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Updating of Attentional and Premotor Allocation Resources as function of previous trial outcome

SUBJECT AREAS:

ATTENTION

COGNITIVE CONTROL

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The neural bases of the inter-trial validity/invalidity sequential effects in a visuo-auditory modified version of the Central Cue Posner's Paradigm (CCPP) are analyzed by means of Early Directing Attention Negativity (EDAN), Contingent Negative Variation (CNV) and Lateralized Readiness Potential (LRP). ERPs results indicated an increase in CNV and LRP in trials preceded by valid trials compared to trials preceded by invalid trials. The CNV and LRP pattern would be highly related to the behavioral pattern of lower RTs and higher number of anticipations in trials preceded by valid with respect to trials preceded by invalid trials. This effect was not preceded by a modulation of the EDAN as a result of the previous trial condition. The results suggest that there is a trial-by-trial dynamic modulation of the attentional system as a function of the validity assigned to the cue, in which conditional probabilities between cue and target are continuously updated.

Organisms must cope with continuous uncertainty between stimuli and outcomes relationships. The Attentional System must deal with this uncertainty and allocate processing resources to guide the organism's actions adaptively. Selective attention allows one to enhance the information received from selected sources and suppress irrelevant, competing sensory inputs²⁶, increasing signal detectability at attended locations²⁵. In a similar manner, the organism must select the more adaptive action between a plethora of simultaneously activated motor programs. The motor attention concept^{20,53} has been introduced to indicate that subjects enhance the activity of certain motor programs, in a similar manner as they bias sensory capacities by sensory attention. Motor attention would also be similar to the concept of motor preparation. In the same vein, the so-called 'premotor theory of attention'^{348,49} proposes that movements can bias sensory processing to action-compatible percepts. Therefore, sensory and motor attention would be dynamically inter-related.

There is a tendency to approach this phenomenon from a mathematical point of view, taking into account the human capacity to process the probabilities of the occurrence of different events^{4,15,46}. Based on these ideas, the present study analyzes the dynamic adjustment of the attentional system in the n trial, given the outcome of the $n - 1$ trial. The Bayesian Brain Hypothesis about the continuous updating of the prior probabilities in the attentional system^{17,60} is applied, hypothesizing that calculating the probability of occurrence of different events guides the attentional resources quickly and accurately to the relevant information and the most likely next scenario. Specifically, this study focuses on the neural mechanisms that are activated when the attention is directed by spatial cues.

The continuous estimate of conditional probabilities between spatial cues and targets^{15,22} would facilitate the allocation of attention to the most probable and relevant stimulus. In this view, the attentional system would carry out two parallel processes. On the one hand, it would guide attentional resources, directing them to relevant stimuli. On the other hand, it would continually try to predict the probability of the occurrence of stimuli, based on the subject's previous experience. Friston proposed the 'Bayesian Brain Model' to explain the continuous updating of conditional probabilities between neural representations of sensory stimuli and their external causes¹⁷. This model includes 'Prediction Error' as the driving force for adaptive changes in synaptic weights, making it possible to modulate the probabilistic relationship between causes and neural representations of causes. Therefore, the dynamic change in the synaptic weights would be due to the effects of neuromodulators, based on the prediction error signal^{15,17,22,60}.

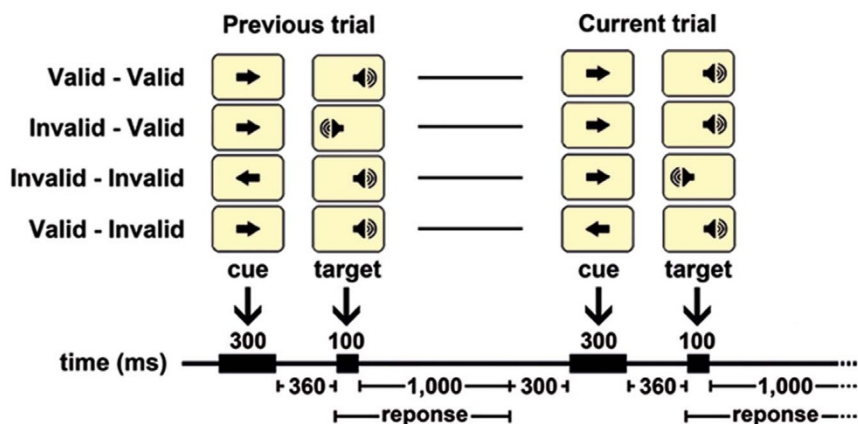


Figure 1 | Experimental paradigm. Examples of dyads used in the experiments showing the temporal organization in previous and current trials. The temporal sequence for stimulus presentation appears in the lower part of the figure. The central arrow (cue) was presented in the center of the screen, and the auditory stimulus (target) was presented monoaurally. Behavioral results in dyads were obtained from the signals in the current trial.

The CCPP is an excellent model to test the change in the predictive value of cues as a function of previous trial outcome. This is a classical task used to study the role of resource allocation in visual perception. An initial cue stimulus indicates that a subsequent target stimulus is more likely to appear at the cued location than at other locations⁴⁰. Based on the CCPP, Posner *et al.* proposed an integrative theory of attention in which three different attentional subsystems are present: alert, orientation and executive^{42–44}. The use of symbolic cues to predict the appearance of a stimulus in a certain spatial position is related to the pre-activation of the neural resources needed to perceive and respond to the predicted stimulus^{10,16,22,27,36}. These predictive neurophysiological signals would be associated with the physiological implementation of the *a priori* probabilities that a target would appear in a certain spatial position. Arjona and Gómez² have shown that the Contingent Negative Variation (CNV), induced by the central symbolic cue, modulates its amplitude as a function of the validity of previous trials. Therefore, the CCPP makes it possible to analyze the attentional effects that occur in subjects as a result of the appearance of expected and unexpected stimuli^{1,21,28}.

The first-order effect in the CCPP correspond to the differences in Reaction Times (RTs) to invalidly and validly cued targets, and would be referred to as the so-called validity/invalidity effect, which is regarded as an indicator of the benefits of being attentionally focused on the location where the stimulus appears, and/or the cost of disengaging and shifting attention from the cued to the uncued location^{40,41}. Behavioral studies have shown that the relation of validity to invalidly cued targets influences attentional allocation, with high cue validities increasing the magnitude of the validity effect^{29,47,58}. In other words, if the information provided by the cue is highly valid, RTs to valid targets decrease, while reaction times to invalid targets increase.

The second-order effect in the CCPP corresponds to the so-called inter-trial validity-invalidity effect^{1,21,28}. This effect would reflect the influence that the assessment of the validity/invalidity in one particular trial ($n - 1$) has on the next trial (n) performance. These studies have observed benefits in RTs when valid trials are preceded by valid trials (VV), compared to valid trials preceded by invalid trials (IV). Meanwhile, invalid trials preceded by invalid trials (II) reflect a reduction in RTs, compared to invalid trials preceded by valid trials (VI). Therefore, there is a clear trend in RTs between the different trial sequences ($VV < IV < II < VI$). These findings support the idea that the brain performs a continuous updating of the predictive value assigned to the cue. On a trial-by-trial basis, the brain would be dynamically modulating the attentional system's operation. The credibility assigned to the cue would change with

each trial, increasing or decreasing the strength in directing the attentional focus to the indicated place.

Orientation to the cue starts with a posterior negativity contralateral to the location indicated by the cue, the so-called Early Directing-Attention Negativity (EDAN)²⁷. During the preparation period, a long-lasting CNV appears with a fronto-central and posterior distribution. The CNV is a signal of negative polarity that appears whenever a subject is expecting the arrival of a significant stimulus in the next few hundreds of milliseconds. It has been observed as an index of different processes such as attention (through the fronto-parietal networks), motor preparation, and sensory activation^{5,10,14,22,27,52}. The CNV is related to the preparation of processes necessary for the task. In the case of CCPP, it occurs within the period between the spatial directional cue (S1) and the target stimulus (S2), reflecting the expectation generated by S1 about the appearance of S2⁵⁹. This late negative component increases in trials in which participants invested preparatory effort¹². In the present study, two periods are analyzed, an initial period called the 'early CNV', which would be related to the sensory orientation process generated by the cue, and a later period called the 'late CNV', which would reflect motor preparation for response to the incoming target^{34,51}. Recently, the later period (late CNV) has also been associated with the preparation of the sensory neural areas needed for processing the expected target^{5,16,22}.

The Lateralized Readiness Potential (LRP) reflects motor activation induced by a warning stimulus. This component is typically observed when subjects make a left-hand response for one stimulus category and a right-hand response for another stimulus category³⁰. Initially, the neural activity is equal across both hemispheres, but it rapidly begins to lateralize, with larger amplitudes found in the hemisphere contralateral to the response side and above the motor cortex¹¹. Some investigations have successfully employed this component to investigate information transmission between perception and response-related processes^{6,22,37}.

The purpose of the present study is to examine the neural implementation of the sequential effects in the CCPP, using behavioral results (RTs and Errors) and Event Related Potentials (ERPs), in a visuo-auditory modified version of the CCPP paradigm (Fig. 1). EDAN, CNV and LRP, induced by the cue, are analyzed to understand the neural implementation of the inter-trial validity/invalidity effect. In order to take into account any possible attentional hemispheric lateralization due to the cue direction (left or right), the CNV is analyzed separately as a function of the cue direction. The EDAN and LRP make it possible to assess sensory attentional orientation and motor preparation as a function of previous trial outcome,

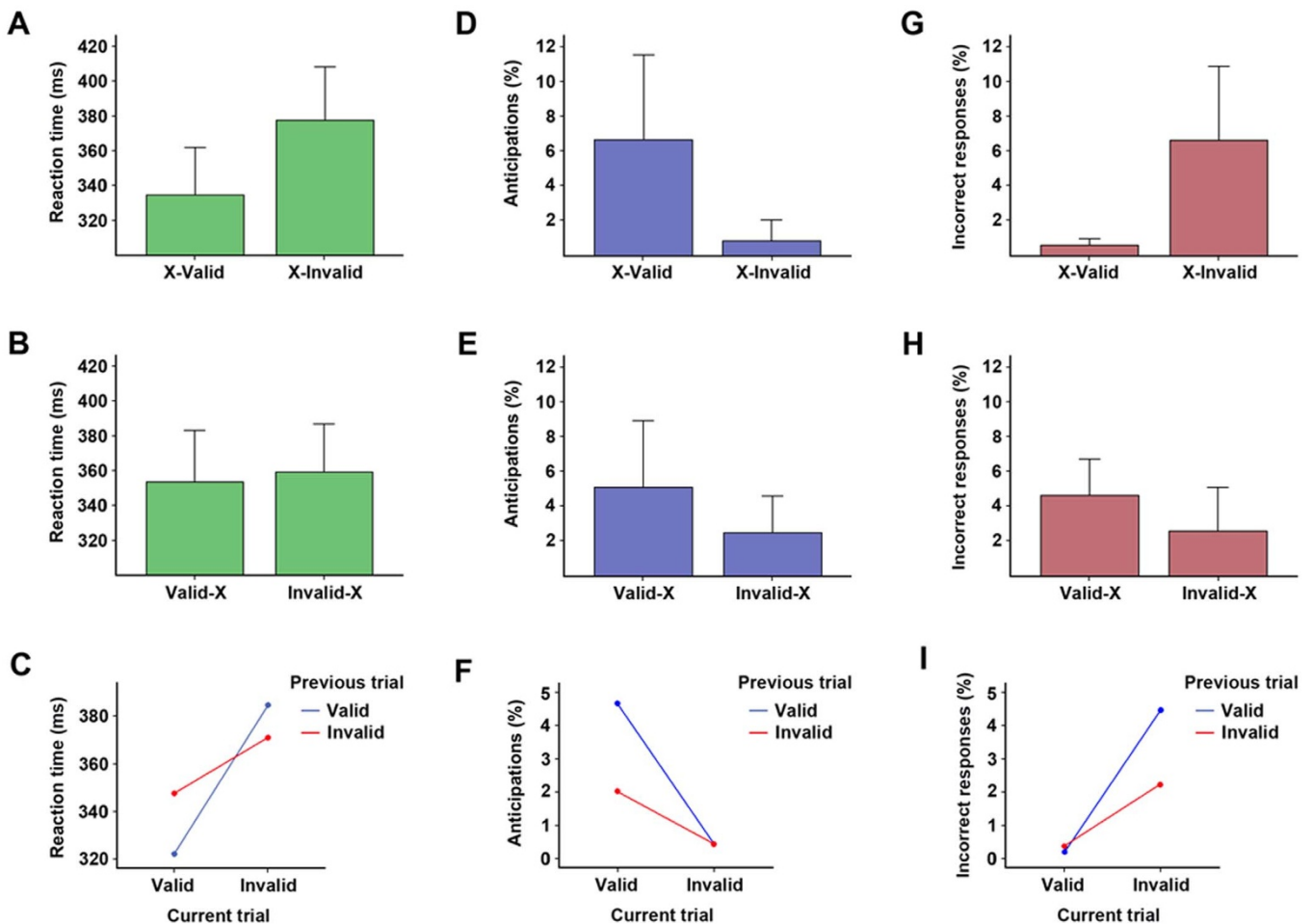


Figure 2 | Comparisons of Reaction times (RTs), Anticipations and Incorrect responses in sequences of two trials (previous and current trial). The ‘X’ means that the condition of that trial was not taken in consideration. Fig. A shows the mean of RTs in Valid and Invalid trials without taking in consideration previous trial condition. Fig. B shows the mean of RTs in trials preceded by Valid and Invalid trials. Fig. C shows the combined effects of condition (Valid/Invalid) and trial position (current/previous) on the RTs. Figs. D, E and F; and G, H and I illustrate, respectively, the percentage of anticipations and of incorrect responses in the same experimental conditions showed in Figs. A, B and C.

respectively. The objective is to relate the sequential effects in CCPP with preparatory ERPs, considering three types of experimental factors: (i) previous trial condition (valid/invalid); (ii) cue direction in the current trial (left/right); and (iii) current trial condition. The third factor only applies for behavioral responses. Therefore, the following three hypotheses to explain the RTs inter-trial validity/invalidity effect are proposed:

- (1) A higher number of anticipations in trials preceded by valid trials compared to trials preceded by invalid trials. This result would indicate an increased preparation induced by the cue as a consequence of validity of previous trial.
- (2) The CNV will be more negative in trials preceded by valid trials compared to trials preceded by invalid trials; reflecting higher attentional setting induced by S1 after confirming predictions in the previous trial. As a corollary of this hypothesis, the EDAN components induced by the cue would also be analyzed in order to find out whether invalidity produces a reduction in the visual attentional orientation.
- (3) The LRP will present greater amplitude in trials preceded by valid trials compared to trials preceded by invalid trials; reflecting a higher preparation for motor response induced by S1 after confirming predictions in the previous trial.

Note that only inter-trial validity/invalidity effect was analyzed in present report; a detailed analysis of the first-order validity/invalidity

effect on ERPs can be found in Arjona and Gómez, 2013². The authors want to state that present results are a reanalysis of previously published data^{1,2}, in which the inter-trial approach on the EDAN, the LRP and the laterality of the CNV corresponds to new insights of the explanation of the behavioral inter-trial validity/invalidity effect.

Results

All the statistical analyses were performed on the second trial of the two trial sequences (Previous trial – Current trial). The ‘X’ means that the cue direction (Left/Right) and the condition (Valid/Invalid) of that trial was not considered relevant in those particular trials.

Statistical analysis of reaction times and errors. Reaction times and errors were analyzed by two-factor repeated measures ANOVA in which valid-valid, invalid-valid, invalid-invalid and valid-invalid condition trials were taken into account. Factors were *Previous trial condition* and *Current trial condition*, each one with two valid-invalid levels.

Reaction times. With respect to the *Current trial condition*, RTs in X-Valid were significantly lower than in X-Invalid sequences ($F [1, 28] = 56.66, p < 0.001$) (Fig. 2A), as expected by the validity/invalidity effect. Furthermore, ANOVA also showed significant differences in RTs with respect to the *Previous trial*



condition ($F [1, 28] = 4.67, p < 0.039$) due to lower RTs in Valid-X than in Invalid-X sequences (Fig. 2B). Interactions between *Previous trial condition* \times *Current trial condition* were also significant ($F [1, 28] = 30.75, p < 0.001$) due to a lower RTs in Valid-Valid with respect to Invalid-Valid sequences ($p < 0.003$) and in Invalid-Invalid with respect to Valid-Invalid sequences ($p < 0.054$) (Fig. 2C). The lower RTs in Valid-X with respect to Invalid-X sequences and the interactions between the previous and current trial effect (inter-trial validity/invalidity effect) suggest an increased preparation after a valid trial than after an invalid trial.

Three additional analyses on Rts were computed to discard or confirm the possible influence on Rts of the change/repetition of the (i) cue direction (collapsing the four conditions), (ii) target location (collapsing the four conditions) and (iii) cue direction-target location combination in the VV condition. For the cue direction-target location combination only the VV sequence was considered, because in the IV, VI sequences there is always a change in subsequent trials with respect to previous trials, and in the II sequences the division in Change and Repetition would produce very few cases. The mean comparison between Rts in current trials when there was a change or a repetition with respect to previous trials only presented a trend to statistical significance in change/repetition of -target location- ($F(1,28) = 3.78, p < 0.062$) with a lower Rts for change (339.42 ms) with respect to repetition (344.76 ms).

Errors. Three main types of errors -anticipation, incorrect responses and omissions- were analyzed taken into account the previous and current trial conditions.

For anticipation errors ANOVA showed significant differences in *Current trial condition* ($F [1, 28] = 8.01, p < 0.009$), due to a higher percentage in X-Valid with respect to X-Invalid sequences (Fig. 2D); in *Previous trial condition* ($F [1, 28] = 7.41, p < 0.011$), due to a higher percentage in Valid-X with respect to Invalid-X sequences (Fig. 2E); and in *Previous trial condition* \times *Current trial condition* ($F [1, 28] = 4.87, p < 0.036$), due to a higher percentage in Valid-Valid with respect to Invalid-Valid sequences ($p < 0.018$) (Fig. 2F).

As in RTs, the effect of the *Current trial condition* in anticipation errors could be related to the validity/invalidity effect in which the anticipatory activity is directed to the target indicated by the cue. The effect of the *Previous trial condition*, with a highest percentage of anticipations in Valid-X than in Invalid-X sequences suggest an increased preparation after a valid trial than after an invalid trial, generating an increased number of endogenously driven responses. The interaction between the previous and current trial effect (*Previous trial condition* \times *Current trial condition*) corresponds to the inter-trial validity/invalidity effect, in which the probability to produce an anticipatory response is increased when previous and current trial are valid.

For incorrect response errors in the *Current trial condition* and also in relation to the validity/invalidity effect, there was a lower percentage in X-Valid with respect to X-Invalid sequences ($F [1, 28] = 8.29, p < 0.008$) (Fig. 2G). This higher percentage of incorrect responses in X-Invalid suggest that in invalid trials there is an endogenous activity related to the location indicated by the cue inducing incorrect responses. With respect to the *Previous trial condition*, there was a higher percentage of incorrect responses in Valid-X than in Invalid-X sequences ($F [1, 28] = 6.23, p < 0.019$) (Fig. 2H). The higher percentage of incorrect responses in Valid-X suggest an increased preparation after a valid trial than after an invalid trial, producing more responses to the opposite side of the target location in next invalid trials (Valid-Invalid sequences). In the interaction of the effects *Previous trial condition* \times *Current trial condition*, significant differences were found ($F [1, 28] = 42.07, p < 0.004$) due to a lower percentage in Invalid-Invalid with respect to Valid-Invalid sequences ($p < 0.008$) (Fig. 2I). 'Omissions' didn't show significant differences. The interaction between the effects of previous and

current trial corresponds to the inter-trial validity/invalidity effect, in which the probability to produce an incorrect response is increased when previous trial is valid (increased preparation to the cue indicated location) and current trial is invalid (target in the opposite side to the indicated location).

Statistical analysis of ERPs. Three post-cue time components induced by the central arrow (EDAN, CNV and LRP) were obtained and statistically analyzed. Two early and late time windows were considered for EDAN (115–155 and 210–325 ms) and CNV (420–520 and 560–660 ms). For LRP, the post-cue time window was 280–660 ms.

Early directing-attention negativity (EDAN). Figures 3A and 3B show the succession of components P1, N1 and P2 generated by the presentation of the central arrow in current trials preceded by valid and/or invalid trials. The ERPs components were generated by spatial orientation of the cue to the left and to the right. These components were more negative over the hemisphere contralateral to the direction indicated by the cue. When ERPs induced by right pointing arrows minus ERPs induced by left pointing arrows were computed, an EDAN component appeared showing an early and a late period (Figs. 3C and 3D).

In the early EDAN, ANOVA showed significant differences for *Hemisphere* ($F [1, 57] = 103.42, p < 0.001$), *Electrodes* ($F [1.68, 95.83] = 5.40, p < 0.009$) and *Hemisphere* \times *Electrodes* ($F [1.93, 110.31] = 4.45, p < 0.015$). In the late EDAN, ANOVA showed statistically differences only for *Hemisphere* ($F [1, 57] = 9.73, p < 0.003$).

Early and late EDAN did not show significant differences for the factor '*Previous trial condition*'. Instead, the significant differences for *Hemisphere* would indicate the establishing of negativity in the contralateral side to the cue direction. Therefore, results from the EDAN component suggest that there was an orientation related to the cue direction, but that the subsequent modulations of ERP components based on the validity or invalidity of the previous trial seems not to be due to an early sensory attention effect.

Contingent negative variation (CNV). In the early CNV, ANOVA showed significant differences for *Previous trial condition* ($F [1, 57] = 14.18, p < 0.001$), *Electrodes* ($F [2.51, 143.27] = 9.58, p < 0.001$) and *Direction of the central arrow in current trial* \times *Hemisphere* ($F [1, 57] = 11.74, p < 0.001$). In the late CNV significant effects were obtained for *Previous trial condition* ($F [1, 57] = 18.08, p < 0.001$), *Electrodes* ($F [3.02, 172.38] = 11.86, p < 0.001$) and *Direction of the central arrow in current trial* \times *Hemisphere* ($F [1, 57] = 7.59, p < 0.008$). These results indicated that the CNV was of higher amplitude in trials preceded by valid trials compared to trials preceded by invalid trials (Figs. 4A and 4B, left side graphics). In both, early and late periods, the topography of the CNV was fronto-central. The subtraction of 'Invalid-Left cue' and 'Invalid-Right cue' from 'Valid-Left cue' and 'Valid-Right cue' sequences, respectively, revealed a lateralization tendency to the contralateral side of the cue (Figs. 4A and 4B, right side maps), which, as already indicated, was statistically significant (*Direction of the central arrow in current trial* \times *Hemisphere*).

Lateralized readiness potential (LRP). A two-factor repeated-measures ANOVA was performed on the voltage data for three selected pairs of electrodes (F3/F4, FC3/FC4 and C3/C4). ANOVA showed significant differences for *Previous trial condition* ($F [1, 57] = 5.57, p < 0.022$) due to a higher amplitude of the LRP in trials preceded by valid trials (Valid-X) than in those preceded by invalid trials (Invalid-X) (Figs. 5A, 5B and 5C). This result suggests an increased motor preparation in trials preceded by valid trials than in those preceded by invalid trials.

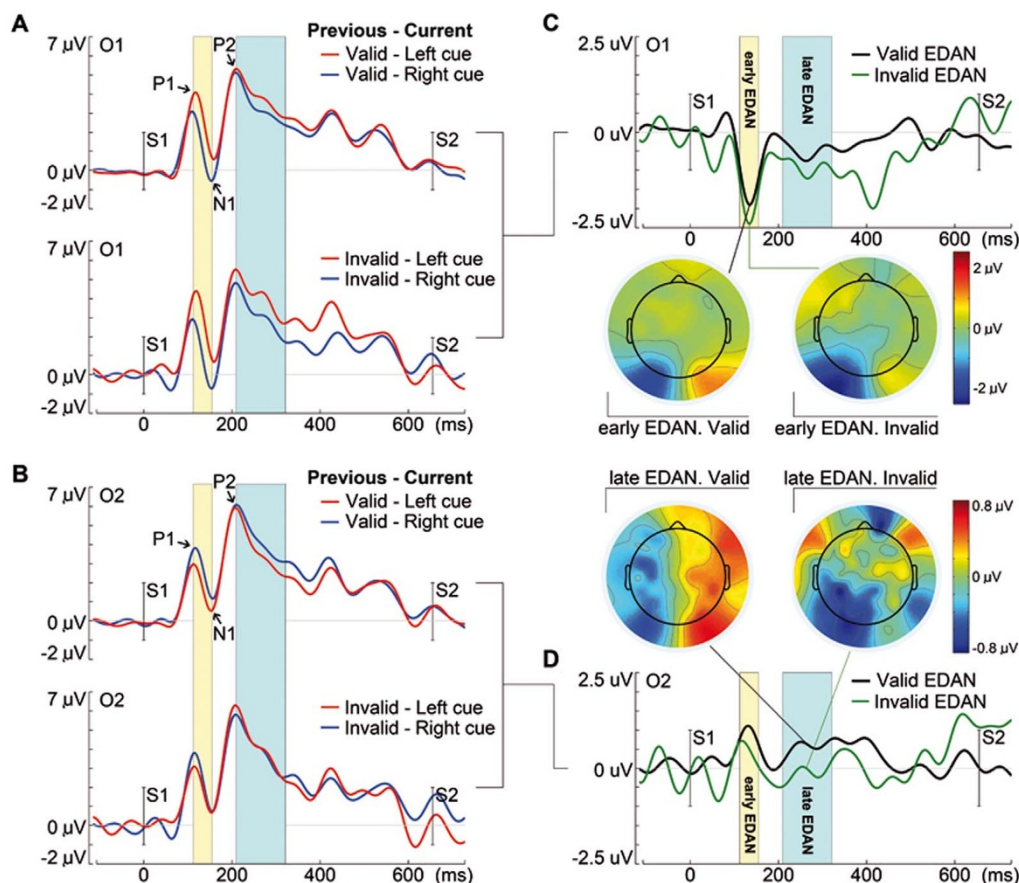


Figure 3 | Effects of the previous valid and invalid trial condition on the Early Directing Attention Negativity (EDAN). Figs. A and B show the Event related potentials induced by the visual cue in current trial after Valid trials (Valid-Left/Right cue) and after Invalid trials (Invalid-Left/Right cue). Figs. C and D show the EDAN waves and topographies generated after Valid and Invalid trials. EDAN was computed by subtracting the ERPs induced by left cues from the ERPs induced by right cues. The shaded areas correspond to the early and late EDAN latencies in which the topographies are represented and where the statistics were computed. The interval -200 to 0 ms before the cue was used as baseline.

Discussion

The present report suggests that attention to spatial cues is continuously modulated as a result of the outcome of the previous trial. CCPP permits the assessment of the deployment of attentional resources needed for responding to a target (S2) validly or invalidly indicated by a previous cue (S1), taking into account the validity or invalidity of the previous trial. The information obtained in each trial would be transmitted to the next trial, producing changes in the processing of the cue, and then influencing the target stimuli processing and the responses (RTs and Errors). The current trial's ERPs modulation by the previous trial would help to explain the inter-trial validity/invalidity effect; lower RTs in trials preceded by valid trials in comparison to trials preceded by invalid trials^{1,22,28}.

ERPs analysis shows different effects based on previous trial outcome. The CNV shows higher amplitude in trials preceded by valid trials compared to trials preceded by invalid trials, reflecting a dynamic adjustment of attentional resources as a function of previous trial outcome (Fig. 4). The LRP shows higher amplitude in trials preceded by valid trials compared to trials preceded by invalid trials, indicating greater preparation of finger motor areas, generated by the cue, after the confirmation of expectations in the previous valid trial (Fig. 5). The lack of statistically significant effects of the factor 'Previous trial condition' in the cue-induced EDAN component indicates that inter-trial validity/invalidity effect seems not to be a consequence of an early attentional bias due to the validity or invalidity of the previous trial. The higher LRP amplitude and percentage of anticipations in trials preceded by valid trials in comparison to

trials preceded by invalid trials, suggest that the RTs behavioral inter-trial validity/invalidity effect is mostly due to an increased motor attentional setting.

Many studies on the first-order validity/invalidity effect in CCPP have demonstrated that subjects respond faster to targets when they have valid information about the location where they will appear⁴⁰. More recently, inter-trial validity/invalidity effect, in which previous trial outcome influences next trial performance, has been demonstrated^{21,28}. The present experiment replicates these findings. One possible explanation for this phenomenon is that previous valid trials increase the credibility of the cue, causing the attentional resources to be more oriented toward the direction indicated by the cue in the next valid trial than in trials preceded by invalid trials, and therefore decreasing response RTs ($VV < IV$). In contrast, previous invalid trials diminish the credibility of the cue in the next valid trial, reducing attentional orientation to the target location and increasing response RTs. In more formal terms, the conditional probability of a valid 'cue-target' combination would increase after a valid trial. Furthermore, it is noted that invalid trials preceded by invalid trials have lower RTs than invalid trials preceded by valid trials ($II < VI$); in this case, subjects would pay less attention to and/or assign less credibility to the cue in invalid trials preceded by invalid trials than in invalid trials preceded by valid trials. Therefore, it would take less time to rectify their attentional resources and process the target in the unexpected location. Also, the errors response pattern is consistent with a motor preparation hypothesis; anticipatory and incorrect response errors are more frequent when previous target was validly

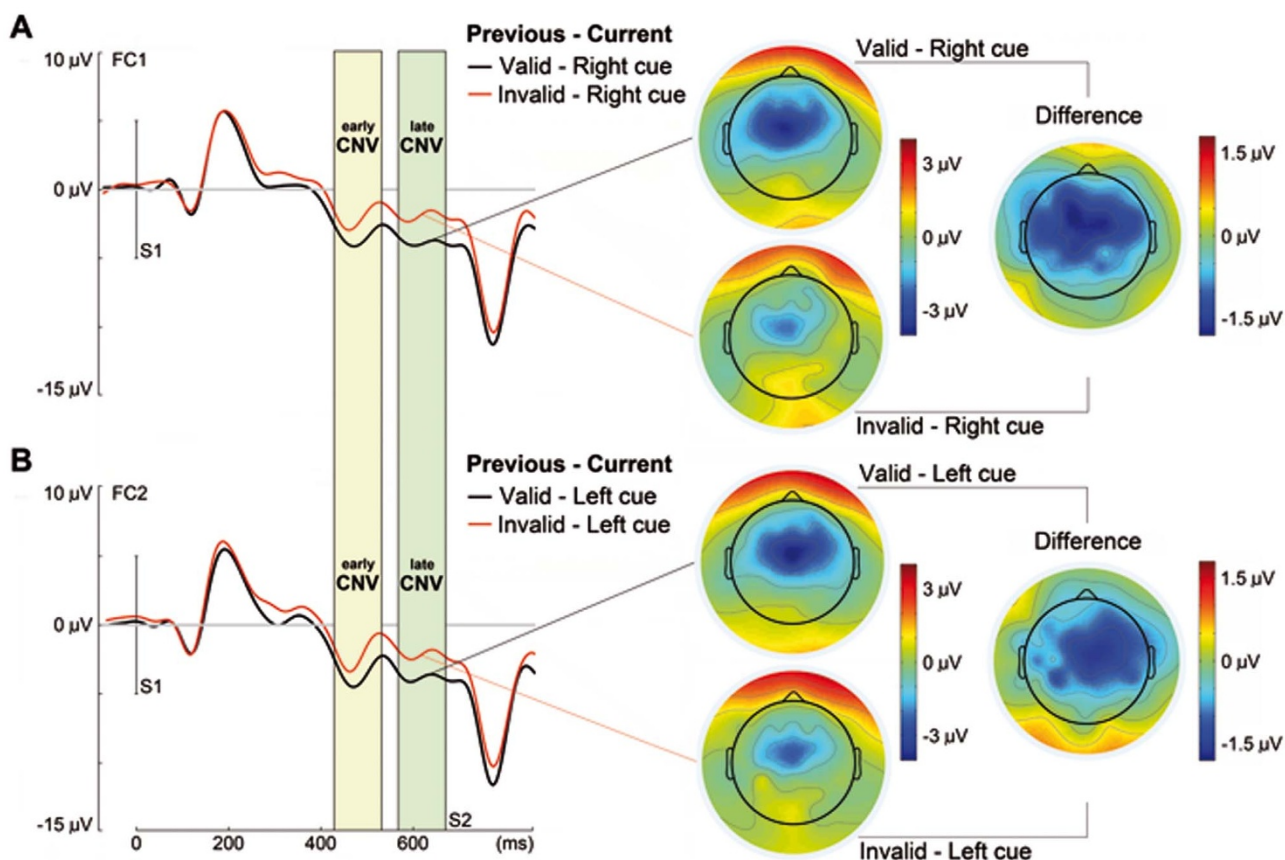


Figure 4 | Effects of the previous valid and invalid trial condition on the Contingent Negative Variation (CNV). Figs. A and B show the early and late waves and topographies of the CNV induced by the cue in current trial (Left/Right cue) after Valid and Invalid trials. The CNV displayed a higher negativity, in both hemispheres, in trials preceded by valid trials compared to trials preceded by invalid trials. Also, the topographies indicate that the CNV is contralateral to the cue direction. The shaded areas identify the latencies in which the topographies are represented and where the statistics were computed. The interval -200 to 0 ms before the cue was used as baseline.

cued, suggesting that endogenously driven responses are more frequent if the credibility of the current cue has been increased due to the validity of previous trial.

Additionally, the analyses show that there is no influence of previous trial in terms of equal or different cue direction, target location or cue direction-target location. These results suggest that the ‘binding effect’ is not related to the sequential validity/invalidity effects in the CCPP⁵⁷. Furthermore, the statistical trend of the factor change/repetition of target location would not have influence on the sequential effect given that change and repetition of target location are equally distributed in VV, VI, IV and II sequences. At this point it would be important to remind that a fundamental difference, that possibly differentiates the sequential effects in CCPP with sequential effects in Stroop, Simon and Flanker paradigms is that in CCPP there is a cue interposed between two target stimuli, which probably induces a different type of phenomena that those induced by successive presentation of target stimuli^{3,13,24,33}.

From a neurophysiological point of view, previous studies have observed frontal activation related to maintenance of attention during the cue-target delay period, and sensory-motor pre-activation, contralateral to the cue, indicating a build-up of attentional and motor resources necessary to adequately perform the task^{16,22,27}. Therefore, the possible modulation of the preparatory signals would be related to the validity/invalidity effect^{10,27,36,38,39}. These results are also consistent with the Biased Competition Model⁹, which refers to a mechanism that increases the processing of items that are currently relevant to the subject. The attentional system would pre-activate the

auditory and motor cortices contralateral to the cue, facilitating target processing. Therefore, in valid trials, attentional resources would be focused on the right place, and take less time to perceive the target and produce the response²².

The neuronal pre-activation would facilitate perceiving and responding to the target in valid trials. This pre-activation would be dominated by the current value of conditional probabilities between the cue direction and the target location ‘P (S2/S1)’. Therefore, the preparatory signals would indicate that subjects are making predictions about the next trial, based on previous trial ‘cue-target’ associations, and the CNV would be a neurophysiological index of these associations²².

The behavioral results on the inter-trial validity/invalidity effect suggest that the assessment of the conditional probabilities ‘P (S2/S1)’ is transferred to the next trial. This idea fits with the Bayesian model of updating the associative weights between cues and targets¹⁷.

The statistical results about the EDAN show that this component seems not to be affected by the condition of previous trial. The absence of this effect would reflect that inter-trial validity/invalidity effect is not a consequence of an early attentional bias due to the validity or invalidity of the previous trial. The attention to the cue is maintained irrespectively of previous trial outcome. However the transfer to the attentional system engaged in the preparation for next cue is biased by result valid/invalid of previous trial.

Present results show that CNV amplitude depends on previous trial outcome². These data, along with the RTs results, support the notion that attention is being modulated trial by trial, based on the previous history of trials. The so-called inter-trial validity/invalidity

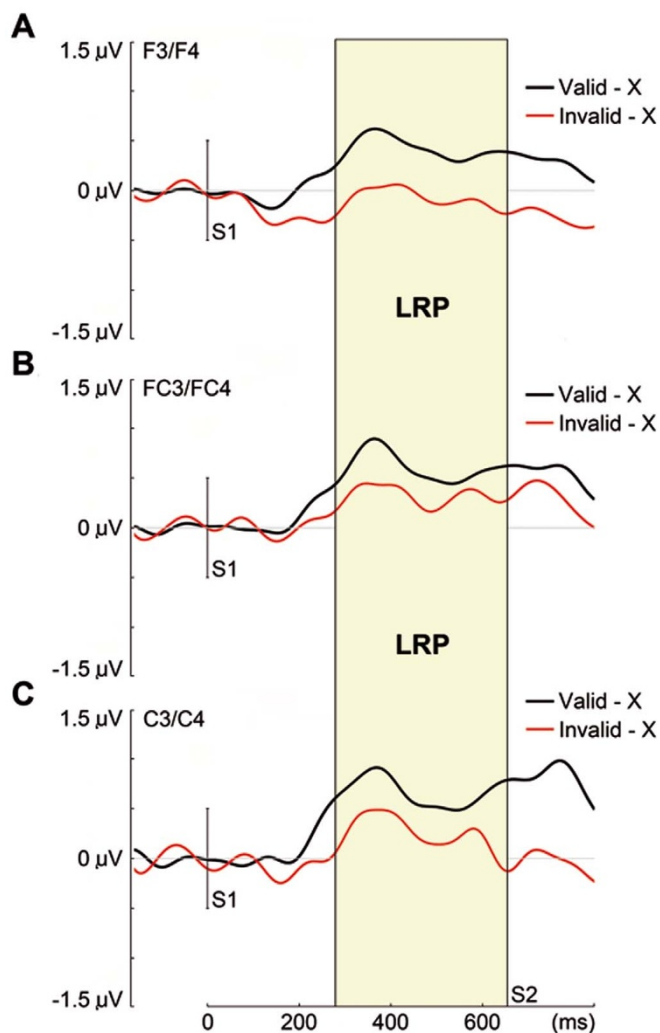


Figure 5 | Effects of the previous valid and invalid trial condition on the Lateralized Readiness Potential (LRP). Figs. A, B and C show the LRP obtained in current trial (X) after Valid and Invalid trials. The ‘X’ means that the cue direction (Left/Right) and the condition (Valid/Invalid) of current trial were not relevant. The LRP shows higher amplitude in trials preceded by valid trials compared to trials preceded by invalid trials. The shaded area corresponds to the latencies in which the statistic was computed. The interval -200 to 0 ms before the cue was used as baseline.

effect would be reflected in the negative amplitude of the CNV, based on the previous trial condition (Valid/Invalid); trials preceded by valid trials showed higher CNV amplitude compared to trials preceded by invalid trials (Figs. 4A and 4B, left side graphics). These results can be interpreted as a reduction in the expectation and preparation generated by the cue after the previous invalid trial. Instead, previous valid trials would strengthen cue credibility and would produce an increased attention for next indicated target. Topographic analysis shows the increased negativity in fronto-central areas for Valid-Left/Right cue sequences compared to Invalid-Left/Right cue sequences (Figs. 4A and 4B, right side maps), indicating that previous trial validity increases the amplitude of a common network activated in both types of sequences.

It was possible to record a posterior ERP, contralateral to the cue-indicated location, which is compatible in topography and polarity with the EDAN. Although the role of EDAN in analyzing the physical characteristics of the central arrow⁵⁶ or indicating attentional orienting²⁷ is still a subject of controversy, its possible role in attentional orientation has been highlighted⁴⁵. The present results,

separating early and late EDAN, would suggest the possibility that both factors (analysis of the physical characteristics of the stimulus and the attentional orienting) would be acting at different latencies. However, for the purposes of the present report, the EDAN seems not to be influenced by the validity or invalidity of the previous trial condition. Therefore, the cue seems to be deeply processed in all trials, but the subsequent deployment of attention (CNV) is the process modified by the inter-trial validity/invalidity effect. It can be suggested that the credibility of the cue must be fully processed to permit the updating of the attentional deployment resources.

CNV amplitude was also measured in two periods (early and late). Both intervals had the same topographic location. This same topography possibly indicates that, given the very short period between S1 and S2, the two CNV periods cannot be easily disentangled in the present experiment. Previous research agrees that the early wave is more related to the salience of the cue value than to response preparation^{31,34}. Furthermore, late CNV is assumed to be an indicator of motor and sensory preparation^{16,19,51}. CNV activity has been correlated with neuronal activity in the prefrontal cortex^{18,50}. This component corresponds to the activation of an attentional fronto-parietal network and sensory-motor areas necessary for the task response^{7,22}. The current experiment showed that a valid trial would elicit higher CNV amplitude in the subsequent trial, which is interpreted as an increased attentional deployment of resources. Therefore, the RTs pattern of $VV < IV$ and $II < VI$ would be partly a consequence of the CNV modulation.

In addition to the main ‘Previous trial condition’ effect, CNV was contralateral to the cue direction. The LRP is an electrophysiological indicator of neuron pre-activation for motor responses. The present study measured the LRP on fronto-central electrodes (F3 – F4/FC3 – FC4/C3 – C4). The exact locations for obtaining an LRP vary between the different research studies, but central electrodes have frequently been chosen^{23,37,54}. This positive wave has one first deflection that is equally large over both hemispheres, but rapidly lateralizes over the motor cortex. This component reflects preparation and initiation of the hand response³². Following this line of interpretation, the present experiment would reflect preparation for responses to the side indicated by the cue. In fact, there was increased amplitude of LRP for Valid-X sequences in comparison with Invalid-X sequences (Fig. 5). LRP results are consistent (i) with the benefits on RTs in valid trials preceded by valid trials in comparison with valid trials preceded by invalid trials ($VV < IV$); and (ii) with the benefits in RTs of invalid trials preceded by invalid trials in comparison with invalid trials preceded by valid trials ($II < VI$), given that if the previous trial is invalid, less preparation for the invalid response in the current trial occurs, and less reorientation for adequate motor response is needed. The anticipation errors pattern would also be explained by a reduced motor threshold in trials preceded by valid trials in comparison to trials preceded by invalid trials.

It should be mentioned that it is not clear whether LRP and the late phase of CNV reflect similar or functionally different processes^{51,55}. In this particular study, LRP might more strictly be described as a lateralized CNV waveform. The different latencies and electrodes used in the analysis of CNV and LRP justify the fact that CNV did not present a ‘Previous trial condition \times Direction of the central arrow in current trial \times Hemisphere’ interaction. Previous MEG studies on visuo-auditory CCPP during the S1–S2 period have shown preparatory activity contralateral to the cue in motor and auditory cortices²². However, in the present experiment, using EEG results, it is difficult to disentangle whether the lateralized aspect of CNV, indicated as LRP, is a product of sensory, motor or both processes. Regardless of the origin of the LRP, the influence of previous trial condition on CNV and LRP amplitude suggests a dynamic updating of the credibility assigned to the cue as a function of previous trial outcome, producing the behavioral pattern of the inter-trial validity/invalidity sequential effect.



In summary, the present results show different ERP effects generated by the transfer of information about the outcome of the previous trial to the next trial performance. Specifically, two different ERP components with different functions are modulated as a result of previous trial outcome: (i) the CNV would reflect the dynamic adjustment of attentional resources; and (ii) the LRP would indicate a dynamic adaptation of the pre-activation of finger motor areas, although the modulation of the auditory cortex might also be participating. Possibly, the RTs pattern for $VV < IV$ can be related to the higher motor preparation (LRP) after a valid trial than after an invalid trial. Likewise, the RTs pattern for $II < VI$ would be related to the more intense incorrect motor preparation (LRP) in VI trials with respect to II trials.

In a more general framework, the results indicate that the brain continuously update the conditional probabilities $P(S2/S1)$ as indexed by CNV and LRP modulation by the condition of previous trial. This amplitude modulation of CNV and LRP is compatible with a computational model in which Bayesian rules are implemented in brain networks¹⁷.

Methods

Participants. Thirty-four subjects participated in the experiment. Five subjects with a high number of ocular blinks, EMG and/or trend-derived contaminations in the EEG, were excluded from the analysis. Therefore, data from only twenty-nine subjects (16 female and 13 male) between 19 and 35 years of age (mean: 24 years old and SD: 2.87) were fully analyzed. 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 and response recording were computer-controlled (E-Prime 2.0). Participants were seated 60 cm from a computer screen. The subjects participated in a modified version of the CCPP, in which the central cues were arrows appearing in the center of the screen, followed by monoaural auditory stimulation (Fig. 1). The central arrow stimulus was considered the spatial orientation cue (S1), and the monoaural auditory stimulus was the imperative one (S2). The auditory stimuli were delivered to the subject's ears through headphones. Participants were instructed to fixate their eyes on a white cross in the center of the screen and pay attention to the ear indicated by the central arrow. They then had to press the right button as quickly as possible if the auditory stimulus appeared in the right ear, or press the left button if the auditory stimulus appeared in the left ear. The response device was the Cedrus model RB-530. The events sequence within a trial was as follows: the central arrow pointer was on for 300 ms, followed by an expectancy period in which a central fixation white cross appeared for 360 ms. Therefore, the total S1–S2 period was 660 ms. The auditory stimulus (1000 Hz) lasted for 100 ms and was randomly presented to the left or right ear with equal probability (0.5). The stimulus had an intensity of 89 db. The window for the response was 1000 ms, followed by a 300 ms period, producing a total inter-trial interval of 1300 ms (Fig. 1).

Each subject was presented with a total of 500 trials divided into five blocks. The central arrow (S1) had directional information: in half of the trials it pointed to the right, and in the other half to the left. In 80% of the trials the central arrow gave correct information about the target location (V: valid trials), and in 20% of the trials the central arrow pointed to the ear opposite to where the auditory stimulus would appear (I: invalid trials). The cued location (left or right ear) and the trial validity or invalidity, were randomly selected. Therefore, the experiment presented four types of trials: left valid (200 trials), right valid (200 trials), left invalid (50 trials) and right invalid (50 trials). Subjects had to respond to the monoaural auditory stimulus with the index finger of the compatible hand. They were informed that the visual cue had informative value, indicating with high probability the location of the auditory stimulus. RTs and percentages of incorrect responses (responses on the side opposite to the stimulated ear), anticipations (responses faster than 180 ms after the onset of auditory target), and omissions (no responses) were computed. The percentage of total errors was computed as the sum of all types of errors. There were ten training trials.

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). Eye movements (EOG) were recorded from two electrodes at the outer canthus of each eye for horizontal movements, and from one electrode under the left eye for vertical movements, referenced to one electrode above the left eye. Impedance was maintained below 5 KOHms. Data were recorded in DC using a common average as reference, and they were not filtered. Ground electrode was localized in the line between Fpz and Fz. The amplification gain was 20000 (ASA-lab EEG/ERP system, ANT, Holland). The data were acquired at a sampling rate of 256 Hz, using a commercial AD acquisition and analysis board (Eemage EEG, ANT, Holland).

EEG recordings were analyzed with the EEGLab v10.0.0.0b⁸ and Matlab R2010a (MathWorks Inc., MA, USA) software packages. To eliminate AC power line interference and blink artifacts in the EEG, an Independent Components Analysis³⁵ was performed. Criteria for determining these artifactual components were their scalp map distribution, time course and spectral power. The eye blink artifact component showed a frontal location, coincided with blinking in the recording of eye movements, and showed low frequency in the power spectrum. These components were discarded, and the EEG signal was reconstructed. The segmented epochs had a duration of 2200 ms. Five out of the thirty-four subjects recorded were excluded from the analysis due to a high number of ocular blinks, EMG, and trend-derived contaminations in the EEG.

Artifact corrected recordings were averaged off-line using a rejection protocol based on voltage amplitude. All the epochs for which the EEG exceeded ± 90 microvolts in any channel were automatically discarded for ERPs analysis. Moreover, for sequential analysis, the first trial in each block (the experiment had five blocks) had to be rejected because there was no preceding trial. The baseline was the 200–0 ms interval before the cue stimuli. The algebraically-linked mastoids were computed off-line and used as a reference for analytical purposes. ERPs were obtained for each subject by averaging the EEG, using the switching-on of the target as a trigger.

Statistical analysis of RTs, errors and ERPs. Statistical analyses of RTs, Errors and ERPs were performed using repeated-measures ANOVAs. The P values were calculated using the Greenhouse-Geisser correction. The very conservative Bonferroni correction for p -values was used to correct statistical significance values for multiple comparisons. The mean voltage in selected time windows was analyzed independently for the different components. Also, the electrode pairs were selected symmetrically in both hemispheres based on previous topography results of every component. All analyses were performed on data extracted from the second trial of sequences of two trials: Previous trial – Current trial.

RTs and Errors ('anticipations', 'incorrect responses' and 'omissions') were analyzed taking into account the condition in previous and current trial. Therefore, four sequences were analyzed by means of a repeated measures two factor ANOVA: valid-valid (VV), invalid-valid (IV), invalid-invalid (II) and valid-invalid (VI). The factors were *Previous trial condition* (2 levels: valid – invalid) and *Current trial condition* (2 levels: valid – invalid).

The mean voltage in the EDAN post-cue time window (Early: 115/155 ms and Late: 210/325 ms) was computed taking into account the condition in previous trial. For computing this component, the ERPs when the arrow pointed to the left was subtracted from the ERPs when the arrow pointed to the right. This arrangement produced negativity in left electrodes and positivity in right electrodes. Trials preceded by valid trials and trials preceded by invalid trials were averaged separately. Electrodes were chosen symmetrically in both hemispheres and compared. These electrode pairs were selected based on previous EDAN topography results (the same criterion was used for the selection of electrodes in the other analyzed components). Therefore, ANOVA was computed with three factors: *Previous trial condition* (2 levels: valid – invalid), *Hemisphere* (2 levels: left – right) and *Electrodes* (PO3/PO4 – PO5/PO6 – O1/O2).

The mean voltage in the CNV post-cue time window (Early: 420/520 ms and Late: 560/660 ms) was computed taking into account the condition in previous trial and the direction of the central arrow in current trial. Electrodes were chosen symmetrically in both hemispheres and compared. Therefore, ANOVA was computed with four factors: *Previous trial condition* (2 levels: valid – invalid), *Direction of the central arrow in current trial* (2 levels: left – right), *Hemisphere* (2 levels: left – right) and *Electrodes* (F1/F2 – F3/F4 – FC1/FC2 – FC3/FC4 – C1/C2 – C3/C4).

The mean voltage in the LRP post-cue time window (280/660 ms) was computed taking into account the condition in previous trial. Three pairs of fronto-central electrodes were chosen and compared. Therefore, ANOVA was performed with two factors: *Previous trial condition* (2 levels: valid – invalid) and *Electrodes* (F3/F4 – FC3/FC4 – C3/C4). The LRP for each type of trial was computed as the mean of the voltage difference between hemispheres when the central arrow pointed to the left and to the right. For instance, to compute the LRP in the Valid-X sequences in C3–C4 electrodes, the following formula was applied to trials preceded by valid trials:

$$((C3 - C4) \text{ Left arrow} - (C4 - C3) \text{ Right arrow})/2$$

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Author contributions

A.A. performed the experiment, analyzed the data, designed the figures and wrote the manuscript. G.C. designed the experiment, analyzed the data and wrote the manuscript. E.M. analyzed the data and wrote the manuscript. All authors reviewed and discuss the results and the final manuscript.

Additional information

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