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Neural correlates of inference-driven attention in perceptual and symbolic tasks: An Event-related Potential study

Antonino Vallesi[$°], Daniela Mapelli[$], Paolo Cherubini[§]

[$]Dipartimento di Psicologia Generale, Universitá degli studi di Padova, Italy

° Now at Rotman Research Institute at Baycrest, Toronto, Canada

[§]Dipartimento di Psicologia, Università di Milano-Bicocca, Milano, Italy

Corresponding author is PC:

Department of Psychology, University of Milano-Bicocca,

1, Piazza dell'Ateneo Nuovo, 20126 Milano (Italy)

Tel: +39 02 6448 3811

Facsimile: +39 02 6448 3706

E-mail: paolo.cherubini@unimib.it

Abstract

The inferential system anticipates the external environment by building up internal representations of its regularities. To that purpose, two sources of information are especially important and attract attentional resources: expected and unexpected events, which are useful for checking the accuracy of internal representations. In the present study, we investigated the behavioural properties and the neural mechanisms underlying the strategic allocation of attention triggered by those events. To that end, Event-related Potentials (ERPs) were recorded during the performance of two tasks requiring detection of predictable and unpredictable response events embedded in a visuo-spatial or numeric sequence. The behavioural results in the two tasks mirror each other, suggesting the recruitment of similar attentional allocation processes between the two domains. The ERPs showed partially similar effects. In both tasks, a P3a-like component signalled the capture of attention by events clashing with previous expectations, whilst a P3b-like component marked the focussing of attention on predicted events, and its redistribution among all possible response events occurring after the detection of an unexpected event.

Keywords: Attention, Inferential processes, Expectations, Surprise, Event-related Potentials.

The cognitive system as an adaptive anticipatory system

Following John Holland's (1995) definition, internal models are representations of the environment that complex adaptive systems, such as living beings, use in order to anticipate future states. Internal models can be tacit and strictly reactive, when they prescribe a current action under the *implicit* prediction, built-in by evolution, of an advantageous future state (e.g., a bacterium swimming up a glucose gradient). Or, they can be overt anticipatory systems, allowing "lookaheads", that is the explicit, internal explorations of alternatives. In this view, human and higher mammals' cognitive systems are, essentially, a sophisticated way for building overt internal models. Evolution endowed some animals with the ability to build models that involve the explicit representation of some environmental features beyond the scope of sensorial experience. The processes mediating lookaheads are the inferential processes, encompassing both the associative, mostly automatic ones, and the rule-based, mostly voluntary ones, commonly called "reasoning" (Holyoak & Spellman, 1993; Sloman, 1996). Internal models serve their adaptive function only as long as they preserve a certain degree of isomorphism to the environment (Newell, 1990). Inferential processes try to preserve the isomorphism by means of a feedback knowledge-revision cycle: environmental data and previous inductive knowledge gathered from past experience allow for predictions that can be later confirmed or disconfirmed via environmental input. When confirmed, previous inductive knowledge is strengthened. Conversely, if anticipations go unfulfilled, the previous knowledge that endorsed them is – or should be – weakened and/or revised (e.g., Anderson & Lebiere, 1998; Rosenbloom, Laird, Newell, & McCarl, 1991; Holland, Holyoak, Nisbett, Thagard, 1986; Neisser, 1976). Accordingly, fulfilled and unfulfilled expectations are of paramount importance for knowledge revision and, consequently, adaptation.

Expectation-related events as critical triggers for attentional deployment

Being so important for adaptation, events which confirm or falsify an expectation should have evolved into critical triggers for the deployment of attention (Horstmann & Becker, in press; Horstmann & Ansorge, 2006; Horstmann, 2006 a and b, 2005, 2002; Cherubini, Burigo, & Bricolo, 2006), that is the cognitive resource that allows enhanced information processing. Many previous studies showed that attention is biased towards unexpected and expected events (for the former, see the studies about *abrupt onsets*, e.g., Hillstrom & Yantis, 1994; Rauschenberger &Yantis, 2001; or the studies about the capture of attention by unexpected, surprising singletons, e.g., Horstmann & Becker, in press; Horstmann & Ansorge, 2006; Horstmann, 2006 a and b, 2005, 2002; for the processing advantage for expected events, e.g., Biederman, Mezzanotte, & Rabinowitz, 1982; Jacoby & Dallas, 1981). That is, expected and unexpected events are rapidly detected and efficiently processed. However – if seen as signals concerning the adequacy of the internal representation of the environment – they have different meaning. Expected events confirm that the cognitive system is adequately anticipating the environment, knowledge needs not to be revised, and anticipations can adequately drive behaviour. Conversely, unexpected events signal that the isomorphism between the internal representations and the environment is not perfect, triggering knowledge revision: the scope of attention should be widened in order to encompass all possible relevant events, to increase the chances of appropriately reacting to other unexpected occurrences. For example, a soldier expecting that an enemy is in some specific location will focus her attention on that location: but, if she later discovers that the enemy is not where she believed (unexpected event), she will be better off by redistributing attention, striving to detect any possible relevant clue that can suggest the actual position of the enemy.

Even though the previous example deals with spatial attention, this triggering mechanism could be quite general. Even in science, the unexpected empirical falsification of a theoretical prediction leads to widening the scope of attention to detect what went wrong, either in the theory, or in the drawing of the prediction, or in the gathering of the empirical data. By using sequences of either visuo-spatial or symbolic stimuli embedded in a continuous flow of events, Cherubini et al. (2006) found behavioural evidence corroborating the hypothesis that the triggering of attention by expectations works in a functionally identical way independently of the specific stimulus domain. Disregarding whether expectations are about the likely continuation of a visual trajectory, or the likely continuation of an arithmetic series, attention is focused on expected events; if those expectations are later disconfirmed by unexpected occurrences, attention is rapidly redistributed in order to encompass all relevant events in the local environment (the authors termed this redistribution of attention triggered by a surprising stimuli "*surprise effect*"). The allocation of attention is at a loss – as shown by critically impaired performance in reacting to all critical events – in "random" environments, that is those environments where, for lack of regularities, inferential processes cannot build any plausible expectation at all.

Neurophysiological bases of inference-driven attentional deployment

The functional identity of some attentional processes in perceptual and symbolic tasks does not imply that the underlying neural mechanisms are the same (Cherubini, Mazzocco, & Minelli, 2007; Cherubini *et al.*, 2006): *convergence* is common in nature, that is a functionally identical, adaptively good solution can be attained in very different ways by different systems adapting to structurally similar features of their environments (e.g., Holland, 1995; see also the principles of *rational analysis* by Anderson, 1990, where the structure of the environment determines the shape of the cognitive processes that deal with it). However, it could also be the case that the functional identity of the inferential triggering of attention in perceptual and symbolic tasks is at least partly grounded on the activity of a common neural network underlying domain-independent strategic properties of attentional deployment. The first aim of this study is to find further support for the inference-driven pattern of attention allocation (for details of the model, and analytic comparisons of its predictions with the preditions of 4 alternative models of spatial attention, please refer to Cherubini et al. 2006), by focusing on a known electrophysiological marker of attention allocation and level of expectancies – namely, the P3b type of the P300 complex (e.g., Polich, 2004). The second purpose is to investigate whether functional similarities between perceptual and symbolic tasks at the behavioural level are mirrored by similar temporal dynamics of the processes involved as revealed by their electrophysiological correlates. To this end, we recorded event-related potentials (ERPs) elicited by perceptual (Experiment 1) and symbolic (Experiment 2) tasks.

Experiment 1: perceptual task

In this experiment we used a slightly modified version of the “clock task” employed in the third experiment by Cherubini et al. (2006), while recording ERPs (Figure 1).

--- Insert Figure 1 about here ---

The participants tracked a simulated clock hand moving inside a circular frame (the clock face), and had to respond to two events: when the hand reached a specified position (e.g., 12 o’clock), or when the hand appeared twice consecutively in the same position (e.g., a hand appearing at 2 o’clock twice consecutively). The hand could behave in three different ways: a) it could follow a regular trajectory that progressively approached the position of the target hour (regular series); b) it could begin moving regularly toward the target, but – just before reaching it – it unpredictably jumped to some other position (interrupted series); finally, c) it could continuously jump randomly to different positions (random series). The previous study

(Cherubini et al., 2006) showed that regular series allow building an expectation concerning when the hand will reach the target hour: if it actually gets there, processing of the event is enhanced, whereas if unexpectedly the repeated-hour event occurs before the target hour is reached, responses to it are very slow. In the interrupted series – which are identical to regular series up to the position next to the target-hour position – participants build expectations concerning the occurrence of the target event that are abruptly disconfirmed by the jump of the hand to an unpredictable position. After detection of the discrepant event, participants redistribute attention in order to encompass both possible response events, thus responding slower to ensuing target-hour events and faster to ensuing repeated-hour events, with respect to the regular series trials. In the random series condition, no expectations concerning response events are either built up or broken, and participants respond slowly to both target events and repeated-hour events. The corresponding predictions for response times (RTs) in the present experiment are:

a) Regular series: target-hour responses < repeated-hour responses;
b) Interrupted series:
    1. target-hour > target-hour in regular series
    2. repeated-hour < repeated-hour in regular series
c) Random series:
    1. target-hour > target-hour in interrupted and regular series
    2. repeated-hour > repeated-hour in interrupted series

Previous ERP literature allows some specific electrophysiological predictions to be made. It is believed that two distinct components may occur within the time-window of the P300, a positive-going waveform peaking at about 300 ms after stimulus presentation (Polich, 2004; 2007). One of them, the P3b or “target P300”, is a centro-parietal component elicited by target stimuli in a sequence, that the participant actively expects and is instructed to attend (e.g., Rosenfeld, Biroschak, Kleschen, & Smith, 2005). This component is modulated by the amount of attentional resources dedicated to a stimulus, and by the level of expectancy (e.g., Sommer, Matt, & Leuthold, 1990). The more a stimulus is expected, the higher is the P3b amplitude elicited by that stimulus (Rosenfeld *et al*., 2005; see also Näätänen, 1990). Accordingly, the imperative stimuli, namely the stimuli requiring a response (from now on, S_n), should elicit a P3b-like wave with a centro-parietal component proportional to the amount of allocated attention in this experiment. Consistent with this view, we expect that the amplitude of this component should comply with the following predictions:

a) Regular series: target-hour events > repeated-hour events;

b) Interrupted series:

  1. target-hour < target-hour in regular series
  2. repeated-hour > repeated-hour in regular series

c) Random series:

  1. target-hour events < target-hour events in interrupted and regular series;
  2. Repeated-hour < repeated-hour in interrupted series.

We also recorded potentials associated with the stimulus that directly preceded the imperative stimulus (from now on, S_{n-1}). In the random series, S_{n-1} is indistinguishable from previous stimuli. In the regular series it is the stimulus immediately next to the target position, but otherwise it is not different from any other previous stimulus in regular and interrupted series. In the interrupted series it is different from previous stimuli, because it is the deviant stimulus that abruptly breaks off the trajectory, disconfirming previous expectations concerning the target event, and thus causing defocusing from the target event and redistribution of attention to both possible response events. Consequently, the most general prediction is that ERPs elicited by the S_{n-1} in the interrupted series should be different from ERPs evoked by that stimulus in other series. Some more specific predictions can be derived from literature. The other P300 component – called the P3a – refers to a typical fronto-central component evoked by rare, new and unexpected events. The P3a has primarily been associated with the orienting response (Donchin, 1981; Friedman, Cycowicz, & Gaeta, 2001; Knight & Nakada, 1998; Polich and Criado, 2006), a rapid physiological response to unexpected stimuli which works as a detector of novelty (Sokolov, 1963; see also Luria, 1973; Pavlov, 1927). The P3a, also called novel or distractor P3, has been associated to attentional capture by deviant stimuli (Sawaki and Katayama, 2008). Donchin and colleagues (see Donchin, 1981; Donchin & Coles, 1988; for reviews), although they did not make an explicit distinction between P3a and P3b, report data consistent with the view that the events likely to modulate the P300 are those that require a revision of an internal model (context-updating process), that is when "the model is revised by building novel representations through the incorporation of incoming data into schema based on long-term memory data" (Donchin, 1981, page 508). Moreover, Näätänen (1990) interprets the anterior P3a as an index of attentional orienting produced by the mismatch between a presented stimulus and the neuronal trace formed from the previous stimuli (i.e., expectancy disconfirmation).

Consistently with this view, detection of S_{n-1} in the interrupted series should be associated with a P3a component with higher amplitude than in the regular and random series. Furthermore, our model assumes that detection of the deviant stimulus in the trial n-1 in the interrupted series elicits redistribution of attention to both possible response events. Accordingly, the P3a component is expected to be followed, in the trial n, by a different modulation of the P300 from those occurring in regular and random series (where redistribution of attention does not occur), reflecting the fact that attention is re-distributed between different possible response events in this condition.

An earlier and usually smaller negative deflection, called N2, is commonly observed before the P300 complex, which in the visual modality peaks around 180 ms (e.g., Squires, Wickens, Squires, & Donchin, 1976). At least two dissociable negative sub-components have been described in the literature in this time range: an anterior N2, which is more pronounced for non-targets, and a posterior one, that is instead sensitive to target detection (see Folstein & Van Petten, 2008, and Pritchard, Shappell, & Brandt, 1991, for reviews). Accordingly, we also analysed this component, that has previously shown modulations from visual attention.

Method

Participants

Twelve adults (9 females) participated in the experiment. Mean age was 25 years (range: 20-31), and all were right-handed. Participants received either 10 euros or university credits as rewards for their participation. No participant reported a history of neurological or psychiatric disorders.

Apparatus and materials

Each participant was tested individually in a silent and dimly lit room. The experiment was implemented by using the E-prime^{TM} software, and was run on a personal computer with a 17” monitor. Subjects sat at a distance of 60 cm from the monitor, using a chin-rest. During the task, the EEG was continuously recorded through Micromed System Plus (Micromed, Mogliano Veneto, Italy) from a pre-cabled elastic cap with 19 Ag/AgCl electrodes positioned in standard locations according to the international 10/20 system (American Electroencephalographic Society, 1994). The ground was Fpz; the reference was provided by two earlobe electrodes shorted together. Two electrodes were placed on the outer cantus and under the left eye, respectively, to record horizontal and vertical electro-oculogram (hEOG and vEOG, respectively). Impedance of each electrode was kept lower than 5 kΩ. Each channel had its own analogical-to-digital converter; signals were digitally filtered in the 0.03–

30 Hz range. The EEG signals were digitalized online; the sampling frequency was 512 Hz and the conversion resolution was 0.19 μV/digit.

Procedure, task and design

A light-grey static circle outline (“clock face”; diameter, 4.8° of visual angle) with a light-grey small fixation dot in the centre was present on the middle of the display throughout the task; the circle had one small placeholder corresponding to 6 or 12 o’clock (balanced across blocks). Participants were required to maintain fixation on the dot at the centre of the clock face and to respond to two response events by pressing one of two keys (“D” and “L” keys on an international keyboard, appropriately labeled): “target-hour” responses, required when the clock hand indicated a specific hour (12 or 6 o’clock, balanced across blocks), and “repeated-hour” responses, required when the hand indicated the same hour twice consecutively. A short segment intermittently flashed within the circle, orthogonal to its circumference (“clock hand”; length, 0.8°; width, 0.1°; duration, 700 ms; ISI, 300 ms), in the positions corresponding to the 12 hours. Response deadline was 1 s from the onset of the clock hand, that is responses had to be given before the ensuing clock hand appeared. Correctness and latencies of the responses were collected. There were two experimental blocks, one per each target position (6 vs 12), balanced within participants. Each block comprised 216 trials and lasted about 30 minutes. Of the total 432 trials, 192 required a target-hour response, 192 a repeated-hour response, and 48 (approximately 11%) were catch trials which required no response whatsoever. Each trial consisted of the clock hand appearing in eight positions. In the regular series condition, the eight positions were arranged so as to form a regular trajectory (clockwise or counterclockwise) up to the position next to the target hour. After that, in non-catch trials half of the times it moved on to the target hour (regular series requiring a target hour response), and then continued on in a regular fashion (for example, a series of 8 clock hands aiming at 7, 8, 9, 10, 11, 12 [target hour response], 1, 2 [end of the series]). In the other half of the trials (that is, regular series requiring a repeated-hour response) the clock hand re-appeared in the position next to the target hour instead of moving on to the target hour; after that, it reprised its movement from the hour following the target hour (for example, a series of 8 hands pointing at 7, 8, 9, 10, 11, 11 [repeated hour response], 1, 2 [end of series]). In regular catch trials, requiring no responses, the series skipped the target hour (for example, 7, 8, 9, 10, 11, 1, 2, 3 [end of series], with the target hour at 12). In the interrupted series, the clock hand approached the target-hour as regularly as in the regular series condition but, after reaching the hour next to the target hour, it jumped to a different position, at least four hours away. After that, in non-catch trials half of the times the hand jumped back to the target hour (interrupted series requiring a target hour response), and then continued on in a regular fashion (for example, a series of 8 clock hands aiming at 7, 8, 9, 10, 11, 8 [discrepant hand], 12 [target hour response], 1 [end of the series]). In the other half of the trials (interrupted series requiring a repeated-hour response) the clock hand repeated itself in the position where it had jumped; after that, it normally reprised its regular movement either clockwise or counterclockwise (for example, a series of 8 hands pointing at 7, 8, 9, 10, 3 [discrepant hand], 3 [repeated hour response], 2, 1 [end of series]). In interrupted catch trials, requiring no responses, after the hand had jumped it reprised its regular movement (for example, 7, 8, 9, 10, 11, 8 [discrepant hand], 9, 10 [end of series]). In the random condition, the series of 8 positions was determined pseudo-randomly (taking care to avoid position repetitions before the response event) (Figure 1). Thus, besides catch trials – requiring no responses – we obtained 6 experimental conditions by crossing two orthogonal factors, type of response (target-hour vs repeated-hour) and the type of series (regular, interrupted, random).

The target-hour event and the repeated-hour event could occur equiprobably on one of the last 4 items of each series. Thus, there were from 4 to 7 previous positions of the clock hand which could be used to build up expectations (and subsequently disconfirm them, for the interrupted series) before the response event. In the regular and interrupted series the response events occurred either immediately after the clock hand had appeared next to the target hour (in regular series), or immediately after the displaced clock hand (in interrupted series). Accordingly, in the regular series target-hour events were the expected continuation of a trajectory, whereas repeated-hour events were unexpected; in the interrupted series, the expectation of the target-hour event was built, but was later disconfirmed by the displaced hand, causing redistribution of attention on both response events. There were no discrete interruptions between trials: All trials were presented one after the other as a continuous flow on the screen, so that participants could not distinctly tell when one trial ended and another began (actually, they were never told that the experiment was divided into “trials”). Participants experienced a clock hand appearing and disappearing continuously, sometimes forming regular trajectories, and some other times jumping at random. They had to remain alert for two possible events requiring different responses. For the appropriateness of this “continuous flow” technique in studying the role of the inferential processes in the deployment of attention, see Cherubini *et al.* (2006, p. 604). Because the imperative hands were in one of the last four positions of the series, when two consecutive trials required a response the distance between the two response events ranged unpredictably from 5 to 11 hands. Considering that 11% of the trials did not require responses, variability in the cyclic occurrence of response events was even higher: The only distinctive rhythm was that after a response event, no other response event was to be expected too soon (the actual minimal distance between response events was 5 hands, but no participants reported such a precise estimation of it in the debriefing session). Furthermore, no predictive statistical association between type of series and type of responses was present. The n-1 stimuli in regular series (the hands next to the target hour) and in interrupted series (the hands that interrupted the series) were recognizable statistical predictors, because they correctly signalled that a response event was forthcoming in 89% of the trials, but nothing could be anticipated about *which* response was likely to be required: either a target-hour response, or a repeated-hour response. Therefore, anticipations of target-hour responses in the regular series were based exclusively on predicting the future course of a trajectory, and did not have a statistical ground. Similarly, since the interrupted and regular series were identical in their initial pattern, in those trials a hand next to the target hour – if present – was a recognizable statistical predictor: half of the times it pertained to a regular series, thus resulting – after discounting the catch trials (11% of 50%) – in a probability of 44.5% that a response event was incoming (half of the response events [22.25%] being target events, and the other half repeated-hour events). However, in the other half of the trials it pertained to an interrupted series, thus allowing to predict that a displaced hand was likely (50%) to occur and – after that (that is, *two* hands after the hand next to the target) – there were 89% chances of an incoming response event (44.5% target hour events, and 44.5% repeated hour events; the remaining 11% were the catch trials in interrupted series). That is, what could be statistically anticipated after seeing an hand next to the target hour was only the likely occurrence of a response event within the next two hands (either at the first one [44.5%], or at the second one [44.5%]); there was no statistical clue whatsoever for anticipating *which* response event was to occur (if any). With these parameters, the hand next to the target position and the interrupting hand have nearly the same strength if they are used as cues for correctly anticipating a response (p=.407 for the former, p=.408 for the latter). Accordingly, the raw higher probability of a response event after an interrupting hand – in absence of any clue to which event is incoming – should not cause faster absolute response times in interrupted series (e.g., Castellan, 1977). In random series, there was no statistical predictor whatsoever. The hands preceding imperative hands were indistinguishable from all other hands in the series, as far as their statistical association to the occurrence of response events was concerned.

Results and Analyses

Response latencies

Latencies of the correct responses are reported in Table 1. RTs were analyzed by means of a 3x2 repeated measures ANOVA with series (regular, interrupted, random) and event (target vs repeated) as within-subject factors. Subsequent two-tailed t-tests were used in order to find the sources of significant effects. Critically, the predicted event by series interaction was significant [$F(2, 22) = 18.9$, $p < .001$]. In the regular series, RTs to target-hour events were shorter than those to the non-anticipated repeated-hour events [$t(11)=8$, $p < .001$]. In the interrupted series, RTs for the two events were not significantly different ($p = .28$). Most importantly, responses to target events were faster in the regular series than in the interrupted series [$t(11)=3.3$, $p < .01$], whilst responses to repeated events were faster in the interrupted series than in the regular series [$t(11)=2.3$, $p < .01$]. Performance deteriorated in the random series. Responses to target events were slower in the random series than in the regular series [$t(11)=6.4$, $p < .001$], and responses to repeated events were slower in the random series than in the interrupted series [$t(11)=2.8$, $p < .05$].

--- Insert Table 1 about here ---

Besides the critical interaction, there was a significant main effect of the series [$F(2, 22) = 11.1$, $p < .001$], with pairwise comparisons showing faster responses in the regular series than in random ones [$t(11)=6.3$, $p < .001$], and a reliable main effect of response event type [F(1,

11) = 73.3, $p < .001$], showing that responses to target-hour events were faster than responses to repeated-hour events.

Accuracy

Error data are shown in Table 2. Responses were classified as incorrect if participant responded by pressing the wrong key, “miss responses” if no response was given to a imperative stimulus (target or repeated), and “false alarms” if participants responded before the onset of a response event. Percentages of false alarms were computed collapsing the response event factor (given that they were produced either before the target event in non-catch trials, or in catch trials).

--- Insert Table 2 about here ---

Errors were analysed with non-parametric Wilcoxon signed rank exact tests. There were significantly more misses to repeated-hour events than to target events (Z = 2.04, $p = .04$). False alarms were more frequent in the regular series than in the random series (Z = 2.84, $p = .004$), and in the interrupted series than in the random series (Z = 2.98, $p = .003$).

Processing of EEG data

Trials with erroneous or anticipated responses (RT < 150 ms), trials with no responses, and those with artefacts (EOG variations exceeding ±50 μV, or variations of any scalp electrode exceeding ±100 μV) were excluded from further ERP analyses. EEG and EOG signals were averaged off-line in the interval starting 100 ms prior to the stimulus onset and ending 900 ms after it. Baseline correction was applied using the 100 ms pre-stimulus sample points. The critical stimuli were S_n (where a response event occurred) and S_{n-1} (immediately preceding S_n). ERPs were averaged accordingly, locked to the S_{n-1} and to the S_n in each trial. The number of artifact- and error-free trials per condition obtained from the subjects in the whole study for ERP averaging ranged from 20 to 60. Nine electrodes (F3, Fz, F4, C3, Cz, C4, P3, Pz, and P4) were selected from the measured head space for analysis of the spatial scalp topography of the ERP effects. They were classified according to their topographical coordinates: 3 laterality (left, medial, right) × 3 regions (frontal, central, parietal).

ERPs at S_n

The ERPs triggered by the S_n were modulated, especially by the anticipated target event after regular series, in the 160-200 ms and in the 350-450 ms time-windows (see Figures 2 and 3 and Table 3).

--- Insert Figures 2 and 3 about here ---

--- Insert Table 3 about here ---

The N2 was analyzed collapsing the mean amplitude in the 3 parietal sites (P3, Pz, P4), since preliminary analyses showed that this component peaked in those sites. These data were submitted to a 3x2 repeated measures ANOVA with type of series (regular, regular, random), and type of response event (target vs repeated event) as factors. There was a significant effect of series [F(2, 22) = 4.3, p < .05]. Subsequent t-tests showed that this was due to the N2 being less pronounced for interrupted series than for regular ones [t(11)=2.5, $p < .05$], and for interrupted series than for random ones as a trend [t(11)=1.9, $p = .08$]. No other effects were significant.

The mean amplitude in the 350-450 ms latency-window was analyzed by means of a 3x3x2 repeated measures ANOVA factoring region (frontal, central, parietal), series (regular,

regular, random), and response event (target vs repeated event). Preliminary analyses did not show any relevant laterality effect. Laterality was therefore collapsed across regions.

The crucial finding was the significant series by response interaction [F(2, 22) = 18.9, p < .001]. Subsequent pairwise comparisons indicated that in the regular series, mean amplitude was more positive for target events than for repeated ones [t(11)=6.2, *p* < .001]. In the interrupted series, positivity for the target event decreases (6.1 μV), whilst positivity for the repeated event increases (7.2 μV), with no difference among the two events (p = .3). This is consistent with the hypothesis that in those series attention is redeployed, and reallocated to both response events. In random series, positivity was at its lowest (again with no difference among the two events (p = .23). The significant response by series by region 3-way interaction [F(4, 44) = 5.0, p < .01, means in Table 4] indicates that the ERP amplitude progressively increases in the antero-posterior direction, particularly for the target events after regular series [parietal vs. central, t(11)=8.7, *p* < .001; central vs. frontal, t(11)=7.9, *p* < .001]. This is consistent with the hypothesis that this is a centro-parietal P3b component of the P300.

Other findings, already embedded in the above described interactions, are the main effect of series [F(2, 22) = 16.3, p < .001] and region [F(2,22) = 46, p < .001], and the region by response interaction [F(2, 22) = 8.4, p <.01].

ERPs at S_{n-1}

Visual inspection of the grand average in Figure 4 suggests that the ERPs triggered by the S_{n-1} show four subsequent modulations: an early parietal negativity (N2), a subsequent fronto-central positivity, a parietal positivity and a final negative frontal component. Accordingly, we focus the analyses of S_{n-1} on mean amplitudes of ERPs in four consecutive latency windows: 160-200, 200-350, 350-420 and 420-650 ms (Table 4).

--- Insert Figure 4 about here ---

--- Insert Table 4 about here ---

As for S_n, the N2 was analyzed by collapsing the mean amplitude in the 3 parietal sites (P3, Pz, P4). These data were submitted to a univariate ANOVA with type of series (regular, interrupted, random) as the only factor. This analysis showed a significant effect of series [F(2, 22) = 16.4, p < .001]. N2 was more pronounced for regular series than for interrupted [t(11)=4.9, *p* < .001] and random ones [t(11)=4.2, *p* < .01].

For the other three components, after preliminary analyses showing no substantial findings related to lateralization, we collapsed data over the laterality factor, and analysed the mean ERP amplitude for S_{n-1}, separately for each latency-window, by means of 3x3 repeated measures ANOVAs, factoring region (frontal, central, parietal) and series (regular, interrupted, random). In the 200-350 ms latency-window there was a reliable main effect of series [F(2, 22) = 71.5, p < .001], showing that the interruption of a previously regular series elicits the highest positive potential [interrupted vs. regular, t(11)=10.1, *p* < .001; interrupted vs. random, t(11)=7.3, *p* < .001]. The effect is more pronounced in the central region, as shown by the significant series by region interaction [F(4,44) = 3.7, p <.05]. For the interrupted series mean amplitude was more pronounced in the central than in the frontal sites [t(11)=11, *p* < .001] and in the central than in the parietal sites [t(11)=2, *p* = .05]. This can be taken as support that this is a P3a component of the P300, associated to the detection of the deviant stimulus.

In the following time-window (350-420 ms), there were main effects of region [F(2,22) = 21.8, p < .001], and series [F(2,22) = 35.6, p < .001], which were better explained by a significant region by series interaction [F(4,44) = 25.4, p <.001, see Table 4]. This interaction indicated that positivity was highest for interrupted series in the centro-parietal regions [central vs. frontal, t(11)=5.7, *p* < .001, parietal vs. frontal, t(11)=6.2, *p* < .001]. This P3b component could correspond to the reallocation of attention following the disconfirmation of previous expectations.

In the last latency-window assessed (420-650 ms), the pattern reverts to a negative fronto-central wave, mostly elicited by the interrupted series. There were main effects of region [F(2,22)=25.3, p < .001] and series [F(2,22) = 10.7, p < .01], that converged in a significant region by series interaction [F(4,44) = 7.1, p < .001, see Table 4], indicating that this wave for interrupted series had an anterior scalp distribution [frontal vs. central, t(11)=4.3, *p* < .01; central vs. parietal, t(11)=4.7, *p* < .001; frontal vs. parietal, t(11)=5.1, *p* < .001].

Discussion

Behavioural findings replicate previous results by Cherubini *et al*. (2006), showing that attention is focused on expected events (as shown by shorter RTs for target events after regular series), and after detection of an abrupt disconfirmation of an expectation it is reallocated to both possible response events. This is demonstrated by the longer RTs for target events in interrupted series than in regular series, matched by shorter RTs for repeated events in the interrupted series than in the regular series. In random environments, where no expectations can be developed, performance is impaired, as shown by responses to target events being slower than those in all other series, and by responses to repeated events being slower than those occurring in interrupted series. These behavioural patterns cannot be fully accounted for by most current theories of spatial attention (Cherubini *et al*., 2006, p. 604-605), nor can they be accounted for by motor preparation of the responses (Cherubini *et al*., 2006, Experiment 3).

The critical ERP findings at S_n fit with the predictions, showing a mostly parietal P300 with an amplitude reflecting the amount of attention allocated to the response events embedded in the different series. This is demonstrated by the reliable region by series by response 3-way interaction. This result is consistent with what is known of the parietal P3b, an ERP component with an amplitude proportional to the amount of expectation (Donchin & Coles, 1988; Sommer *et al.*, 1990; Rosenfeld *et al.*, 2005) and attention (Wickens, Kramer, Vanasse, & Donchin, 1983) associated to the stimuli. A caveat derives from the possibility that differences in the amplitude of this condition may partly derive from across condition differences in the amount of intra-trial latency jitter for this component. However, low variability is also an index of efficiency in cognitive processing (e.g., Stuss, Murphy, Binns, & Alexander, 2003). Therefore, whether these differences derive from consistently higher P300 amplitude for target S_n following a regular series than for the other conditions, or from less inter-trial variability in the P300 peak latency, this finding suggests that events that confirm a pre-existing mental representation are processed more efficiently.

A modulation in the posterior N2 was also observed, in that this earlier component was less pronounced for interrupted series than for the other two series, suggesting that detection of either response event is less efficient in interrupted series. However, the critical prediction of our model concerned the response event by series interaction: this interaction was not significant, hinting at the possibility that the N2 waveform is less involved than the P300 in the mechanism of strategic deployment of attention that we are investigating.

Ancillary ERP findings, related to the S_{n-1}, show a negative component in the N2 range, followed by a positive biphasic wave for the interrupted series. The posterior N2 was more pronounced in the regular series than in the other two series. This finding is in keeping with visual ERP literature showing that posterior negativities in the N2 time range are more pronounced for expected events (Folstein & Van Petten, 2008).

The positive wave was more pronounced for interrupted series than for the other two series. This component was initially (200-350 ms) mostly central and then (350-420 ms) it appeared in parietal regions. The finding is suggestive of a P3a component, associated to the processing of the deviant stimulus, followed by a P3b component, associated to the ensuing reallocation of attention (e.g., Friedman, Cycowicz, & Gaeta, 2001). However, a third, unexpected modulation occurred. After being positively modulated from 200 to 420 ms after the event, the waveform reverts to a negative component, reliably more pronounced for the interrupted series. Similar components, although with different scalp distributions, have been also described for deviations from expectancies using semantic material (Kutas & Hillyard, 1980, 1984; Holcomb & Neville, 1990), pictures (Barrett & Rugg, 1990), emotional faces (Balconi & Pozzoli, 2005), non-linguistic special symbols (Hoen & Dominey, 2000), olfactory material in relation with pictures (Sarfarazi, Cave, Richardson, Behan, & Sedgwick, 1999) and words related to musical stimuli (Koelsch, Kasper, Sammler, Schulze, Gunter & Friederici, 2004). Thus, irrespective of the input code, a negativity around 300-500 ms is typically related to re-processing of information at odds with the previous context.

Experiment 2: Symbolic task

Experiment 1 found electrophysiological evidence supporting the model of inference-driven allocation of attention in tracking a visual trajectory. Behaviourally, the same pattern of response latencies observed in tracking a visual trajectory can be observed in the symbolic domain, when tracking simple arithmetic series. In this experiment we tested whether the behavioural similarities between these perceptual and symbolic tasks extend to the electrophysiological domain. To that end, we used a numeric task similar to that used in Cherubini and colleagues' (2006) experiments 2 and 3, while recording ERPs from a new group of participants. Predictions at S_n are the same as in the previous experiment (see the introduction to Experiment 1). Even the predictions at S_{n-1} remain the same, namely a biphasic P300 should be observed for interrupted series, with a P3a component associated with detection of the deviant stimulus and a P3b component associated with reallocation of attentional resources. As far as the unexpected N400 component observed in Experiment 1 is concerned, we do not have *a priori* theoretical reasons for predicting it. Furthermore, in similar studies, when participants were presented with consecutive series of numbers (e.g., 2, 4, 6, 8…), a stimulus discordant with the expected completion of the series elicited a large P300, with both visual (Polich, 1985) and auditory (Lang & Kotchoubey, 2002) modalities but it did not elicit a N400 modulation.

Method

Participants

A total of 13 young adults (10 females) volunteered for the experiment. They were 24 years old on average (range: 20-27), and were all right-handed (writing hand). Each of them was paid 10 euros or received credits for a university psychological course. The ERP results of 2 female participants were not available for technical reasons (too many EEG artefacts and triggering failure, respectively). No participant reported a history of neurological or psychiatric disorders.

Apparatus, procedure, and task

The apparatus and design was the same as in Experiment 1. The procedure was similar, but was adapted to numerical series. Each trial was composed of 8 three-digit numbers (see Figure 1), each one appearing at the centre of the screen with a black background (Courier New 18-point white characters, average dimension: 2.2° x 0.95°) and remaining on the screen for 700 ms; the ISI between two subsequent numbers was 300 ms. Participants were instructed to pay attention to the series and respond to two events. They had to press a key whenever a specific target number was presented (*target-number responses*), and a different key whenever any number appeared twice consecutively (*repeated-number responses*). The series could be regular – either increasing or decreasing by twos – when the number progressively approached the target number, inducing its expectation. Interrupted series began as regular series, but after the number preceding the anticipated target number a deviant number appeared, abruptly breaking the series and disconfirming previous expectations.

Finally, response events could be embedded in pseudo-random series (see examples in Figure 1). Accordingly, there were six experimental conditions requiring responses, according to a 3 x 2 orthogonal design factoring the required responses (target-number vs repeated-number) and the type of series (regular, interrupted, random). Of the total 432 trials, 192 required a target-number response, 192 a repeated-number response, and 48 (approximately 11%) were catch trials which required no response whatsoever. In non-catch trials, target numbers always occurred within the last 4 numbers in the series, so that participants had 4 to 7 numbers prior to the imperative stimulus. The structure of the trials was the same as in Experiment 1. No statistical associations allowed to predict which response event was likely to occur in a given trial. Other perceivable predictive statistical associations – concerning exclusively the likely occurrence of response events, and not their type – were the same as described in Experiment 1. The experiment was divided into two blocks of trials. A different target number was used for each of the two blocks. Target numbers were also counterbalanced across participants.

Results and Analyses

Response latencies

Latencies of the correct responses are shown in Table 1. RTs were analysed by means of a repeated-measures ANOVA factoring type of series and type of response, and paired two-tail t-tests were used to find the source of significant effects. The main effect of series was significant [$F(2, 24) = 20.4$, $p < .001$]. Responses to the regular series were faster than those to the interrupted series [t(12)=3.4, $p < .01$], and responses to the interrupted series were faster than those to the random series [t(12)=3.3, $p < .01$]. More relevant for the present purposes, the predicted response by series interaction was significant [$F(2, 24) = 21.2$, $p < .001$; see Table 1]. In the regular series, responses to anticipated target numbers were faster than those to the unexpected repeated numbers [t(12)=4.65, $p < .001$]. Responses to the target numbers were slower in the interrupted series than in the regular series [t(12)=4.6, $p < .001$], whilst responses to repeated numbers became faster in the interrupted series than in regular series [t(12)=2.2, $p < .05$]. Latencies of the two response types were not reliably different from each other in the interrupted series. In the random series performance decayed, as shown by the main effect of series; nonetheless, responses to repeated events were faster in the random series than in the regular series [t(12)=2.8, $p < .05$], where they clashed with the expectation of the target number [random vs. regular, t(12)=6.2, $p < .001$, random vs. interrupted, t(12)=3.3, $p < .01$].

Accuracy

Table 2 reports the overall percentage of errors. Errors were analysed with non-parametric Wilcoxon signed rank exact tests. The rate of incorrect responses was generally low. Misses were more frequent for repeated-number events than for target events [$Z = 3.2$, $p = .001$]. Frequency of misses was not different among the series. There were more false alarms in the regular series than in the random one [$Z = 2.8$, $p = .005$], and in the interrupted series than in the random ones [$Z = 3.4$, $p = .002$].

Electrophysiological effects at S_n

EEG data were pre-processed as in Experiment 1. Because preliminary analyses showed no interesting laterality effects, the side factor was collapsed. The resulting Grand Means for the target-number events and the repeated-number events are reported in Figure 5 and 6, respectively, and the mean amplitudes in Table 3 (referring to the 350-450 ms latency-window).

--- Insert Figure 5 and 6 about here ---

As for experiment 1, the N2 was analyzed after averaging together the mean amplitude in the 3 parietal sites (P3, Pz, P4), which were those where the component was at its highest amplitude. N2 mean amplitude was submitted to a 3x2 repeated measures ANOVA with series (regular, interrupted, random), and response event (target vs repeated event) as factors. No effect was significant, even though there was a trend for a main effect of Series [F(2, 20) = 2.7, p = .088]. Similarly to Experiment 1, N2 tended to be less pronounced for interrupted series than for regular and for random ones.

Mean amplitudes in the 350-450 ms latency-window were analyzed by means of a 3x3x2 repeated measures ANOVA, factoring region (frontal, central, parietal), type of series (regular, interrupted, random), and type of response event (target-number vs repeated-number). Replicating Experiment 1, the most important finding is the reliable series by response interaction [$F(2, 20) = 10.5$, $p < .01$]. It shows that, in a regular series, this component was more positive for the target-number events than for the repeated-number events [t(10)=5.9, $p < .001$] whereas, in interrupted series, there was no difference among the two response events: positivity increased for repeated events, and decreased for target events, with respect to regular seires. These results are consistent with the idea that attention is focused on the target number in the regular series, but – in the interruptede series – after detection of the deviant number attention is redeployed to both response events. Positivity is at its lowest point in random series where, for target-number events, amplitude is significantly lower with respect to interrupted series [t(10)=3, $p < .05$] and to regular series [t(10)=5, $p < .001$]. Also in this case, this pattern fits the observed response latencies. The ERP amplitude progressively increases in the antero-posterior direction, and mostly so for the target events after regular series, as shown by the significant response by series by region 3-way interaction [F(4, 40) = 4.9, p < .01, means in Table 3]. This pattern suggests that the observed component is likely to be a P3b component.

Other findings, embedded in the effects reported above, are the main effect of region [F(2, 20) = 10.9, p < .01], series [F(2, 20) = 5.9, p <.05] and response [F(1, 10) = 20.1, p < .01].

Electrophysiological effects at S_{n-1}

The grand means of ERPs evoked by S_{n-1} are shown in Figure 7. Visual inspection suggests two differences with respect to Experiment 1: here, there is no N400 modulation and the positive modulation begins at an earlier time and lasts longer. Yet, similarly to Experiment 1, there is a posterior N2, and the P300 shows a late peak mostly in the centro-parietal regions, even though waveforms had different temporal durations from the previous experiment. For the analyses we selected three latency-windows: 160-200, 200-300 ms, and 300-600 ms.

For the N2, mean amplitude in the 3 parietal sites averaged together (P3, Pz, P4) was submitted to a univariate ANOVA factoring type of series (regular, regular, random). The effect of series was significant [F(2, 20) = 8.6, p < .01]. N2 was more pronounced for regular series than for interrupted [t(10)=3.6, $p < .01$] and random ones [t(10)=2.5, $p < .05$], even if in the latter case the difference was of only 0.4 μV. The interrupted series was significantly less pronounced than the random one (t(10)=2.5, $p < .05$).

For the other two components, mean amplitudes were analyzed by means of a repeated-measures ANOVA factoring region (frontal, central, parietal) and series (regular, interrupted, random). Preliminary analyses showed no substantial findings related to lateralization. Accordingly, also for these time-windows the laterality factor was collapsed across regions.

--- Insert Figure 7 about here ---

Amplitudes in the two latency-windows are shown in Table 4. In the earlier window, the only reliable effect was the main effect of series [F(2, 20) = 19.2, p < .001], showing that the interrupted series (those where S_{n-1} was deviant) were associated with a more positive waveform than the other two series [interrupted vs. regular, t(10)=5.6, $p < .001$; interrupted vs. random, t(10)=4.7, $p < .001$]. In the later latency-window, there was a main effect of region [F(2, 20) = 24.1, p < .001], showing that activity increased progressing in the anterior-posterior direction [frontal vs. central, t(10)=5.1, $p < .001$; central vs. parietal, t(10)=4, $p < .01$]. The main effect of series was also significant [F(2, 20) = 14.8, p < .001], again showing that the interrupted series elicited the most pronounced potentials [interrupted vs. regular, t(10)=4.4, $p < .001$; interrupted vs. random, t(10)=3.9, $p < .01$].

Discussion

Behavioral findings replicate previous results by Cherubini *et al*. (2006). As in Experiment 1, ERPs at S_n corroborate the pattern of allocation of attention predicted by the inference-driven view of attentional deployment. A mostly parietal P300 is observed. This P3b component is sensitive to the amount of expectations/resources allocated to incoming response events. As predicted, in regular series it is more pronounced for target-numbers than for repeated numbers; positivity associated to target-numbers become less pronounced in interrupted series, whereas ERPs to repeated numbers have a higher amplitude, with respect to regular series. Finally, ERP waves to both events are less pronounced in the random series than in interrupted series. Despite some differences from Experiment 1, mostly in the absolute amplitudes of potentials (which were higher in the perceptual task), the observed statistically reliable effects in the P3b are the same as in Experiment 1. A pattern similar to Experiment 1 is also observed in the N2 component, even if only as a trend. However, as in Experiment 1, the lack of a Series x Response interaction modulating the N2 amplitude suggests that the N2 – contrary to the P300 – is not sensitive to the inference-driven mechanism of strategic deployment of attention.

The positive P3 complex for S_{n-1} has an earlier onset and lasts longer than in Experiment 1. Despite these differences, it bears a structural resemblance to that observed in Experiment 1: it is biphasic, with the later component mostly parietal, suggestive of a two-stage process where, first the deviant stimulus is detected, and then disengagement and reallocation of attention for the incoming response event is undertook. The N2 for S_{n-1} was also modulated in a similar fashion as in Experiment 1, in that this component was more pronounced for regular series than for the other two series. No N400-like component was found.

Cross-experimental results

We tested whether the RTs and the ERP components found in the two experiments showed a similar pattern by submitting these measures to mixed ANOVAs. For the RTs, a 2x3x2 mixed ANOVA was performed with experiment (perceptual vs. symbolic) as the between subjects factor, and series and response event as the within subject factors. The 3-way interaction Experiment x Series x Response event was not significant, showing that the critical Series x Response interactions were not reliably different in the two experiments. The only significant effect involving experiment was the interaction with the response event type [F(1, 23) = 9.9, p < .01]: in the perceptual task, responses to target events were globally faster than responses to repeated events (t(11) = 6.6. p < .001), whereas the two responses were not different in the symbolic task (p = .22). Faster responses to target events were observed in Cherubini *et al*. (2006): together with the increased number of errors for the repeated events, they point to the fact that responses to target events are generally easier, a result of no consequence for the experimental hypotheses. All the more, this trend not reaching significance in the present Experiment 2 is not of concern for the main results of this study. There was a trend for a main effect of experiment [F(1, 23) = 4.1, p = .054], suggesting that responses in the perceptual experiment were faster than those in the symbolic experiment. Even this trend is consistent with previous results of the 2006 study, where responses to perceptual tasks were reliably faster than responses to symbolic tasks. No other effect involving task reached significance.

For the ERP analysis, all the components were evaluated through mixed ANOVAs with experiment as the between factor, with the exception of the late frontal negativity associated to S_{n-1} in the perceptual experiment, since this component did not appear in the symbolic experiment. Preliminary analyses indicated that absolute amplitude of ERPs was much greater in the perceptual task than in the symbolic one. To focus on the effects of experimental manipulations on ERPs independently of differences in absolute magnitude of ERP amplitudes, we first standardized mean amplitudes using z-scores. For each condition and experiment, z-scores were obtained by subtracting the mean amplitude from each subject’s amplitude value and dividing this difference value by the standard deviation. As a result of this transformation, the amplitude data from both experiments were centered to the zero value, thus cancelling out the absolute differences between the two experiments.

The mean amplitude z-scores of the N2 elicited by S_n was evaluated through 2x3x2 mixed ANOVA with experiment as the between subjects factor, and series and response event as the within subject factors. This analysis yielded a main effect of series only [F(2, 42)=5.8, p = .01], which strengthens results from the separate ANOVAs by showing that N2 was less pronounced for interrupted series than for the other two series in both experiments. The mean amplitude z-scores of the P3b elicited by S_n was submitted to a 2x3x3x2 mixed ANOVA with Experiment as the between subjects factor, and region, series and response event as the within subject factors. Besides the significant effects confirming results from ANOVAs carried out separately for each experiment, no effect involving the factor experiment was found.

The mean amplitude of the N2 elicited by S_{n-1} was submitted to a 2x3 mixed ANOVA with experiment as the between subjects factor, and series as the within subject factor. This analysis yielded a significant main effect of series only [F(2, 42) = 23.2, p < .001]. As in the separate ANOVAs, this effect mainly indicates that N2 for was more pronounced for regular series than for the other two series in both experiments.

The mean amplitudes of the P3a and P3b elicited by S_{n-1} were submitted to a 2x3x3 mixed ANOVAs with experiment as the between subjects factor, and region and series as the within subject factor. For the P3a, the only effect involving the experiment was an experiment by series interaction [F(2, 42) = 6.6, p < .01]. It is noteworthy that this was not a cross-over interaction, and was instead due to the fact that the difference between P3a amplitudes for interrupted and target series was larger in the perceptual task than in the symbolic task, although for both tasks this difference was significant, as confirmed by subsequent t-tests [for the perceptual task: t(11) = 10.1, p < .001; for the symbolic task: t(10) = 5.6, p < .001].

For the P3b, there was a region by series by experiment interaction [F(4, 84) = 7, p < .001]. This interaction was mainly due to differences in the topography of the components. As already shown in the separate ANOVAs, and also corroborated by planned comparisons here, the difference between the interrupted and the regular series was strongest in the parietal region and smallest in the frontal region for the perceptual task (planned comparison F(1, 21) = 19, $p < .001$), whereas this difference was equally distributed across the scalp in the symbolic task (planned comparison F(1, 21) = 2.3, p = .14). Notably, the series by experiment interaction was not significant (p = .6), a result that suggests that the three way interaction was mainly due to differences in the scalp topography of an otherwise similar modulation.

General Discussion

The present study investigated the electrophysiological correlates of inference-driven attention, that is the strategic control of attention driven by expectations and by their disconfirmations. Events confirming or contrasting with an expectation are critically important for the revision of our internal models of the environment. Both classes of events are rapidly and efficiently detected and processed (e.g., Horstmann & Becker, in press; Horstmann & Ansorge, 2006; Horstmann, 2006 a,b, 2005, 2002). However, as shown by Cherubini *et al*. (2006), expected and unexpected events trigger different patterns of attentional deployment. Specifically, when a set of regularities in the previous stimuli induce the expectation of a specific response event, attention is focused on it. If that event later occurs (as it happened for the target events in the regular conditions of the present experiments), its processing is enhanced, whereas if a different, unexpected response event occurs (as it happened for repeated events in regular series), its processing is hindered. After an unexpected event occurs in a previously regular context (e.g., interrupted series conditions), attention is redeployed and distributed among the two possible response events. Finally, lack of regularities impedes the building of expectations, and thus it impedes inference-driven attentional orienting, resulting in poor performance for both response events. These patterns of attentional deployment work similarly for some perceptual tasks (tracking of perceptual trajectories) and for a symbolic task (tracking of simple arithmetic series). The behavioral results of the present experiments consistently replicate the findings of Cherubini *et al.* (2006).

In this study, by capitalizing on the notion that a centro-parietal component of the P300, namely the P3b, is likely modulated by the amount of allocated attention (Sommer et al., 1990; Wickens *et al.* 1983), and by the amount of expectancies toward an incoming response event (Rosenfeld et al., 2005; Näätänen, 1990), we directly checked the electrophysiological correlates of the inference-driven attention model. In two tracking tasks, one using visual trajectories (perceptual task, experiment 1) and the other using arithmetic series (symbolic task, experiment 2), we actually found a P3b component associated with the response events, which was modulated as predicted by the inference-driven model of attention. In regular trajectories, its amplitude was higher for anticipated target events than for unpredictable repeated events. By contrast, after an abrupt interruption of a trajectory the P3b for target events was less pronounced than in regular series, and the P3b for repeated events was more pronounced than in regular series, reflecting the redistribution of attention following the detection of an abrupt disconfirmation of previous expectancies. Finally, in random trajectories, the amplitude of the P3b associated to both response events was similar, and less pronounced than in the interrupted trajectories, reflecting the lack of a consistent attentional deployment strategy in those conditions. These electrophysiological findings corroborate the hypothesis that the behavioral differences observed in response latencies are indeed the result of a mechanism of attentional deployment..

A second purpose of the study was to check whether behavioral similarities in the pattern of distribution of attention in perceptual and symbolic tasks were matched by electrophysiological similarities. In this way we test whether behavioral similarities between the two tasks are caused by “convergent evolution” of different, domain-specific neural mechanisms of attentional orienting acting in different domains, or can be at least partly caused by a common, non-specific neural mechanism concerned with the high-level control of attentional deployment in different domains. Results suggest the latter possibility. Despite differences in the absolute amplitudes and in the time course of the P3b, the patterns of the potentials related to the response events (S_n) were very similar in the two experiments. Cross-experimental analyses showed that the series by response interaction, critically important for the theoretical predictions, was not reliably different in the perceptual task (Experiment 1) and in the symbolic task (Experiment 2). This finding suggests that the P3b is at least partly modulated by the activity of a neural substrate concerned with attentional orienting in a general, cross-domain way. The other electrophysiological attentional marker that we checked was the N2, a posterior component which reflects visual selective attention (Folstein & Van Petten, 2008). It reliably showed the lowest modulation after an interrupted series in both task (although only as a trend in the symbolic task), suggesting that the early stages of detection of a response event are hindered after an abrupt disconfirmation of expectancies. However, this main effect of the type of series did not interact with the type of response events, thus showing that the N2 waveform – contrary to the P3b – is probably not affected by the high-level mechanism of attentional redeployment that we are investigating.

Trials immediately preceding response events were also assessed. In one condition of our experiments, those events were stimuli that abruptly deviated from a previously regular trajectory/series. According to the inference-driven model of attention, after a deviant event is detected, the scope of attention is widened in order to better explore the “surprising” environment (in the artificial environments used in our experiments, this amounts to redistributing attention to the internal representations of both possible response events). In both experiments we found biphasic ERPs, including an anterior P3a component, marking the detection of the deviant stimulus, and a later parietal P3b component, reflecting the reallocation of attention. Even though both P3a and P3b can be elicited by deviant events and they usually show spatial and temporal overlap, previous studies using principal component analysis (Dien, Spencer, & Donchin, 2003) and independent component analysis (Debener, Makeig, Delorme, & Engel, 2005) have shown that they reflect two distinct components (see also Friedman *et al.*, 2001). Moreover, source analysis has suggested two different anatomical sources for P3a and P3b, namely anterior cingulate and temporal parietal junction, respectively (Dien, *et al.*, 2003). The interrupted series elicited an earlier P3a-like component that was central in the Experiment 1, and diffused across the scalp in Experiment 2, followed by a late P3b-like component, that was mainly parietal in both experiments. This pattern is in line with the existence of an attentional system, involving prefrontal and temporo-parietal regions, that is specialized for the detection of behaviorally relevant stimuli, mainly when they are unexpected and salient (Corbetta & Shulman, 2002), and the strategic redistribution of attentions that occurs after it.

The critical stimulus in the interrupted series eliciting a P3a, not only was deviant, but also conveyed task-related information, because after that stimulus subjects were alerted that the two response events were equally likely to occur, whereas they previously focused on only one of those events. Recent work on the P3a has shown that this component is modulated more by the amount of task-related information that the eliciting stimulus provides, than by other factors such as its novelty and probability of occurrence *per se* (Barcelo, Escera, Corral, & Perianez, 2006).

Another earlier potential was also sensitive to the series which the S_{n-1} belonged to. The posterior N2 was more pronounced for the regular series than in the other two series in both experiments. This finding corroborates previous studies showing that posterior negativities in a similar time window as the one analysed here for the N2 (around 180 ms) are more pronounced for expected events such as targets (Folstein & Van Petten, 2008; Pritchard *et al.*,

1991) in both spatial (e.g., Luck & Hillyard, 1994a & b) and non-spatial (e.g., Eimer, 1997) selective attention paradigms. In both tasks, the lowest N2 was present to interrupted series, a finding that suggests that early selective attention was less focused on deviant stimuli.

However, beyond the many similarities in the electrophysiological patterns in the two Experiments, some differences were also observed between the two tasks. One reliable difference was observed in the topography of the P3a orienting component between experiments 1 and 2 (central vs. diffused, respectively). This finding suggests that more neural areas are recruited when detecting deviant numbers in a numerical string than when detecting deviant positions in a spatial trajectory, possibly because the former require attendance to semantic properties (even though quite simple, in our task), whereas the latter is grounded on spatial attention.

The second important ERP difference between the two experiments is a frontal negativity waveform associated to the deviant stimulus in the perceptual task in a similar time-window as the N400, which was not observed in the symbolic task. While the absence of this late negativity from arithmetic tasks is consistent with previous literature (Polich, 1985; Lang & Kotchoubey, 2002), its presence in the visual tracking task was unpredicted, because the N400 is mostly associated to *semantic* incongruencies, even though there are examples of N400 observed in non-semantic tasks in previous literature (Barrett & Rugg, 1990; Niedeggen & Rösler, 1999; Balconi & Pozzoli, 2005; Hoen & Dominey, 2000; Sarfarazi *et al.*, 1999). It is more likely that, given also differences in scalp distribution (frontal here vs. parietal in the case of the N400), this component corresponds instead to a re-orienting negativity (RON), a negativity developing at around 400-600 ms that follows a P3a in paradigms using irrelevant distractor stimuli. This component has been described both in the auditory domain (Schröger & Wolff, 1998) and, under certain circumstances, in the visual domain (Berti & Schröger, 2001). RON is usually interpreted as an index of attentional reorienting towards the task-relevant stimulus features. In the case of deviant clock hands, it could indicate a reorienting of attention towards the positions where the hand could possibly appear next (same position or target position). It is possible that RON is sensitive exclusively to perceptual deviations from the attended stimulus, rather than to symbolic ones, as suggested by the fact that this component was absent in the number task, thus marking another difference between the reorienting mechanism involved in the two tasks.

However, further data would be required in order for us to interpret the meaning of these differences in the ERPs in terms of information-processing stages. We acknowledge that their presence suggests that *some* of the neural networks and mechanisms underlying the two tasks were different and domain-specific. This conclusion is not mutually exclusive with the previous one based on the similarities of ERPs elicited by the response event, which suggested the existence of a non-specific, cross-domain structure in charge of strategic, inferential-driven allocation of attentional resources.

Finally, it should be noted that all the expectations concerning the type of incoming response event used in this study were not statistically grounded: in all series, the target event and the repeated event were equally likely. Of course, statistical regularities are an important class of inferential expectations, but they are not the only ones: the inferential system generates expectations by using its own regularity detection strategies, which – even though they often emulate a statistical processor (e.g., Cosmides & Tooby, 1996) – in many instances deviate from it (for example, see the literature about the perception of randomness, e.g., the review by Nickerson, 2002; or the studies on illusory correlations, e.g., the model by Garcia-Marques, Hamilton, & Maddox, 2002). The present results show that inferential expectations and their violations affect deployment of attention in a structured, cross-domain way, even when they are not based on valid statistical regularities.

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Table 1. Mean Response Times (and standard errors) of correct responses in Experiments 1 and 2, in milliseconds.

	Series		
Response	Regular	Interrupted	Random
Experiment 1			
Target	482 (24)	568 (22)	589 (19)
Repeated	627 (19)	587 (19)	628 (19)
Experiment 2			
Target	656 (74)	745 (68)	798 (82)
Repeated	771 (73)	737 (75)	752 (74)

Table 2. Mean percentages of errors (and standard errors) in Experiments 1 and 2.

Response	Error Type	Series		
		Regular	Interrupted	Random
Experiment 1				
Target	Wrong	2.0 (0.9)	0.8 (0.5)	0.9 (0.4)
	Miss	3.0 (1.3)	2.7 (1.1)	2.7 (1.2)
Repeated	Wrong	1.2 (0.5)	2.3 (0.7)	1.3 (0.6)
	Miss	6.4 (1.3)	8.9 (2.5)	5.7 (1.5)
False Alarm		5.9 (1.1)	5.5 (0.8)	1.8 (0.6)
Experiment 2				
Target	Wrong	0.7 (0.3)	0.1 (0.1)	1.0 (0.4)
	Miss	4.3 (1.1)	4.6 (0.6)	5.3 (1.5)
Repeated	Wrong	1.4 (0.3)	0.5 (0.2)	1.1 (0.5)
	Miss	16.8 (3.0)	19.2 (3.0)	20.3 (2.9)
False Alarm		3.0 (0.8)	3.8 (0.9)	0.8 (0.3)

Table 3. Mean ERP amplitude (and standard error) at S_n, according to series, response types, time-windows and scalp regions in Experiments 1 and 2, in micro-volts.

		Series		
Region	Response	Regular	Interrupted	Random
Experiment 1, latency-window 160-200 ms				
Parietal	Target event	-0.6 (.7)	1.3 (0.9)	0.04 (0.9)
	Repeated event	-0.2 (0.7)	0.1 (0.7)	-0.04 (0.44)
Experiment 1, latency-window 350-450 ms				
Frontal	Target event	7.0 (0.9)	3.5 (1.1)	3.6 (0.9)
	Repeated event	4.2 (1.1)	4.9 (1.2)	2.6 (1.3)
Central	Target event	11.1 (0.9)	6.2 (1.4)	6.0 (0.9)
	Repeated event	6.5 (1.1)	7.5 (1.2)	5.3 (1.2)
Parietal	Target event	13.2 (.8)	8.5 (1.4)	8.4 (1.0)
	Repeated event	7.7 (1.1)	9.3 (1.3)	7.4 (1.1)
Experiment 2, latency-window 160-200 ms				
Parietal	Target event	4.8 (0.7)	4.7 (0.6)	3.5 (0.7)
	Repeated event	3.6 (0.7)	4.7 (0.9)	3.8 (0.6)
Experiment 2, latency-window 350-450 ms				
Frontal	Target event	3.5 (0.6)	3.3 (0.7)	0.6 (0.6)
	Repeated event	1.2 (0.5)	2.1 (0.7)	0.4 (0.5)
Central	Target event	5.2 (0.9)	3.9 (0.9)	1.5 (0.6)
	Repeated event	1.5 (0.5)	2.7 (1.2)	1.2 (0.5)
Parietal	Target event	7.0 (1.2)	5.1 (1.1)	3.0 (0.9)
	Repeated event	2.7 (0.6)	4.4 (1.2)	3.1 (0.6)

Table 4. Mean ERP amplitude (and standard error) at S_{n-1}, organized according to the three series, the three scalp regions, and the different latency-windows in Experiments 1 and 2 (in micro-volts).

		Series		
Latency window	Region	Regular	Interrupted	Random
Experiment 1				
160-200 ms	Parietal	-1.4 (0.5)	1.3 (0.6)	-0.4 (0.6)
200-350 ms	Frontal	2.5 (0.4)	8.4 (1.1)	4.7 (0.8)
	Central	2.7 (0.5)	10.1 (1.1)	5.3 (0.7)
	Parietal	2.5 (0.4)	8.8 (0.8)	4.9 (0.5)
350-420 ms	Frontal	1.8 (0.8)	5.2 (0.7)	1.8 (0.9)
	Central	2.8 (0.8)	8.5 (0.9)	3.4 (0.8)
	Parietal	3.5 (0.8)	9.8 (1.0)	4.4 (0.7)
420-650 ms	Frontal	-1.3 (0.5)	-4.6 (0.3)	-2.3 (0.4)
	Central	-0.4 (0.4)	-2.8 (0.7)	-1.1 (0.3)
	Parietal	0.2 (0.3)	-1.6 (0.6)	-0.4 (0.3)
Experiment 2				
160-200 ms	Parietal	2.6 (0.4)	3.9 (0.5)	3 (0.4)
200-300 ms	Frontal	3.7 (0.4)	5.5 (0.5)	3.4 (0.5)
	Central	4.2 (0.4)	6.0 (0.5)	4.0 (0.4)
	Parietal	4.3 (0.4)	5.8 (0.5)	4.3 (0.4)
300-600 ms	Frontal	-1.1 (0.5)	1.4 (0.6)	-0.8 (0.5)
	Central	0.1 (0.5)	2.5 (0.6)	0.1 (0.4)
	Parietal	1.3 (0.6)	3.1 (0.6)	0.8 (0.5)

Figure Captions

Figure 1. Some examples of (a) regular, (b) interrupted, and (c) random series, in Experiments 1 (visual trajectories) and 2 (arithmetic series) (for the visual trajectories, the regular-repeated and random-repeated conditions are not exemplified). In the experiments each series was equally associated with target-event responses and repeated-event responses. The small numbers near the clock hands in Experiment 1 were not present in the real task: they are displayed here to show the sequential order of presentation of the hands. In Experiment 2, all the numbers appeared at the center of the screen.

Figure 2. Grand Averages of the ERPs elicited by a *target event* at the imperative stimulus (S_n), as a function of Series, in Experiment 1 (visual trajectories task). Analysed electrodes only are displayed. F is frontal, C is central, P is parietal; electrodes numbered 3 are on the left hemisphere, 4 on the right one, and z are on the midline. Amplitude (in microvolts) is plotted in the y-axis, and latency (in milliseconds) in the x-axis.

Figure 3. Grand Averages of the ERPs evoked by a *repeated event* at S_n, as a function of Series in the Experiment 1 (visual trajectories task). See figure 1 for details.

Figure 4. Grand Averages of ERPs for the S_{n-1} as a function of Series, in Experiment 1.

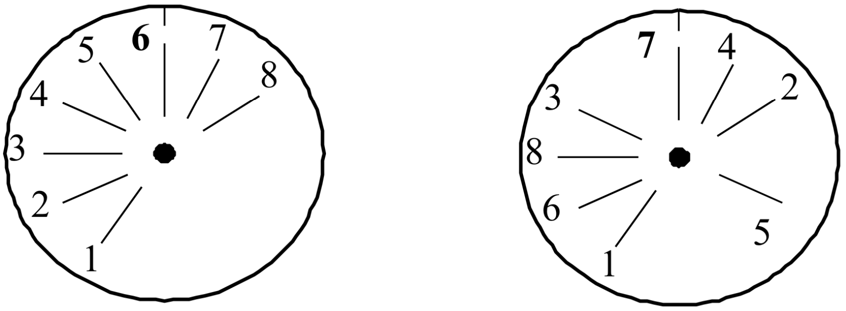
Figure 5. Grand Averages of the ERPs evoked by a target event at S_n, as a function of Series, in Experiment 2 (arithmetic task). See figure 1 for details.

Figure 6. Grand Averages of the ERPs elicited by a repeated event at S_n, as a function of Series, in Experiment 2. See figure 1 for details.

Figure 7. Grand Averages of the ERPs at S_{n-1}, as a function of Series, in Experiment 2. See figure 1 for details.

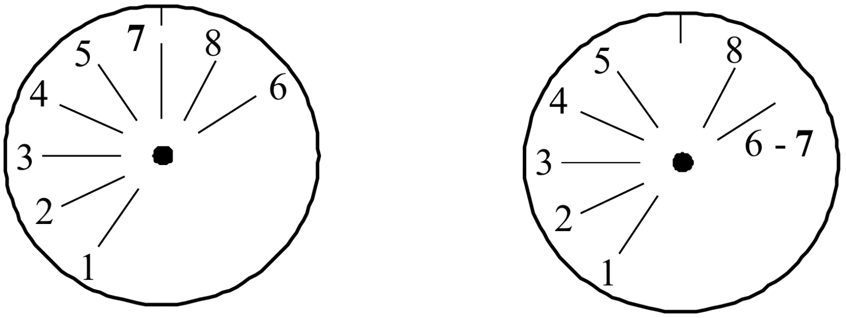
Figure 1.

Experiment 1: visual trajectories (target hour: 12 o’clock)



(a) Regular, with response to target hour

(c) Random, with response to target hour



(b) Interrupted, with response to target hour

(b) Interrupted, with response to repeated hour

Experiment 2: arithmetic series (target number: 342)

...332 334 336 338 340 342...
Regular, with response to target number

... 334 336 338 340 271 342...
Interrupted, with response to target number

...272 235 417 314 124 342...
Random, with response to target number

...332 334 336 338 340 340...
Regular, with response to repeated number

... 334 336 338 340 271 271...
Interrupted, with response to repeated number

...272 235 417 314 124 124...
Random, with response to repeated number

Figure 2.

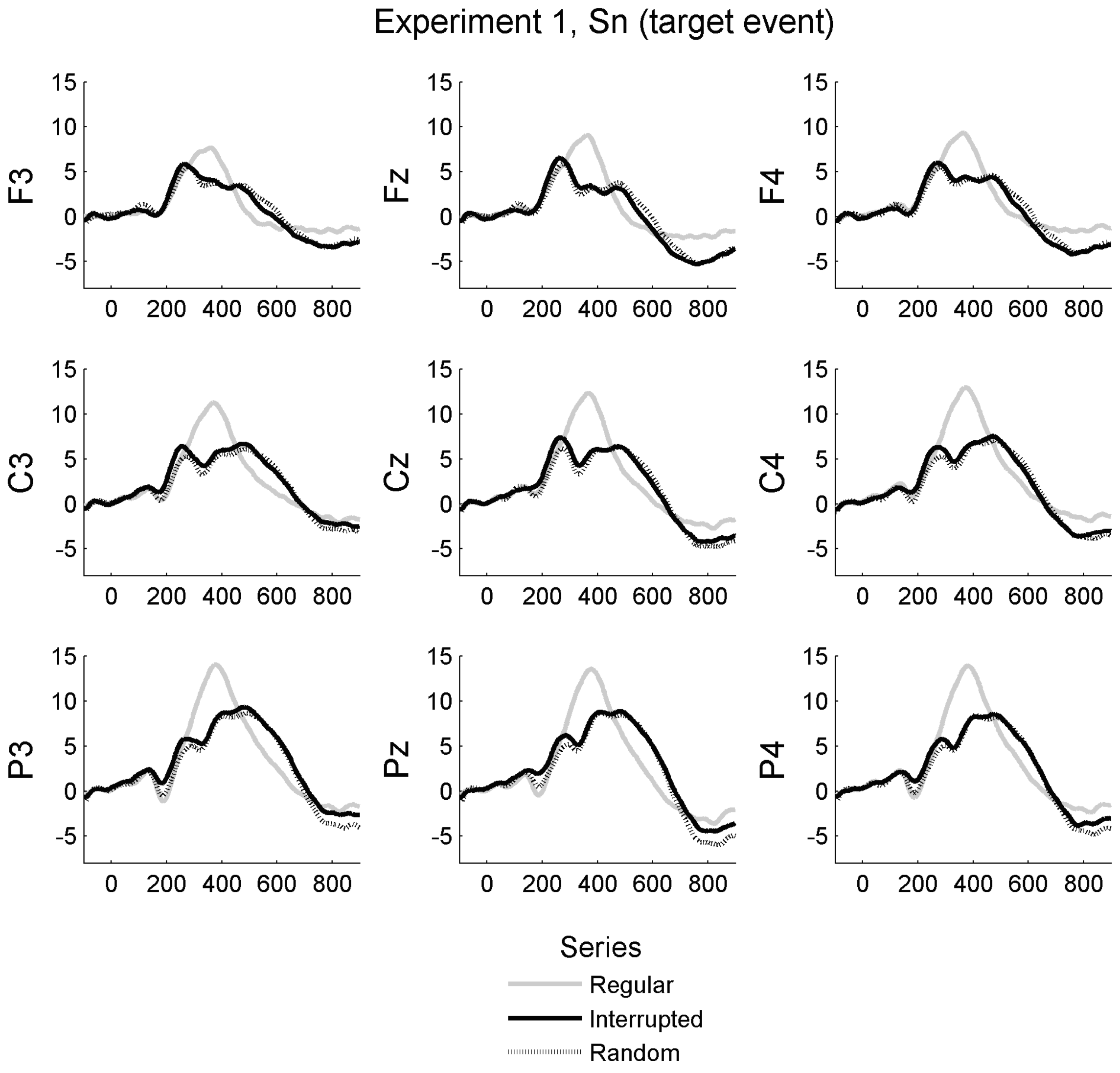

Experiment 1, Sn (target event)
F3
Fz
F4
C3
Cz
C4
P3
Pz
P4
15
10
5
0
-5
0
200
400
600
800
Series
Regular
Interrupted
Random

Figure 3.

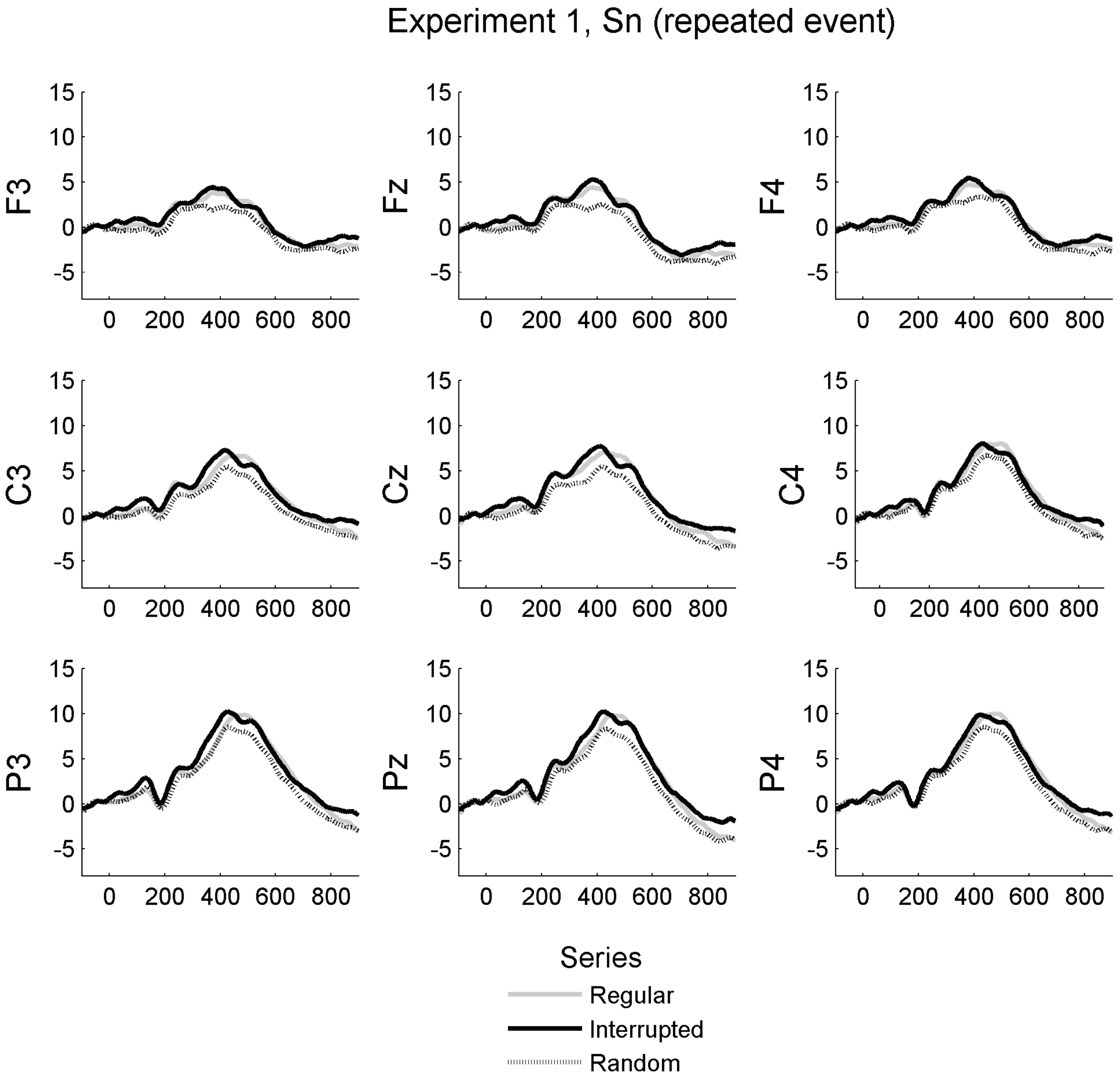

Experiment 1, Sn (repeated event)
F3
Fz
F4
C3
Cz
C4
P3
Pz
P4
15
10
5
0
-5
0
200
400
600
800
Series
Regular
Interrupted
Random

Figure 4.

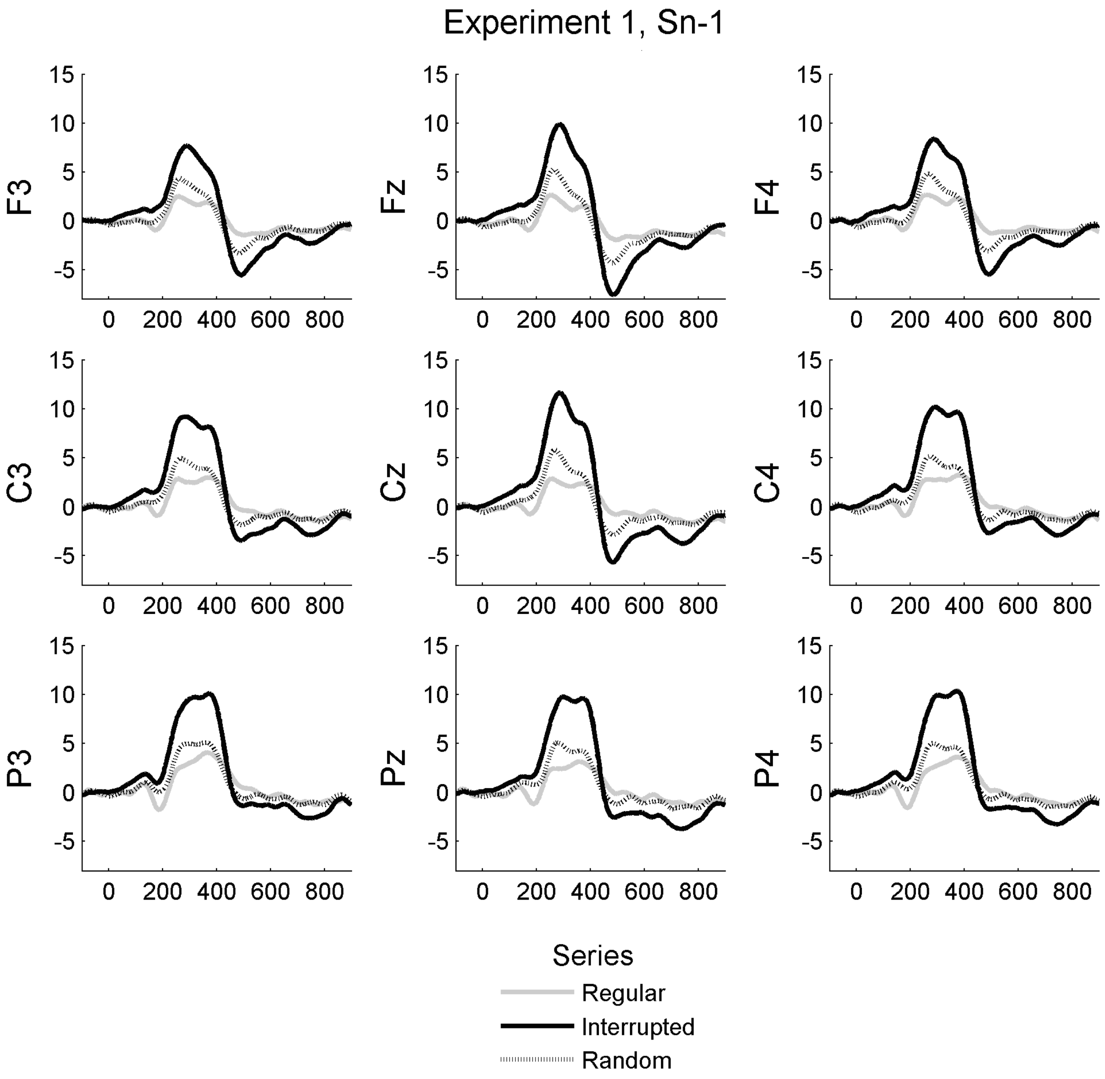

Experiment 1, Sn-1
F3
Fz
F4
C3
Cz
C4
P3
Pz
P4
15
10
5
0
-5
0
200
400
600
800
Series
Regular
Interrupted
Random

Figure 5.

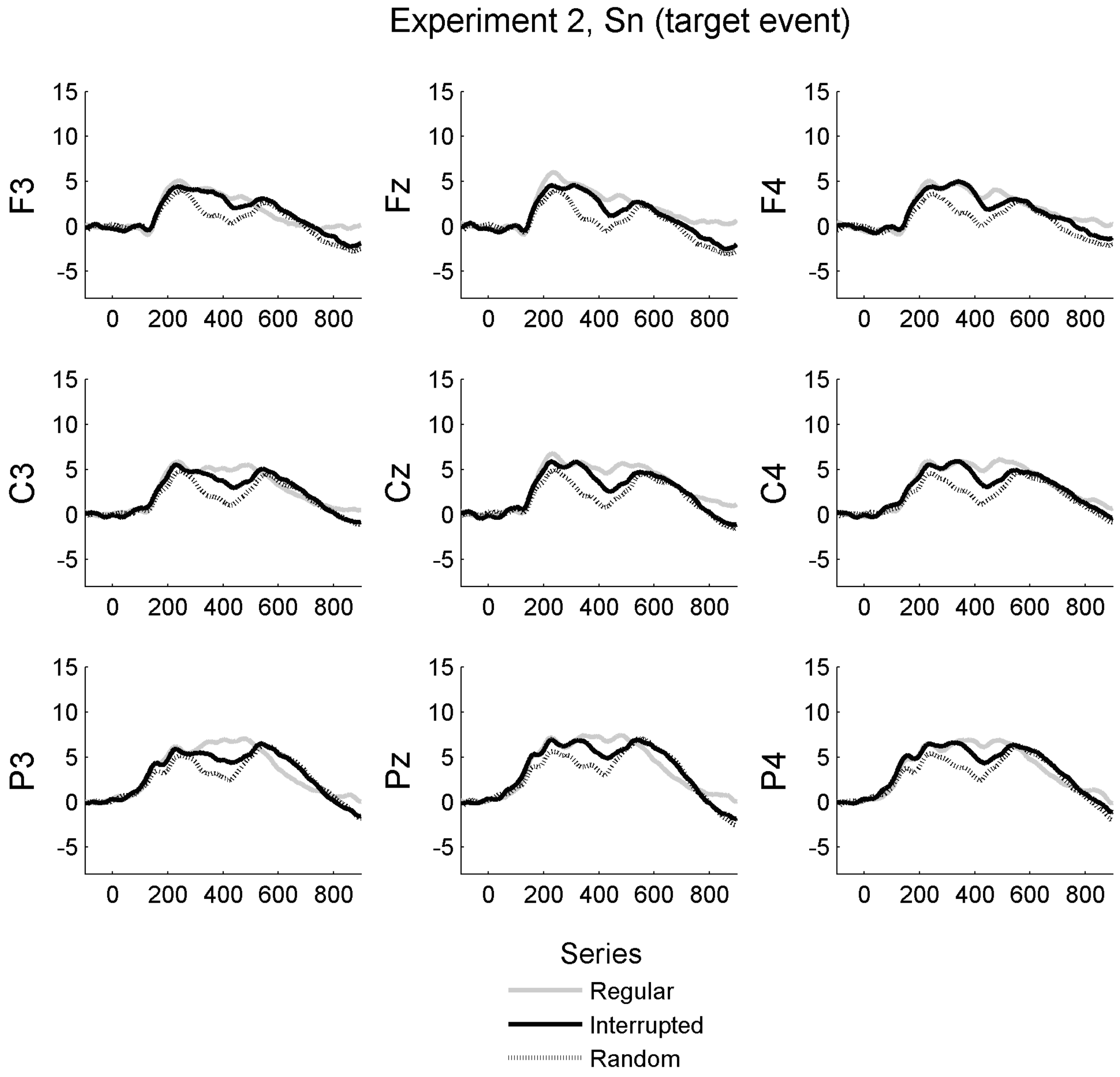

Experiment 2, Sn (target event)
F3
Fz
F4
C3
Cz
C4
P3
Pz
P4
15
10
5
0
-5
0
200
400
600
800
Series
Regular
Interrupted
Random

Figure 6.

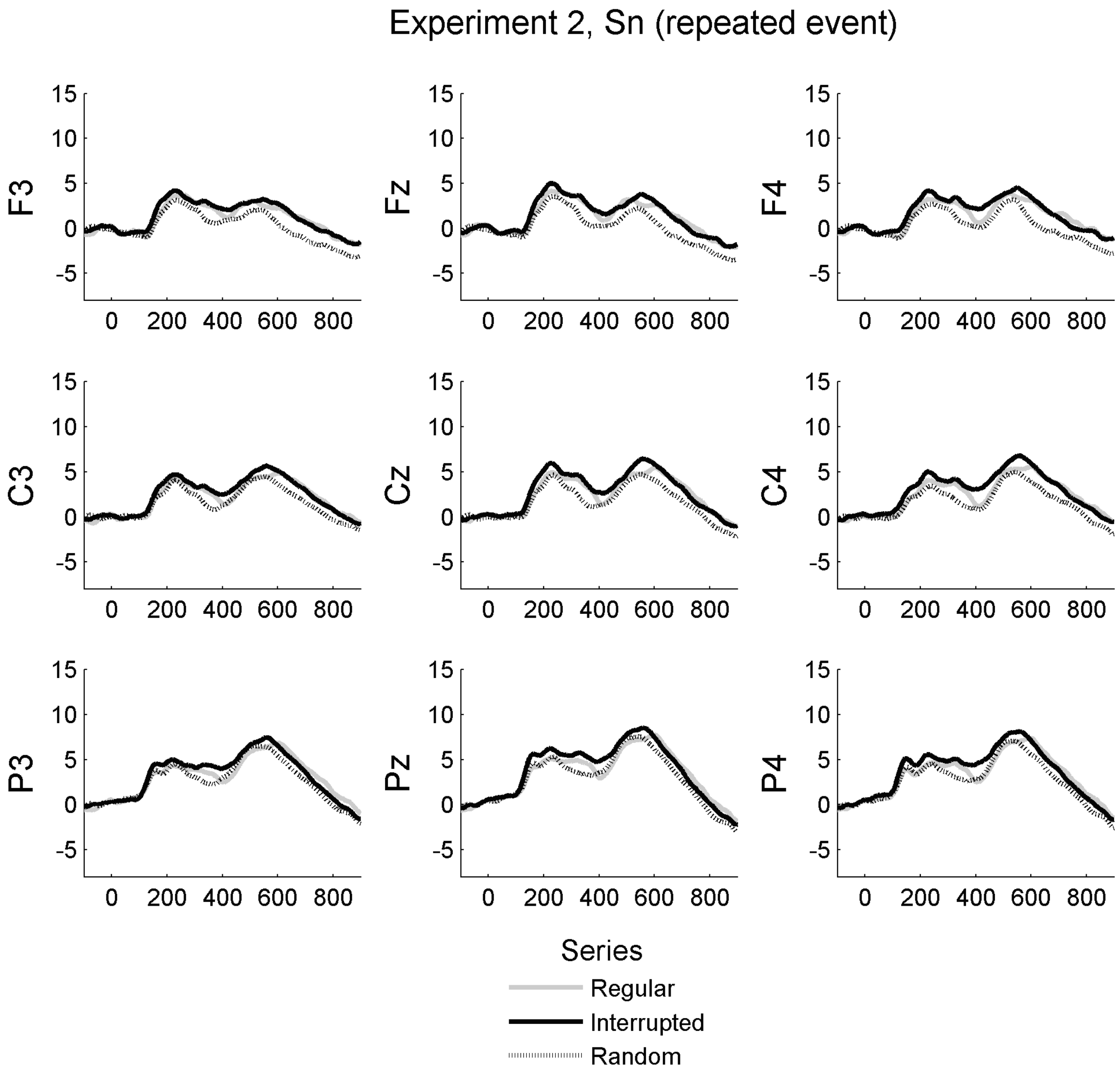
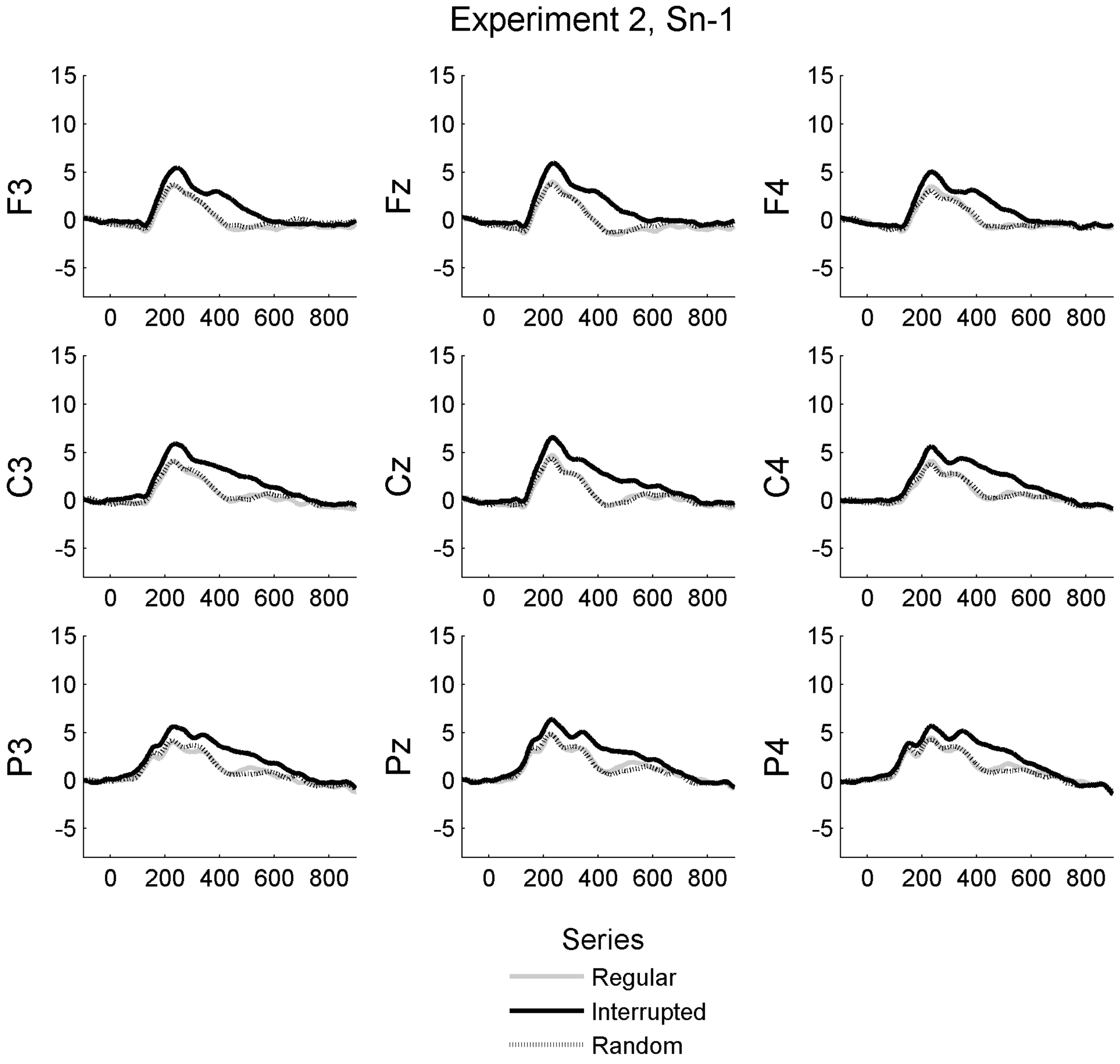

Experiment 2, Sn (repeated event)
F3
Fz
F4
C3
Cz
C4
P3
Pz
P4
15
10
5
0
-5
0
200
400
600
800
Series
Regular
Interrupted
Random

Figure 7.


Experiment 2, Sn-1
F3
Fz
F4
C3
Cz
C4
P3
Pz
P4
15
10
5
0
-5
0
200
400
600
800
Series
Regular
Interrupted
Random