VI condition than the VV and IV conditions. ANOVA showed an effect of the type of trial sequence ($F_{2,26}$=4.81, P=0.016) and an interaction between the type of trial sequence and the electrodes ($F_{2.26}$=4,21, P=0.025). *Post-hoc* analysis showed effects at all the electrodes for the comparisons IV vs. VI (Table III). Comparisons between VV and VI yielded statistically significant differences at the electrodes Fcz and Cz. There were no statistically significant differences between VV and IV at any of the electrodes considered.

P3b

ANOVA showed that the interaction "type of trial sequence × hemisphere × electrodes" was statistically significant ($F_{10,130}$=2.75, P=0.004). *Post-hoc* comparisons,

Table II

Percentage of errors in the stimulus sequence of Experiment 1

	Condition	Percentage of no response	SD	Percentage/S1	SD	Percentage/S2	SD
Error	Invalid	0.33	0.84	0.17	0.62	1.99	2.56
	Valid	0.62	1.15	0.44	0.48	0.29	0.56

Omissions (percentage of no response), false alarms to the S1 of the second trial of the sequence (i.e. S1 before target, indicated as percentage/S1), and false alarms to the target stimuli (percentage/S2) are shown.

Table IV

Post-hoc results for the component P3b in the Experiment 1

	P3	P4	P7	P8	O1	O2	PO3	PO4	PO5	PO6	PO7	PO8
VV vs. VI	<0.001	<0.001	<0.001		<0.001	0.045	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
IV vs. VI	<0.001	<0.001	<0.001		0.006				<0.001		<0.001	
VV vs. IV				<0.001				0.004		0.002		

In all cases Bonferroni correction was applied

using the very conservative Bonferroni test, showed statistically significant differences between the IV and VV conditions at the electrodes PO4, PO6 and P8 (Table IV). Figures 3 and 4 show a higher P3b in the IV condition than in VV at the posterior right side of the scalp. *Post-hoc* comparisons between VI and VV or IV were statistically significant at most of the electrodes considered.

Experiment 2

Behavioral results

The RTs in the different trial sequences appear in Table V. ANOVA showed an effect of the type of trial sequence ($F_{3,45}$=9.081, P=0.001). The fastest condition was VV, followed by IV, II and finally VI. Bonferroni analysis showed that the RTs in the condition VV were significantly faster than in IV (P<0.046) or VI (P<0.001), and that the RTs in the IV condition were significantly faster than in the VI condition (P<0.01). II did not differ from any other condition, probably because there were so few cases of II. The preceding results indicate that the attentional cueing manipulation was effective, but they also show that the IV condition is intermediate in status between the VV and VI conditions.

Table VI shows the percentages of different types of error in the valid and invalid trials. Comparisons showed a statistically significant difference between these percentages (Table VI): there were significantly more errors in the invalid trials than in the valid ones

Table V

Reaction times of the four experimental stimulus sequences analyzed in Experiment 2

Condition	Reaction Times/ Mean	SD
Valid / Valid	346.37	86.38
Invalid / Valid	363.78	83.69
Invalid / Invalid	382.64	103.46
Valid / Invalid	401.99	87.81

Table VI

Percentage of errors in the stimulus sequence of Experiment 2

	Condition	Percentage of no response	SD	Percentage/ S1	SD	Percentage/ S2	SD
Error	Invalid	7.72	6.44	0.29	0.79	1.78	3.08
	Valid	5.054	3.5	0.41	0.5	0.25	0.52

Omissions (percentage of no response), false alarms to the S1 of the second trial of the sequence (i.e. S1 before target, indicated as percentage/S1), and false alarms to the target stimuli (percentage/S2) are shown.

Table VII

Post-hoc results for the component P3a in the Experiment 2.

	Fz	Fcz	Cz
VV vs. VI	<0.001	<0.001	<0.001
IV vs. VI	<0.001	<0.001	<0.001
VV vs. IV			

In all cases Bonferroni correction was applied. The cells with no values were not statistically significant.

(P<0.04). No other comparisons (responses to S1 and omissions to S2) were statistically significant. Comparison between Tables II and VI shows that the main difference between the two experiments was a greater number of omission errors in Experiment 2 than Experiment 1, probably because it was more difficult to discriminate the targets. In any case, any erroneous trial or sequence of trials was eliminated when the ERPs and RTs were computed.

Event-Related Potentials

P3a

Figure 5 shows a greater positivity for the VI condition than for the VV and IV conditions. The waves are entirely similar to those depicted in Fig. 3 for Experiment 1. ANOVA showed an interaction between the type of trial sequence and the electrodes ($F_{4,60}$=2.71, P=0.038). *Post-hoc* analysis revealed effects at all the electrodes considered when the VI condition was compared to IV and VV (Table VII). There were no statistically significant differences between VV and IV at any of those electrodes.

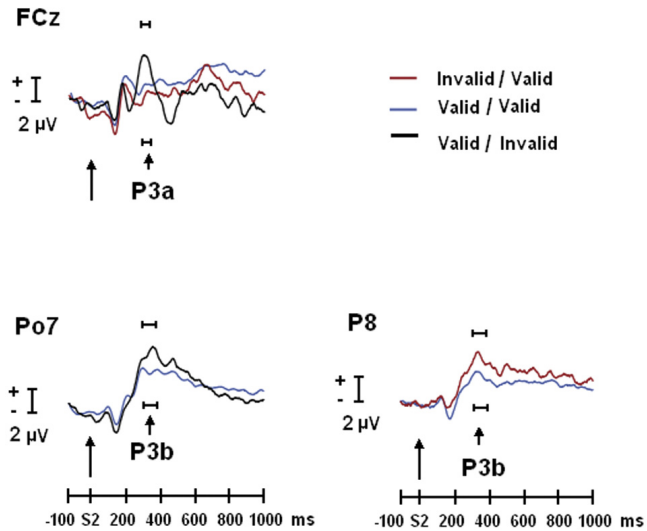

Fig. 3. ERPs for the different sequences of trials in Experiment 1. Notice that the P3a component at the FCz electrode is greater for the valid–invalid condition than the valid–valid or invalid–valid conditions. The P3b is greater in the valid–invalid condition than in the valid–valid condition at the PO7 electrode, and greater in the invalid–valid than the valid–valid condition at the P8 electrode. The horizontal bar indicates the time window of the maps shown and the statistic referred to in the text.

P3b

ANOVA showed that the interaction between the type of trial sequence and electrodes was statistically significant ($F_{4,60}$=7.51, P<0.001). *Post-hoc* comparisons revealed statistically significant differences between the IV and VV conditions at electrode P4 (Table VIII), the posterior positivity being greater in the IV than the VV condition. Figures 5 and 6 show a larger P3b in the IV than the VV condition at the posterior right side of the scalp. *Post-hoc* comparisons between VI and VV

Table VIII

Post-hoc results for the component P3b in the Experiment 2

	P3	P4	P7	P8	O1	O2
VV vs. VI	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
IV vs. VI	<0.001	<0.001	<0.001	0.046	<0.001	<0.001
VV vs. IV		0.017				

In all cases Bonferroni correction was applied

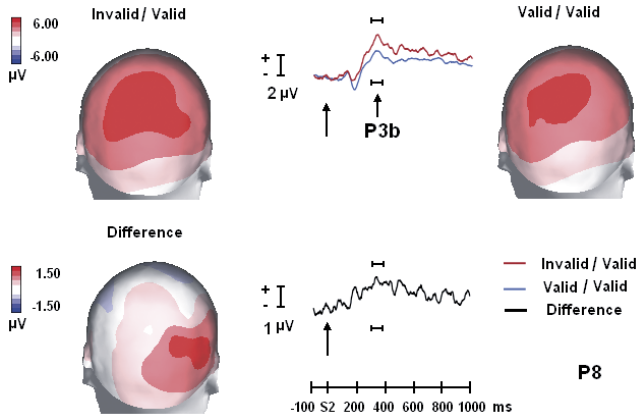

Fig. 4. ERPs (P8) and voltage maps of invalid–valid and valid–valid trials and the difference wave in Experiment 1. Notice the presence of a posteriorly-distributed P3b component under both IV and VV trial conditions. The difference wave shows that the amplitude of the P3b component is greater in the IV than the VV condition. The horizontal bar indicates the time window of the maps shown and the statistics referred to in the text.

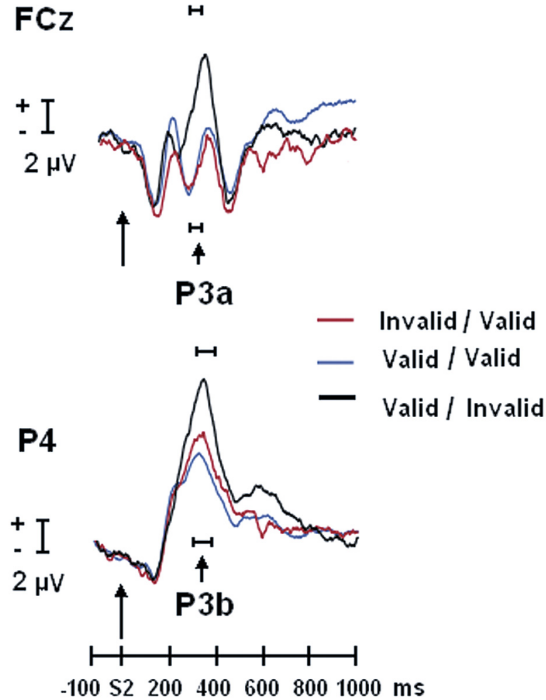

Fig. 5. ERPs for the different sequences of trials in Experiment 2. Notice that the P3a component at the FCz electrode is higher in the valid–invalid than the valid–valid and invalid–valid conditions. For the P3b at the P4 electrode, notice the gradual increase of amplitude from the valid–valid to the valid–invalid condition; the invalid–valid condition presents an intermediate value. The horizontal bar indicates the time window of the maps shown and the statistic referred to in the text.

or IV were statistically significant at all electrodes considered.

CNV during the S1–S2 period

Further analysis was conducted to test the possibility that the S1–S2 preparatory period was modified, as indicated by the CNV, as a function of the outcome of the previous trial. Figure 7 shows the CNVs for trials preceded by an invalid or a valid trial in the two experiments. Although there were some differences in the CNV as a function of the outcome of the previous trial, those differences were not consistent across experiments and were not analyzed further.

DISCUSSION

Both experiments gave the same type of results: the RTs showed the trend VV < IV < II < VI. However, the VV condition was significantly faster than the IV condition only in the second experiment. In both experiments, P3a and P3b were larger in the VI condition than in VV or IV. However, the comparison most relevant to the sequential effects in these experiments was VV vs. IV. P3a showed no statistically significant differences between these two conditions. However, comparison of P3b in IV and VV showed statistically significant differences: it was larger to valid targets preceded by an invalid trial than to valid targets preceded by a valid trial. Therefore, the general trend for P3b amplitude was VV < IV < VI. These results suggest trial-by-trial learning of the predictive value of the cue.

Behavioral results

RTs were longer for invalidly cued targets (II and VI conditions) than for validly cued ones (VV and IV conditions). This is a general result for the central cue Posner's paradigm (Posner 1980) and has been interpreted as a consequence of allocating spatial attentional resources in the pre-cued position, producing the typical cost-benefit pattern to invalid and valid targets. Both experiments showed more errors in the invalid conditions than valid ones.

Although the two experiments showed statistically significant differences in only some RTs under the four different experimental conditions, the general pattern

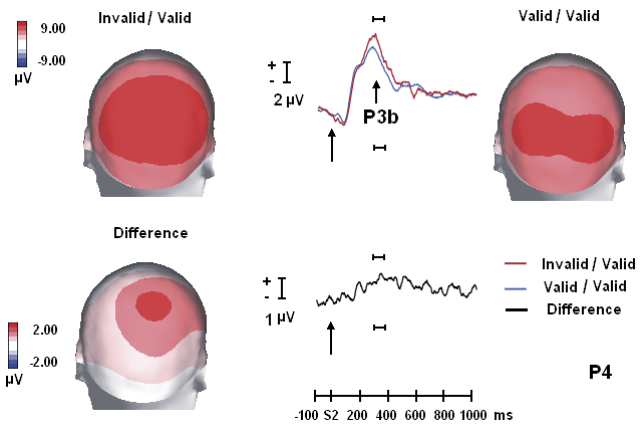

Fig. 6. ERPs (P4) and voltage maps of invalid-valid and valid-valid trials and the difference wave in Experiment 2. Notice the presence of a posterior distributed P3b component in both IV and VV trial conditions: The difference wave shows higher P3b component amplitude in the IV than the VV condition. The horizontal bar indicates the time window of the maps shown and the statistic referred to in the text.

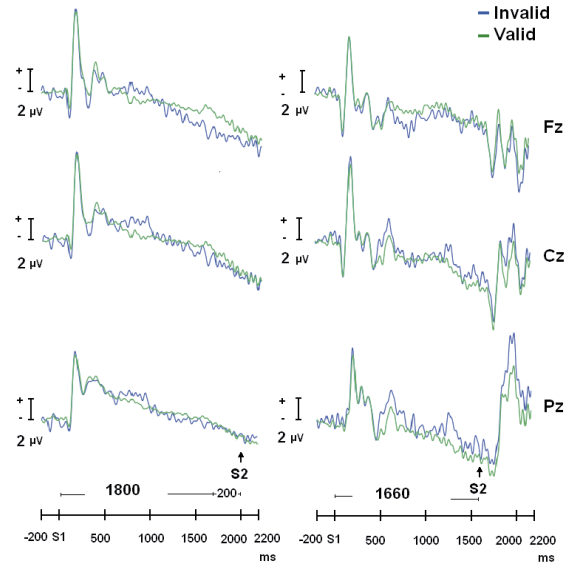

Fig. 7. The CNV induced by presenting the S1 stimuli after invalid and valid trials. The results of Experiment 1 (vertical targets) appear on the left side of the figure, and those corresponding to Experiment 2 (horizontal targets) on the right. Notice that the previous trial outcome does not have consistent effects on the CNV and ERPs induced by the S1.

was the sequence: VV < IV < II < VI. A similar inter-trial validity–invalidity result was obtained by Jongen and Smulders (2007). Only experiment 2 showed significant differences between the VV and IV conditions, the critical issue for the objectives of this paper. Behavioral differences between those two conditions were found in an experiment involving a total of 2 349 trials (Jongen and Smulders 2007). Such a high number would have been impracticable in the present experiment with EEG recording; but it suggests, as expected, that sequential effects are small and difficult to capture.

The finding in experiment 2 that RTs are longer in the IV than the VV condition recalls the classical reduction of the compatibility effect observed in conflict tasks, as in the Simon effect (Stürmer et al. 2002, Burle et al. 2005, Notebaert et al. 2006), or in congruent trials following incongruent trials in the Stroop task (Kerns et al. 2004), and in the flanker task (Gratton et al. 1992). In such experiments, RTs are longer when a compatible trial follows an incompatible one than when it follows a compatible one. This could be explained in accordance with the conflict-loop theory, presuming higher cognitive control in compatible trials following incompatible ones (Botvinick et al. 2001, 2004). However, none of the previously-cited conflict tasks presented cues, and the inter-response periods were much shorter than those found in the present experiments. Moreover, the CNV obtained in the present study reflected no consistent modulation as a function of previous trial outcome. Since the CNV reflects the state of preparation of the subjects (Gómez et al. 2004, 2007) it should be modulated if control is greater in trials preceded by invalid trials. It is still possible that cognitive control of the next trial would be greater because of the previous trial outcome, but this is not detected by the CNV.

Another possible explanation for the longer RTs in the IV than the VV condition is continuous updating of the predictive value that subjects assign to the spatial cue. Yu and Dayan (2005) proposed that the central cue Posner paradigm is a good example of how probabilistic Bayesian learning occurs. In trials in which expectations are violated, the subjects would pay less attention to top–down signals (cues) and more attention to bottom–up processes. In other words, the cue value would change on a trial-by-trial basis. This value would be lower in the IV than the VV condition, consequently producing longer RTs in the IV condition. It must be noted that a comparison between the VV and the IV conditions would reflect a local effect of the outcome of the previous trial, superimposed on the more robust cost–benefit effect because of global contingencies on the task and the implicit spatial value of the cues (Posner 1980).

Event-Related Potentials

The effects of the central cue Posner paradigm on ERPs have been extensively described, as reviewed in the introduction: typically, P1 and N1 are greater, and posterior P3 components are lower, in validly cued trials than in invalid ones (Mangun and Hillyard 1991, Eimer 1993, Perchet and Garcia-Larrea 2000, Perchet et al. 2001, Gómez et al. 2008a). More recently, an increase of the P3a-like component during processing of invalidly cued S2 targets has been described. All these results suggest that validly cued targets are attentionally facilitated (Coull 1998), but also that invalidly cued targets produce a novelty-like effect indicated by the increased P3a (Gómez et al. 2008a), accompanied by the need to update the context in which the working memory is operating, indicated by the increased P3b (Duncan-Johnson and Donchin 1977, 1982). An alternative to the "context-updating" hypothesis of P300 has been proposed by Verleger and colleagues (2005). This states that the P3b represents a mediating function between stimulus and response. The present results deal with the modulation of P3 in the IV and VI conditions compared to the VV condition. We think that the P3b modulation can be explained by "context updating" and the P3 component in which this modulation acts may be understood perfectly in terms of the operation of the stimulus-response transition (Verleger et al. 2005). In addition, the neural mechanism may be related to the inhibition needed in temporo-parietal areas to allow the memory system to act on the S1–S2 contingencies (Polich 2007).

The present results represent a more careful reanalysis of previously published data (Experiments 1 and 2, Gómez et al. 2008a, Digiacomo et al. 2008). Here, we have sub-divided the VC into the critical sub-conditions VV and IV in order to study sequential effects. Both experiments confirmed that P3a and P3b are greater in the invalid condition (VI) than the two valid conditions (VV and IV). Moreover, both experiments showed a greater P3b for IV than for VV trials. This result suggests that hypotheses about the predictive value of the cue are more revised in the IV than the VV condition, but less than in the VI condition (P3b amplitude VV < IV < VI). However, P3a showed no significant effect when the VV and the IV conditions were compared. The only condition in which the P3a response was significantly increased was VI. Taken together, these results about P3 allow us to suggest that, during IV trials, there is an implicit change in the predictive value of the cue that is not reflected in P3a because the global predictive value of the cue predominates in IV trials, while in invalid trials (VI), both explicit and implicit changes appear (P3a and P3b effects).

In the central cue Posner paradigm, a central cue can validly (V trials) or invalidly (I trials) indicate the spatial position of the upcoming target. Because of preparation, there is a faster response (benefit) when the spatial position of a target is validly predicted, and a slower response (cost) when it is invalidly predicted (Posner 1980). Part of this effect is due to the preparation of the incorrect response for invalidly-cued target stimuli (Eimer 1993, Gomez et al. 2004), but also to preactivation of the corresponding sensory cortex relative to the expected sensory stimulation (Harter et al. 1989, Gómez et al. 2004). When a cue indicates the probable position of the target, as in the central cue Posner paradigm, a CNV-like component is generated, which indicates specific activation of the sensory and motor cortex for the proposed task in the S2 and activation of the attentional fronto-parietal networks (Hopfinger et al. 2000, Gómez et al. 2004, 2007, Fan et al. 2007). Since the CNV represents preparation for the incoming stimulus (Eimer 1993, Gómez et al. 2003, 2004, 2007), and comparisons of the CNV after valid and invalid trials yielded inconsistent results between the two experiments, we suggest that the sequential effects obtained are not due to increased cognitive control in the trial following an invalid trial (Botvinick et al. 2001, 2004). Moreover, intensity effects related to the orientation of the cue should predominate in the early CNV, but the early CNV did not show consistent modulation between the experiments depending on the nature (valid or invalid) of the previous trial. Therefore, it was not evident that greater cognitive control after invalid trials explained why the RTs were longer in IV than VV trials. It must be remarked that the experiments in which increased cognitive control has been proposed to explain longer RTs after incongruent trials had shorter ISIs than the present experiments, and no cue was interposed between two target stimuli (Gratton et al. 1992, Stürmer et al. 2002, Kerns et al. 2004, Burle et al. 2005, Notebaert et al. 2006).

The alternative hypothesis would be reduced motor and sensory attention to the cued side after an invalid trial. Yu and Dayan proposed that the central cue Posner paradigm would be a good example of probabilistic Bayesian learning in which the predictive value of the cue would change as a function of the outcome of the previous trial. This hypothesis can be supported by the RT pattern obtained. The CNV during cueing paradigms presents lateralized motor and sensory aspects (Eimer 1993, Gomez et al. 2004), so if deployment of focused attention decreases after an invalid trial, a less lateralized CNV would be expected after invalid than valid trials. However, as validity and invalidity effects predominate over sequential effects, the possibly lower lateralization in IV than VV trials would be very difficult to observe in the CNV lateralization pattern. However, the pattern of increased P3b amplitude obtained (IV > VV) would reflect the post-processing of the target (the amount of attention deployed to the cued side, VV > IV). Therefore, the IV trials induce more revision of the current working memory state than VV trials (Duncan-Johnson and Donchin 1982). It is possible that the cue-target contingency learning that occurs on a trial by trial basis, as reported here, depends on awareness of expectations between the cue and the target, as has already been clearly demonstrated in the trace conditioning of the blink reflex in humans (Clark et al. 2002), where the conscious (declarative) perception of contingencies between the conditioned (S1) and unconditioned (S2) stimuli is crucial for establishing conditioning.

The results obtained can be assimilated into a more naturalistic approach as in the framework provided by Fuster (2003, 2004), where the consequences of prediction, sensation, action and their outcomes are in continuous feedback interplay favoring adaptation of the organism.

CONCLUSION

The behavioral and ERP results suggest that there is a trial by trial evaluation of the outcome of each trial, inducing a change in the *a priori* validity that subjects assign to the next spatial cue.

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