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Barceló, Francisco; Cooper, Patrick S.; "An information theory account of late frontoparietal ERP positivities in cognitive control". Published in Psychophysiology Vol. 1, Issue 19 (2017)

Available from: http://dx.doi.org/10.1111/psyp.12814

This is the peer reviewed version of the following article: Barceló, Francisco; Cooper, Patrick S.; (2017), "An information theory account of late frontoparietal ERP positivities in cognitive control", **Psychophysiology**, which has been published in final form at http://dx.doi.org/10.1111/psyp.12814. This article may be used for non-commercial purposes in accordance with Wiley Terms and Conditions for Self-Archiving.

Accessed from: http://hdl.handle.net/1959.13/1349452

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Title page

An information-theory account of late frontoparietal ERP positivities in cognitive control

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Running head: Information theory and the P300

Keywords: Context-updating, Executive function, Information theory, P300, Task-set inertia,

Task-set reconfiguration

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Abstract

Event-related potential (ERP) research on task-switching has revealed distinct transient and sustained positive waveforms (latency circa 300-900 ms) while shifting task rules or stimulusresponse (S-R) mappings. However, it remains unclear whether such switch-related positivities show similar scalp topography and index context-updating mechanisms akin to those posed for domain-general (i.e., classic P300) positivities in many task domains. To examine this question, ERPs were recorded from 31 young adults (18-30 yo) while they were intermittently cued to switch or repeat their perceptual categorization of Gabor gratings varying in color and thickness (switch task), or else they performed two visually identical control tasks (go/nogo and oddball). Our task cueing paradigm examined two temporarily distinct stages of proactive rule updating and reactive rule execution. A simple information theory model helped us gauge cognitive demands under distinct temporal and task contexts in terms of low-level S-R pathways and higher-order rule updating operations. Task demands modulated domaingeneral (indexed by classic oddball P3) and switch positivities –indexed by both a cue-locked late positive complex (LPC) and a sustained positivity (SP) ensuing task transitions. Topographic scalp analyses confirmed subtle yet significant split-second changes in the configuration of neural sources for both domain-general P3s and switch positivities as a function of both the temporal and task context. These findings partly meet predictions from information estimates, and are compatible with a family of P3-like potentials indexing functionally distinct neural operations within a common frontoparietal "multiple demand" system during the preparation and execution of simple task rules.

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Introduction

Event-related potentials (ERPs) measured during task-switching have consistently shown several distinct positive waveforms present when shifting task rules/stimulus-response (S-R) mappings (e.g., Karayanidis, Coltheart, Michie, & Murphy, 2003; Karayanidis, Mansfield, Galloway, Smith, Provost, & Heathcote, 2009; Karayanidis, Provost, Brown, Paton, & Heathcote, 2011; Rushworth, Passingham, & Nobre, 2002). These ERP positivities, which typically occur 300-900 ms post switch stimulus, are often interpreted as reflecting switchspecific control processes (Kopp & Lange, 2013; Lavric, Mizon, & Monsell, 2008; Nicholson, Karayanidis et al., 2011). However, some authors have suggested switch positivities may actually have a functional relationship with the ubiquitous P300 component observed across many task domains (hereafter, the "domain-general" P3), probably reflecting higher-order context-updating mechanisms akin to those hypothesized for P3 potentials in simpler target detection tasks (Barceló, Escera, Corral, & Perianez, 2006; Barceló, Perianez, & Knight, 2002; Barceló, Perianez, & Nyhus, 2008; Kieffaber & Hetrick, 2005; cf., Donchin, 1981).

Switch-related and P300 positivities appear to have similar scalp topographies, suggesting they both recruit activity from a common cluster of frontoparietal regions (Bledowski et al., 2004). Given that frontoparietal networks are readily associated with cognitive control across many task domains (Cole et al., 2013; Petersen & Posner, 2012), the notion of such a "multiple demand" system (Duncan, 2013) may underpin the link between P3 and switch potentials. While many authors have interpreted the similar scalp topographies between the canonical P300 and switch positivities as reflecting context-updating mechanisms akin to those posited for P300 elicitation (Barceló et al., 2008; Kieffaber & Hetrick, 2005), to date this link remains unconfirmed. Few ERP studies have directly examined whether switch positivities are comparable to the canonical P300 both in their scalp topographies and in their purported context-updating function across task domains (cf., Holig & Berti, 2010; Lavric et al., 2008).

Many practical difficulties hinder progress toward a theoretical integration of domain-general P3 and switch positivities. First, one prominent issue is the temporal contingencies among task stimuli and responses (i.e., the "temporal context" of goal-directed actions; Fuster, 2001). For example, in oddball paradigms, it is widely accepted that P300 potentials can be elicited by both the targets of goal-directed behavior, and also by infrequent oddball distracters that are not to be responded to (Polich, 2007; Squires, Squires, & Hillyard, 1975). These targets and rare distracters elicit two functionally distinct P300 potentials whose scalp topographies differ along a fronto-parietal axis, with a more centroparietal scalp distribution for the former, and a more frontal distribution for the latter (Polich & Comerchero, 2003; Spencer, Dien, & Donchin, 1999). However, many P300 studies use oddball targets and thus confound the "oddballness" and "targetness" aspects of cognitive control, akin to the stages of proactive strategic preparation and reactive execution of simple sensorimotor rules, as defined in task-cueing paradigms (Braver 2012). That is, when an oddball target occurs within a sequence of repetitive standard distracters, one has to process its oddballness first, and then process its target or distracter features in order to select the appropriate motor response, and these two processes overlap in the summated ERP waveforms. Therefore, to clarify whether the frontal and parietal aspects of P300 index strategic resolution of contextual uncertainty (oddballness), as distinct from reactive execution of simple sensorimotor rules (targetness), targets need to be presented at predictable intervals within the trial run. Task-cueing procedures have revealed distinct frontoparietal switch positivities for these two distinct processing stages, with parietal maxima to temporally predictable targets during rule execution, and more anterior maxima to infrequent unpredictable task cues that anticipate a switch in rules (Barceló et al., 2002; Kieffaber & Hetrick, 2005). This evidence highlights the temporal dynamics of two distinct modes for the control of task-switching, with proactive rule updating and reactive rule execution stages differentially engaging the frontoparietal control network

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(Braver, 2012). Presumably, these same temporal dynamics also apply in simpler task domains. For instance, proactive interference in first target trials following an unexpected interruption has been proposed as a prime determinant of residual (restart) costs under single task conditions (Allport, Styles, & Hsieh, 1994; Barceló et al., 2008).

A second key limitation toward an integrative view of the P300 and switch positivities is the strict dichotomy between the two sub-components of the P300, with the frontal P3a linked to rare, novel and ignored stimuli, and the centroparietal P3b linked to attended, relevant and consciously-processed stimuli (for a review, see Polich, 2007). Such a sharp and dichotomous taxonomy impedes a theoretical integration of P3a/P3b sub-components with modern views about a graded contribution from both frontal and temporo-parietal nodes of frontoparietal cortical networks while dealing with a continuum of gradually increasing cognitive demands (Bledowsky et al., 2001; Cole et al., 2013). For example, Barceló et al. (2006) used Principal Component Analysis (PCA) to demonstrate that P3-like potentials to irrelevant novel sounds and relevant tones that signaled an upcoming task switch both showed similar peak latencies and scalp topographies, with more frontal or parietal maxima depending on their task context (for P3a potentials with parietal maxima see Polich, 2007; Kopp & Lange, 2013). This finding suggests that both irrelevant novel stimuli and familiar task cues may evoke a gradient of activity across frontal and parietal regions depending on their task context. Here we assume a common frontoparietal network for dealing with a whole gamut of cognitive demands beyond the traditional extreme "ignore" vs. "attend" dichotomy (Barceló & Knight, 2007).

A third limitation is the use of notional rather than formal definitions of *context*, which hinders examination of the prevailing "context-updating" hypothesis of P300 (Donchin 1981) across different task contexts, and impedes a direct comparison with switch positivities. Traditional views consider the stimulus context (i.e., mean stimulus probability) to be a major

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determinant of P300 amplitudes (Polich, 2007). However, the above examples highlight the influence of both temporal and task contexts on frontoparietal P300 dynamics, as a function of the cognitive demands associated with similar stimuli delivered under different task contexts. This highlights the importance of S-R links and *sensorimotor* information transmission –over and above stimulus properties alone- to completely explore the link between P3 and switch positivities (Verleger, Baur, Metzner, Smigasiewicz, 2014; Verleger, Jaskowoski & Wäscher, 2005). To this end, here we adopted a simple model of cognitive control based on information theory to compare cognitive demands associated with equally infrequent grey Gabor gratings, which set the temporal context for implementing the same visuomotor rule upon ensuing colored Gabor gratings delivered under three different task contexts (Switch, Go/NoGo, and Oddball tasks). This approach helped us to mathematically operationalize the construct of "context-updating" (Donchin, 1981), and to control for the confound between oddballness and targetness by factoring out the influence of the temporal context on neural activity and behavior. In doing so, we estimated the sensorimotor information transmitted between contextually related task stimuli and their associated motor responses (or "input-output correlations"; Miller, 1956) at both lower and higher order levels in a putative hierarchy of sensorimotor control (cf., Barceló & Knight, 2007; Barceló et al., 2008).

Information theory allows us to assign task properties binary digit values or bits (Attneave, 1959; Cooper, Garrett, Rennie, Karayanidis, 2015). In this way, S-R contingencies can be ascribed an information value, permitting simple contrasts between tasks. Information theory allows us to gauge cognitive demands associated with dissimilar stimulus and response sets, and distinct S-R mappings in order to predict the intensity and scalp topography of ERP positivities across different task domains. For instance, Barceló et al. (2008) relied on information theory estimates to demonstrate the distinct functional roles of cue-locked (i.e., context) P3 and target P3 potentials elicited by the same sequence of red and blue shapes

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interspersed with infrequent black symbols administered under oddball, go/nogo and taskcueing instructions. These authors found similar frontocentral scalp topographies -albeit with different magnitudes- for context-related P3s and switch positivities to the infrequent black symbols, consistent with their information estimates. In sharp contrast, target P3 amplitudes were not modulated by task demands, and showed similar midparietal amplitudes and topographies across all task contexts. Thereby, hereafter we will adopt the term "context P3" to describe positivities elicited by infrequent grey Gabor gratings that are predicted to index context-updating operations proactively, in anticipation to target onset, and regardless of the task context. Conversely, we will adopt the term "target P3" to describe ERP positivities elicited by temporally predictable colored gratings thought to recruit mostly reactive target detection, without the temporal unpredictability of *oddball targets*. Finally, we circumvent limitations of an earlier study (Barceló et al., 2008) by using a within-subject task design, larger sample sizes, and surface Laplacian values to minimize volume conduction of scalp potentials.

In sum, this study aimed to examine the similarities and differences in the intensities and scalp distribution of domain-general P3 (300-400 ms) and switch-related (300-900 ms)¹ ERP positivities while participants were intermittently cued to switch or repeat their categorization of Gabor gratings varying in color and thickness (switch task). Two perceptually identical tasks served as controls with varying cognitive and response demands (go/nogo and oddball). Following the discussion above, we addressed one important question: are switch positivities topographically similar and functionally compatible with a context-updating mechanism akin to that proposed for the canonical P3 component recorded in simpler oddball and go/nogo tasks? This question was addressed by testing two specific hypotheses: (1) If the *temporal context* of goal directed actions (i.e., proactive strategic preparation versus reactive execution of a simple visuomotor rule) modulates the frontoparietal scalp distribution of late P3-like positivities, then more frontal positivities will be elicited during proactive preparation (e.g.,

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higher-order rule updating) than during lower-order sensorimotor control of reactive rule execution at target onset (Barceló et al., 2008; Braver, 2012). (2) If the parametric increase in cognitive demands posed by three different task contexts (oddball, go/nogo, switch) modulates the frontoparietal distribution and magnitude of late P3-like positivities, then gradually more frontal positivities will be elicited with gradually higher cognitive demands, in line with predictions from an information theory model of cognitive control (Koechlin & Summerfield, 2007). These two predictions relied on the hypothetical contribution from a common frontoparietal "multiple demand" system (Duncan, 2013) to both domain-general P3 and switch P3-like positivities. To test these two hypotheses, we recorded P3 potentials to oddball and go/nogo Gabor gratings and compared their scalp distributions with switch P3-like potentials to identical stimuli delivered under switch task conditions. To favor integration with the extant literature, we analyzed mean amplitudes and surface Laplacian values from four midline regions (frontopolar, frontal, central and parietal), under the assumption that distinct scalp topographies and functional dissociations to experimental factors characterize distinct ERP components (Kappenman & Luck, 2012). For simplicity, we modeled sensorimotor information transmission only at two levels in the putative hierarchy of cognitive control, namely, low-level sensorimotor control (i.e., changes in single S-R pathways), and higher-order episodic control of task rule retrieval and updating (Dayan, 2007; see Supplementary material).

Methods

Participants

Thirty-one participants (25 female, mean= 21.8, \pm 2.7 years) took part in the current study and received course credit for their collaboration. All were graduate or postgraduate students at the University of the Balearic Islands with normal or corrected-to normal vision and reported no history of neurological or psychiatric disorders. Informed consent was obtained from all

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participants and experimental procedures and behavioral testing was performed in accordance with the Declaration of Helsinki, and the approval of the Ethics committee of the university.

Stimulus Materials and Procedures

Participants sat in a sound attenuated and dimly lit room at a viewing distance of 150 cm from a 27-inch video LCD monitor (800 x 600 at 75 Hz). Stimuli were displayed against a grey background (2.85 cd/m²) at a visual angle of 6.5° to the left or right of a central fixation cross with 0.5° x 0.5° of visual angle². A central fixation cross remained continuously present throughout each experimental run. Stimuli consisted of four equally probable (p = 0.21), colored Gabor gratings with horizontally oriented gratings (either red or blue, 4 or 10 cpd, 25% contrast, 1° visual angle, 3.5 cd/m²), and two infrequent (p = 0.08) grey Gabor gratings (oriented either vertically or horizontally, 2 cpd, 25% contrast, 1° visual angle, 3.5 cd/m²). Participants responded via a hand-held response pad with their left or right index fingers.

The experimental procedures have been described elsewhere (Cooper, Darriba, Karayanidis & Barceló, 2016), and consisted of three different tasks: *switch, go/nogo* and *oddball*, yoked for stimuli and trial sequences but involving different response and cognitive demands each (Fig. 1). A test sequence included 976 trials of colored and grey Gabor gratings that was semi-randomly generated offline, with the constraint that consecutive grey Gabors gratings were separated by four to eight colored gratings. This trial sequence was divided into eight blocks to allow for short self-paced breaks approximately every five minutes. Each trial consisted of a Gabor grating presented for 100 ms in the left or the right visual hemifield. On designated target trials, participants had to respond within a maximum of 1200 ms after stimulus onset. Instructions emphasized both response speed and accuracy. All error trials (i.e., incorrect, late responses and false alarms) were followed by visual feedback and the following trial was delayed by 500 ms to help subjects keep on task. Hence, stimulus onset asynchrony (SOA) was

 either 1900 or 2400 ms on correct and error trials, respectively. The present ERP analyses were based on correct trials only. The stimulus display and behavioral response recording were implemented using Presentation[®] software (Neurobehavioral Systems Inc., Albany, CA).

Each participant was presented with a unique pseudorandomly generated test sequence that was repeated three times under different task instructions for the oddball, go/nogo and switch tasks. Tasks were administered in counterbalanced order to control for inadvertent order effects. Thus, the three tasks involved an identical stimulus context but different cognitive and response demands (Fig. 1).

The *switch task* (Fig. 1A) was a variant of the intermittent-instruction paradigm (Monsell, 2003; Rushworth et al., 2002). The grey Gabor stimuli were cues, indicating whether to switch or repeat the task. The colored Gabor stimuli were targets and required a left or right hand response based on either the color (blue or red grating) or the grating's spatial frequency (thick or thin grating). Hence, the orientation of the grey grating (cue) instructed participants whether to switch or repeat the task they completed on the previous trial run. Grey grating orientations and instructions were counterbalanced between participants. A short training session was administered to ensure that participants reached a criterion of 80% correct responses and had understood task instructions.

The *go/nogo task* (Fig. 1B) served as a control for the switch task. It involved an identical stimulus sequence and again participants responded only to the colored Gabors. However, importantly, here the grey Gabors had no predictive significance regarding the task to be performed, but set the temporal context for the next target onset. Rather they were defined as nogo stimuli and participants were asked to withhold their response while implementing color classifications across the entire block of trials. In essence, this task is similar to a single-

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task block. In sum, the go/nogo task involved sorting Gabors by their color, an identical stimulus sequence and similar S-R mappings as the switching task.

The *oddball task* (Fig. 1C) served as a control for both switch and go/nogo tasks, having an identical stimulus context but with different response demands. Specifically, a response was required only to red Gabor gratings, which were defined as oddball targets. All other stimuli did not require a motor response. This oddball task was inspired on regular novelty oddball tasks (Barceló & Knight, 2007), except that all targets, standard and rare distracters included an additional irrelevant stimulus dimension (e.g., thickness of gratings).

Insert Figure 1 around here

Information Theory Estimations

We adopted an information theory approach to cognitive control as a formal tool to help us operationalize both temporal and task *contexts* in terms of low- and high-order sensorimotor (S-R) information transmission within a putative hierarchy of fronto-parietal control processes (cf., Barceló & Knight, 2007; Cooper et al., 2016). These estimates allowed us to define the informational structure of our tasks in terms of, not only mean stimulus probabilities, but also joint and conditional probabilities among stimuli, their associated motor responses, and any relevant cognitive operations involved (e.g., rule updating). Thus, the task context was modeled at two hierarchically distinct levels: (1) low-level sensorimotor control of single s-r pathways, and (2) higher order episodic control of task rule updating (Dayan, 2007; Koechlin & Summerfield, 2007). The temporal context was separately modeled for infrequent grey Gabors and for the relatively more frequent colored Gabors. Thus, while infrequent grey Gabors were visually identical in all tasks, and appeared with identical probability, the type of information provided varied. Oddball grey Gabors transmitted the lowest sensorimotor information for

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response selection (as they did not anticipate target onset on the following trial), and no episodic information given that the same task rule was used for all Oddball targets and nontarget distractors. Alternatively, increased sensorimotor information was conveyed by nogo grey Gabors as these stimuli were associated with less frequent nogo responses (r_0) compared to the Oddball task, and they did anticipate target onset on the next trial. As with grey Gabors in the oddball task, no episodic information can be assumed for nogo grey Gabors given that the same task rule was consistently used across all trials. Finally, similar sensorimotor information was transmitted by all grey Gabors in the Switch task, plus an additional amount of episodic information was transmitted only by 'switch' grey Gabors, as these served as cues requiring anticipatory updating of episodic task rules. Note that these information estimates can be seen as a more formal and accurate way to translate into bits the mean probabilities of task events that are common practice in experimental psychology studies. Yet bits provide a common metric to compare our manipulation of context across different task domains. For instance, instead of saying that a grey Gabor distractor occurs with an overall mean probability of p = 0.08 throughout our Oddball task, we chose to quantify this in bits by saying that the sensory entropy of this distractor is: $H(s_1) = -0.08 \cdot \log_2 0.08 = 0.29$ bits (cf., x-axis of Fig. 2). A similar formalism was used to quantify in bits the relative probabilities of specific sensorimotor processes, such as the joint probability of specific s_i - r_i mappings using the concept of transmitted information: $I(s_i, r_i) = \log_2 p(s_i, r_i) - \log_2 p(s_i) - \log_2 p(r_2)$. For simplicity, additional sources of contextual information (i.e., stimulus-response congruency effects, stimulus repetition effects, etc.) were randomized and not modeled in these estimates. Fig. 2 presents a summary of these information estimations, in line with the two specific predictions of our study; for a technical description see Supplementary material and Cooper et al. (2016).

Insert Figure 2 around here

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Behavioral Analyses

Reaction times (RTs) are reported from correct trial runs only, while trial runs containing any false alarm, omission, or other errors were discarded. Errors were used to compute accuracy indexes. Only the first three target trials following a grey grating entered the analyses, since behavioral costs typically reach an asymptote in later trials (Monsell, 2003). Restart costs were defined as the difference in mean RTs and errors between the first and second target responses following any grey grating. Equivalent indices were obtained for the two control tasks. Mixing costs were estimated for the switch task only as the difference in mean RTs and errors between third target responses in the switch vs. go/nogo tasks. Third targets provided a relatively pure index of mixing costs independent from restart costs. Finally, although we did not expect to find switch-specific behavioral costs due to our long cue-to-target intervals (cf., Foxe, Murphy, & De Sanctis, 2014), local switch costs were also computed as the difference in mean RTs and errors between first target responses after switch versus repeat cues. Only color-rule trials were considered in the behavioral analyses of switch trials, to limit any task switch asymmetries. Mean RTs and percentage error trials were subjected to repeatedmeasures analysis of variance (ANOVA) with the following factors: Grey grating (vertical vs. horizontal), Target trial (1st, 2nd, 3rd target in the trial run), and Task context (oddball, go/nogo, switch). All participants had an overall hit rate better than 89% in the switch task, with at least 60% correct trial runs to the initial three targets following any grey Gabor (cf., Cooper et al., 2016). These strict selection criteria were meant to avoid posterror slowing effects, and ensured that participants had complied with task instructions.

EEG Recordings and ERP Analyses

Continuous EEG data (0.05–100 Hz bandpass) were collected using SynAmps RT amplifiers (NeuroScan, TX, USA) from 60 scalp sites using tin electrodes mounted on an elastic cap (Synamp2 Quikcap, Compumedics, TX) at a sampling rate of 500 Hz. EEG electrodes were

placed following the extended 10–20 position system with a left mastoid reference, and later re-referenced offline to the algebraic average of the right and left mastoids. Four additional electrodes were placed above and below the left eye and on the outer canthi of both eyes to monitor blinks and eye movements. Sensor impedances were kept below 10 k Ω , as in Cooper et al. (2016).

EEG data were processed using MATLAB (Mathworks, Navick, MA) through a pipeline utilizing EEGLab (Delorme & Makeig, 2004), CSD Toolbox (Kayser & Tenke, 2003), and in-house functions. Preprocessing was performed in EEGLab as follows. EEG data were re-referenced offline to linked mastoids and band-pass filtered (0.1 - 30 Hz). Epochs for each stimulus type were extracted from -200 ms to +1200 ms relative to stimulus onset, with a 200 ms prestimulus baseline. Trials with non-stereotyped artifacts (e.g., cable movement, swallowing) were removed, and stereotyped artifacts (e.g., blinks, eye movements) were deleted using independent components analysis (extended infomax algorithm; Bell & Sejnowski, 1995). Note, only color-rule trials were considered for analysis of switch trials (to limit any influence of task asymmetries relative to the control tasks), which resulted in an average of $142.8 (\pm 9.6)$ SD) grey distractor, 73.5 (\pm 4.9) target 1, and 75.3 (\pm 5.4) target 3 trials for oddball; 126 (\pm 16) nogo, 130 (\pm 16) target 1 and 122.2 (\pm 15.6) target 3 go trials for go/nogo; and 28.4 (\pm 4.6) repeat cues, $30.7 (\pm 4.8)$ repeat target 1 and $30.9 (\pm 4.8)$ repeat target 3 trials; $31.4 (\pm 3.7)$ switch cues, $31.1 (\pm 3.7)$ switch target 1 and $31.2 (\pm 3.6)$ switch target 3 trials for the switch task. This same dataset was employed to examine EEG oscillatory dynamics of task-switching in the same sample of young participants (cf., Cooper et al., 2016).

Neighboring electrodes were combined into topographical ROIs (frontopolar: including Fp1, Fpz, Fp2; frontal: F1, Fz, F2; central: C1, Cz, C2; and parietal: P1, Pz, P2) to preserve statistical power (Picton et al., 2000). Time windows for ERP analyses were selected based on visual

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inspection of the corresponding grand mean waveforms. Two groups of ERP measures were obtained: context-locked and target-locked; based on the assumption that grey gratings provided the temporal context for subsequent target detection. Thus, five distinct ERP components were measured and analyzed in the context-locked waveforms: P3 (350-400 ms), two windows of a late positive complex (LPC₁: 550-600 ms, LPC₂: 750-850 ms), and a frontally distributed slow negativity towards the end of the recording epoch (contingent negative variation, CNV; 1000-1200 ms). In the target-locked waveforms, maximal signal amplitudes were observed at one latency window: P3 (350-400 ms), and only for the first target following any grey grating, two more latency windows captured a sustained positivity starting around 300 ms post-target onset and lasting to the end of the epoch (SP₁: 550-600 ms and SP₂: 750-850 ms; see Figure 4). The latency of P300 potentials is known to vary with task complexity (Kappenman & Luck, 2012; Kutas et al., 1977), and hence, switch positivities were examined using a wider (300-900 ms) latency window. Accordingly, our distinction between domaingeneral P3 and switch positivities relied on their distinct scalp topographies and sensitivity to experimental factors, rather than on any differences in peak latencies.

Mean ERP amplitudes were analyzed using repeated-measures analysis of variance (ANOVA) to examine our manipulation of *temporal* and *task contexts* on domain-general P3s –common to all tasks while uninfluenced by task switching demands- and switch positivities. Firstly, a Temporal context (grey grating, target3) factor examined differences in P3-like amplitudes between infrequent and temporally unpredictable grey gratings, and temporally predictable third targets following those grey gratings. Secondly, and given the highly different P3-like task effects observed for grey gratings (i.e., context P3) and third targets (i.e., target P3), the Task context factor was tested separately for context-locked and target-locked ERP waveforms. Thus, context-locked ERP waveforms were analyzed considering the following within-subject factors: Task context (switch, go/nogo, oddball), Grey grating (vertical, horizontal), and ROI

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(frontopolar, frontal, central, parietal). Target-locked ERP waveforms were analyzed with the within-subject factors: Task context (switch, go/nogo, oddball), Grey grating (vertical, horizontal), Target trial (target1, target3), and ROI (frontopolar, frontal, central, parietal). The Greenhouse-Geisser sphericity correction was applied as needed. Corrected *p* values are reported, but original degrees of freedom are kept for easier reading. A significance level of *p* < 0.05 was adopted for all main statistical analyses, and a Bonferroni-corrected threshold (0.05/4= *p* < 0.0125) was used for multiple tests at the four midline regions.

Analyses of ERP Scalp Topographies

As in many past studies (Polich & Comerchero, 2003; Squires et al., 1975), to assess the effects of temporal and task contexts on ERP positivities, we examined the scalp distribution of mean amplitudes across four midline regions (frontopolar, frontal, central, parietal), two temporal contexts (grey grating, target3) and three task contexts (switch, go/nogo, oddball). Further, to identify switch P3-like positivities as distinct from domain-general P3, we looked for significant interactions with the Grey grating factor (switch vs. repeat) in the switch task only. Next, to address our first and second hypotheses, we examined changes in the scalp distribution of domain-general P3 across the three task contexts, as well as for the two temporal contexts, namely, for proactive (grey gratings) and reactive (target3) processing modes, respectively. Accordingly, answers to our first and second hypotheses were addressed by looking for significant ANOVA interactions between the ROI factor and the Temporal and Task context factors, respectively. Further, we specifically tested the null hypothesis of similar scalp distributions for switch positivities and domain-general P3 by examining the interaction between ROI x ERP component in the switch task only. To minimize the effects of volume conduction on the analyses of scalp topographies and favor integration with past studies, data were also compared by using a surface Laplacian filter (smoothing = 10-5, number of iterations = 10, spherical spline order = 4; Kayser & Tenke, 2006; Urbach & Kutas, 2002).

Results

Behavioral Results

All three tasks were performed very efficiently, with an average of only 6.3% incorrect trials in the switch task (95% CI [5.1, 7.4]), 4.5% in the go/nogo (95% CI [3.5, 5.5]), and 0.4% in the oddball (95% CI [0.3, 0.5]). A main effect of Task ($F(2, 60) = 47.6, p < 0.0001; GG = 0.83; \eta^2 =$ 0.61), confirmed differences in overall error rates among all three tasks (all *p*'s< 0.001; Fig. 3A). Accuracy did not vary across target trials in the oddball, but larger error rates were observed in first relative to second target trials following any grey gratings in both switch and go/nogo tasks (all *p*'s< 0.001), with no further differences between second and third target trials, as revealed by a 2-way interaction between Task and Target trial (F(2, 120) = 5.1, p < 0.003; GG =0.73; $\eta^2 = 0.15$). The 3-way interaction with Grey grating was marginally significant (F(4, 120) =2.72, *p* = 0.08; *GG* = 0.52; $\eta^2 = 0.08$), pointing to significantly greater error rates to the first target trial following 'switch' compared to 'repeat' grey gratings in the switch task only (9.5% vs. 6.5% errors respectively, *p* < 0.02), which thus confirmed the presence of local, restart and mixing costs for accuracy data in the switch task. No other effects reached significance.

The speed of correct target responses differed among all tasks (p's< 0.001; Fig 3B), as revealed by a main Task context effect (F(2, 60) = 99.9, p< 0.0001; GG= 0.76; η^2 = 0.77). A 2-way interaction between Task context and Target trial (F(4, 120) = 17.8, p< 0.0001; GG= 0.59; η^2 = 0.37) revealed the presence of restart costs in the switch and go/nogo tasks, both showing slower responses to the first than the second or third targets (all p's< 0.001), without any further slowing observed between the two latter trials. In contrast, the oddball task did not show any first trial slowing. Mixing costs were inferred from the larger mean RTs to third target trials in the switch compared to both control tasks (all p's< 0.001; Fig. 3B). The third order interaction with Grey grating failed to reach significance, suggesting the absence of local

switch costs in the mean RTs to correct first target trials in the switch task, an expected outcome given our long 1900 ms cue-target intervals (cf., Foxe et al., 2014).

Insert Figure 3 around here

Electrophysiological Results

 Fig. 4 summarizes the grand ERP waveforms over midfrontal and midparietal regions to grey gratings, and to the first (target1) and third (target3) target trials across all tasks. Since ERPs to second target trials (not shown) present an intermediate stage, analyses focused on first and third target trials to maximize trial differences. Through visual inspection, three distinct ERP positivities could be identified in the context-locked ERP waveforms of the switch task, showing maximal amplitudes over centroparietal regions: P3 (350-400 ms), LPC₁ (550-600 ms), and LPC₂ (750-850 ms). These two aspects of the LPC best captured switch-related contextual effects. Finally, a sustained frontally distributed CNV-like negativity extended from circa 800 ms until the onset of the first target stimulus. A target P3 (350-400 ms) was present in the target-locked waveforms, with similar amplitudes and centroparietal scalp distribution across all three task contexts, as shown in Figs. 4 and 5. In addition, a sustained positivity (SP) starting 300 ms post-target onset and lasting until the end of the recording epoch was observed to target1 in the switch and -to a lesser extent– also the go/nogo tasks. Modulations of these context- and target-locked ERP waveforms are described below. The visual P1 and N1 were not modulated by task conditions, and will not be discussed further.

Context Effects on Domain-General P3s

Two domain-general P3s with 350-400 ms peak latencies were present across all three tasks (labeled as "context P3" and "target P3" in Figs. 4 & 5), and their mean amplitudes were not modulated by the Grey grating factor in any of the three tasks. Instead, as reported below,

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these two P3s showed distinct scalp topographies and were differently modulated by temporal and task contexts, which justifies their consideration as two distinct P3 components.

As predicted by our model, both the temporal and task contexts modulated the intensity and scalp topography of domain-general P3s, as reflected by significant Temporal context x Task context (F(2, 60)= 17.6, p< 0.0001; GG= 0.86; η^2 = 0.37) and Temporal context x Task context x ROI interactions (F(6, 180)= 35.5, p< 0.0001; GG= 0.53; η^2 = 0.54). Given the very different P3-like modulations elicited by grey gratings and colored targets, Table 1 presents the relevant ANOVA results separately for context P3 and target3 P3. Firstly, increasing task demands elicited larger context P3 amplitudes, as revealed by a main Task effect. Follow-up contrasts revealed a larger context P3 for the switch as compared to the other two tasks (all p's< 0.005), with no such differences between oddball and go/nogo tasks (Figs. 4, 5A). A Task context x ROI interaction revealed that these larger context P3 amplitudes in the switch compared to the other two tasks occurred only at central and parietal regions (all p's< 0.01; Figs. 4, 5A & 6A,C left panels). In sharp contrast, mean target3 P3 amplitudes were larger in the oddball compared to the other two tasks, and only at the parietal region (p's< 0.005), as revealed by a significant Task context x ROI interaction (see Table 1; Figs. 4, 5C & 6B,D).

Secondly, the significant interaction between Temporal context and Task context was further examined by comparing mean amplitudes of context P3 and target3 P3 in each task domain separately. Significantly larger target3 P3 than context P3 mean amplitudes were observed in the oddball and go/nogo tasks (main Temporal context effect: F(1, 30)=46.1, p<0.0001; $\eta^2=$ 0.61, and F(1, 30)=7.7, p<0.01; $\eta^2=0.20$, respectively), with differences at central and parietal regions (Temporal context x ROI: F's(3, 90)>30.4, p's<0.0001; $\eta^{2'}s>0.52$). In contrast, the Temporal context x ROI interaction failed significance in the switch task (F(3, 90)=1.4, p=0.24), suggesting no differences in mean P3 amplitudes elicited by grey gratings and third targets

trials in the switch task (Figs. 6B, A left panel). This pattern of results was confirmed with surface Laplacian values (Table 1; Figs. 6C, D left panel), which attest to different topographies with varying task demands for both context P3 and target3 P3. Thus, whereas target3 P3 showed a centroparietal maximum under the simplest oddball task, context P3 to the grey gratings showed maximal frontal intensities under the most difficult switch task (Fig. 4).

Of note, mean target P3 amplitudes differed for target1 versus target3 trials, as suggested by a main Trial effect (F(1, 30) = 10.4, p < 0.003; $\eta^2 = 0.26$), but this was true only in the switch task, as revealed by a 2-way Task context x Target trial interaction (F(2, 60) = 6.8, p < 0.003; GG = 0.86; $\eta^2 = 0.18$). Simple tests of effects revealed that neither oddball nor go/nogo target P3 amplitudes changed from first to third target trials (see Figs. 4 and 5C). In contrast, target1 P3 in the switch task was larger than target3 P3 across all midline regions (all p's< 0.005), owing to an overlapping slow positivity as described below.

Context Effects on Switch P3-like Positivities

The Grey grating factor yielded significant main effects and 3-way interactions with Task context and ROI for context-locked LPC₁ (*F*(6, 180) = 9.5, *p*< 0.0001; *GG*= 0.39; η^2 = 0.24) and LPC₂ positivities (*F*(6, 180) = 24.3, *p*< 0.0001; *GG*= 0.38; η^2 = 0.45), as well as for the sustained positivity (SP) to the first target following a switch cue (*F*'s(1, 30) > 10.7, *p*'s< 0.003; $\eta^{2'}$ s > 0.26). In all cases, LPC₁ and LPC₂ amplitudes in the switch task were larger for switch than for repeat grey gratings over midcentral and midparietal regions (all *p*'s< 0.01; Fig. 7A), whereas only LPC₁ also differed among grey gratings over frontopolar and frontal regions (all *p*'s< 0.02; Figs. 4, 5 & 7A). Mean amplitudes for the sustained positivity (SP₁ and SP₂) to target1 were largest for switch grey gratings across all midline regions (Figs. 4, 5B & 7B). This effect was present already in the latency window of target1 P3 (Grey grating main effect: *F*(1, 30) = 11.5,

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 p< 0.002; η^2 = 0.28), with differences at frontal, central and parietal regions (all p's< 0.005; interaction Grey grating x ROI: F(3, 90) = 3.5, p< 0.04; $\eta^2 = 0.11$).

In sum, two distinct switch-related positivities were apparent: a context-locked late positive complex (500-850 ms; described as a "switch positivity" by Karayanidis et al., 2009), and a sustained slow positivity (300-1200 ms) elicited by the first target (target1) following a switch cue (cf., Barceló et al., 2008).

Insert Table 1 around here

Insert Figure 4 around here

Insert Figure 5 around here

Scalp Topography of Domain-General P3s vs. Switch Positivities

The main question of this study specifically required testing the null hypothesis of similar scalp distributions of switch positivities and domain-general P3s, as indicated by the absence of an interaction between ROI x ERP component. Thus, differences in the midline scalp distribution of P3-like amplitudes and Laplacian values were examined in response to "switch" grey gratings (Table 2, Figs. 7A,C) and first switch target trials (Table 3, Figs. 7B,D).

Firstly, significant differences in midline topographies of context P3 and two aspects of a late positive complex (LPC) to the switch cues were revealed by 2-way interactions between ERP and ROI for mean amplitudes and surface Laplacian values (Table 2; Figs. 7A,C). Follow-up tests of effects revealed different topographies for P3 and LPC₁ (amplitudes: P3< LPC₁ at all sites, all p's <0.002, Fig. 7A; Laplacian: P3> LPC₁ at frontal; P3< LPC₁ at central and parietal, all p's <0.005; Fig. 7C). Likewise, scalp topographies differed between P3 and LPC₂ (amplitudes: P3> LPC₂ at all ROIs; all p's <0.004, Fig. 7A; Laplacian: P3> LPC₂ at frontal, p <0.002, Fig. 7C).

Secondly, the scalp topography of target1 P3 and the early SP₁ and late SP₂ aspects of a slow positivity to first switch targets also differed as revealed by 2-way interactions between ERP and ROI for mean amplitudes and surface Laplacian values (Table 3; Figs. 7B,D). Simple tests of effects showed different topographies between target1 P3 and SP₁ (amplitudes: P3> SP₁ at all ROIs; all *p*'s <0.02, Fig. 7B; Laplacian: P3< SP₁ at frontopolar and P3> SP₁ at frontal; *p*'s <0.001, Fig. 7D). Topographies of target1 P3 and SP₂ differed for mean amplitudes: P3> SP₂ at frontal, central and parietal (all *p*'s <0.002, Fig. 7B), but not for Laplacian values (Table 3; Fig. 7D).

In sum, these analyses of scalp topographies resulted in significant ERP x ROI interactions when comparing domain-general P3s in the switch task with two switch P3-like positivities identified in the preceding analyses (Tables 2 and 3). These analyses failed to support the null hypothesis, thus disconfirming our original visual impression of apparently similar scalp topographies for switch P3-like and domain-general P3 potentials in the switch task (cf., Figs. 4 & 5). On the contrary, these analyses suggested significant –albeit subtle– split-second changes in the disposition of frontoparietal sources with varying contextual and task demands (see Fig. 7; cf., Kappenman & Luck, 2012; Urbach & Kutas, 2002).

Insert Tables 2 and 3 around here

Insert Figure 6 around here

Insert Figure 7 around here

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Linear Regression Analyses

Finally, to further assess the reliability of our model's predictions, we performed linear regression analyses using mean P3 and P3-like amplitudes from midfrontal and midparietal ROIs as criteria; predictors were the values of transmitted sensorimotor (S-R) information estimated for the six Gabor gratings used in each task (Fig. 2; see Table s7 in Supplementary material). Given the very distinct P3-like modulations elicited by grey gratings and colored targets, regression analyses were performed separately for either temporal context. For a more sensitive analysis of this linear association, the same regression analyses were run separately for each subject, and t-tests were used to examine whether the standardized (beta) regression weights averaged across all participants differed significantly from zero. The significance of mean beta regression weights across subjects is provided in brackets next to R² coefficients for the grand ERP averages. For the grey gratings, a direct association was found between increasing information and midparietal amplitudes for context P3 (R^2 = .664, p= .05; Fig. 8A) [beta= .49, t(30)= 6.12; p= .0001)], and context LPC₁ ($R^2= .881$, p= .008; Fig. 8A) [beta= .73, t(30) = 11.8; p = .0001], and midfrontal amplitudes for context LPC₁ ($R^2 = .920$, p = .002; not shown) [beta= .40, t(30)= 3.8; p= .01)]. Of note, mean context LPC₂ amplitudes were not predicted by sensorimotor information neither at parietal (R^2 = .473, p = .13; Fig. 8A) [although this reached significance across subjects: beta = .34, t(30) = 3.7; p = .01], nor frontal regions ($R^2 =$.524, p = .104) [beta = .14, t(30) = -1.39; p = .096)], reflecting that this switch P3-like component was present in the switch task only (cf., Figs. 2 and 8A). For the targets, an inverse relationship was apparent between increasing sensorimotor information and smaller target P3 amplitudes, although this did not reach significance neither at parietal (R^2 = .284, p = .28; Fig. 8B) [beta = -.09, t(30) = -.82; p = .42], nor frontal regions ($R^2 = .445, p = .14$) [beta = .09, t(30) = .83; p = .41]. This is consistent with our model's predictions (Fig. 2) in that the strongest modulations of P3like positivities across tasks were linked to the processing of unexpected grey gratings rather than to target detection per se (cf., Posner & Petersen, 1990).

Insert Figure 8 around here

Discussion

This study addressed one important question for a theoretical integration of past P300 research on the hypothesis of context-updating (Donchin, 1981) with newer ERP studies on the cognitive control of task-switching, as hypothetically regulated by a common frontoparietal network of cortical regions. Our results provide new evidence about our main research question, and two ancillary hypotheses about the relationship between domain-general P3s and switch P3-like positivities. Firstly, the results clearly support that switch positivities are functionally distinct from P3s recorded in simple oddball and go/nogo tasks, including subtle – albeit significant– changes in scalp topography. Secondly, our results support the hypothesis that the temporal context (i.e., proactive preparation versus reactive execution of visuomotor rules) was a crucial determinant of the scalp distribution of both domain-general P3s and switch positivities. Finally, results also lent support to our second hypothesis that gradually larger frontoparietal P3-like positivities were elicited under higher cognitive demands, but only for those P3-like potentials elicited by temporarily surprising events that proactively prompted for future rule execution (Cooper et al., 2016; Kopp & Lange, 2013; Verleger et al., 2014).

These findings suggest that the present switch positivities are compatible with two types of context-updating mechanisms as defined by a model of cognitive control based on information theory: the updating of low-level sensorimotor S-R pathways (a domain-general mechanism common to many tasks), and the updating of higher-order task rules from episodic memory. When considered alongside domain-general P3s, the current results are compatible with the hypothesis of switch positivities as part of an extended P300 family of late positive potentials,

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and also as plausible neural indexes of a multiple demand system (Duncan, 2013) of frontoparietal generators being rapidly engaged under varying contextual demands. These findings carry far-reaching implications for a redefinition of "the P300" component in terms of an extended family of late P3-like positivities involved in cognitive control.

Two Domain-General P3s Index Distinct Proactive and Reactive Control Modes

The present analyses identified two functionally distinct domain-general P3s: one contextlocked P3 (350-400 ms) and one target-locked P3 (350-400 ms). These two ERP positivities were examined in its simplest form in response to the infrequent grey gratings and target gratings in the oddball task, respectively; although they were also clearly apparent in the go/nogo and switch tasks. These two domain-general P3s fit well with the two aspects of conventional P300 potentials, namely, an anterior P3a to rare distracters, and a target P3b with its characteristic midparietal scalp distribution (Polich, 2007). However, these P3-like modulations cannot be explained by the updating of stimulus features alone, but are better accounted for in terms of sensorimotor S-R links and amount of task-set information held in memory while upholding, preparing, or executing goal-directed actions (Verleger et al., 2014). Mean amplitudes and surface Laplacian values of context P3 and target3 P3 were differently modulated by increasing task demands (Fig. 4, 5, 6A,B). This is consistent with the extant literature that describes two functionally and topographically distinct P300 aspects, namely, novelty P3a and target P3b (Spencer et al., 1999; Squires et al., 1975), only that our formal operationalization of both temporal and task contexts allowed us a much richer and finergrained functional characterization beyond the conventional "ignore" vs. "attend" dichotomy.

Critically, third target trials elicited very similar ERP waveforms across all tasks, a paradoxical outcome given the intuitive differences in task difficulty also supported by behavioral results. However, this outcome concurs with our model's prediction that, on average, target gratings

transmitted similar amounts of sensorimotor information for response selection in all three tasks (Fig. 2). The only reliable difference affected mean target3 P3 amplitudes parietally, which were largest in the simplest oddball task. This effect is consistent with the reduced target P3b observed in relatively more complex tasks (Donchin, 1981), and is also compatible with carryover interference from competing S-R mappings that may result in reduced mean P3b amplitudes several trials after a task transition (Barceló et al., 2002). These findings suggest that target P3b –when disentangled from temporal unpredictability (*oddballness*)– reflects one type of reactive control shared across many task domains, such as the execution of simple s_i-r_i pathways (i.e., press a button to designated targets; cf., Verleger et al., 2014).

The model accurately predicted contextual effects upon mean P3 amplitudes to the grey gratings (hence described as "context P3") that were mostly sensitive to task differences in cognitive demands. Overall, context P3 showed a relatively more frontal scalp distribution for oddball grey gratings, and a relatively more parietal distribution for the most informative switch grey gratings. One critical aspect that might account for the functional dissociation between context P3 and target3 P3 is the need to uphold a motor response to unpredictable onset of grey gratings within a context of infrequent 'nogo' responses in the go/nogo and switch tasks, which confer those stimuli with higher order sensorimotor information relative to the grey gratings in the oddball task (cf., Verleger et al., 2014; see Supplementary material). Importantly, stimulus *oddballness* alone (i.e., the temporal unpredictability of grey gratings relative to the more predictable colored target gratings) cannot explain the present results. Instead, context P3 amplitudes captured the *oddballness* of specific S-R links involved in the strategic resolution of contextual uncertainty, as formally estimated in terms of low- and high-level sensorimotor control (Verleger et al., 2014). This contextual predictability hypothesis would agree with evidence that infrequent and unexpected distracters convey large amounts

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of information that may overshoot working memory capacity, thus eliciting novelty P3a with a more anterior scalp distribution (Barceló et al., 2006; cf., Kopp & Lange, 2013).

In sum, target3 P3 potentials suggest similar reactive control processes across all task domains, whereas switch positivities overlaying context P3 and target1 P3 potentials hint at distinct proactive and early reactive control operations across tasks (Rubinstein, Meyer, & Evans, 2001). This functional dissociation is consistent with model's predictions, and with carry over effects due to the temporal contiguity between the highly informative grey gratings and the first targets, not only in the switch task (Monsell, 2003), but also in the simpler go/nogo task (Allport et al., 1994; Barceló et al., 2008).

A Late Positive Complex (LPC) Indexes Proactive Task Rule Updating

A late positive complex (LPC, circa 500-900 ms) with a centroparietal scalp distribution was elicited by grey gratings both in the go/nogo and switch tasks, and was sensitive to the spatial orientation of grey gratings (i.e., switch cues) in the switch task. Both the early LPC₁ and late LPC₂ aspects showed larger mean amplitudes for switch than repeat cues over centroparietal regions (Figs. 7A,C, central and right panels). In line with previous results from task-cueing paradigms, this effect may reflect higher-order context-updating operations, such as memory uploading of new S-R mappings in preparation for upcoming targets that need to be classified with new rules. This could be seen as one type of proactive control operation, presumably one requiring episodic memory retrieval of task rules (Dayan, 2007), consistent with our model's predictions (see Table s5). Topographic profiles of early LPC₁ and late LPC₂ showed larger intensities for switch than repeat cues over centroparietal regions (Fig. 7A, central and right panels). Further, subtle differences in the scalp topography of early LPC₁ and late LPC₂ pointed to their distinct roles in proactive rule updating. The early LPC₁ showed maximal frontal intensities in response to switch cues, with lesser centroparietal intensities for repeat and

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nogo grey gratings. In contrast, the late LPC₂ was elicited only by switch cues with a distinctly larger intensity over parietal regions, and a comparatively lesser frontal involvement (Figs. 4 & 7A,C, right panels). This functional and topographical dissociation portrays LPC₁ as a process shared by both task cues and nogo distracters (e.g., the stopping or inhibition of active s_i-r_j mappings), which is a prerequisite for subsequent rule updating, specifically indexed by the late LPC₂ aspect. Hence, LPC₁ cannot be regarded as a pure switch-specific positivity, given that it partly encoded lower-level sensorimotor control also shared by nogo and repeat grey gratings. All in all, LPC modulations matched well our information estimates for grey gratings in the switch and go/nogo tasks (Figs. 2 and 8; Table s7 in the Supplementary material), with an early LPC₁ aspect indexing a mixture of both low-level sensorimotor control and high-order task rule updating, followed by a late LPC₂ more specifically related to rule updating.

Switch LPC₁ and LPC₂ showed distinct scalp topographies, indicative of significant –albeit subtle– changes in the configuration of underlying sources relative to classic P3 potentials. In general, LPC amplitudes were larger over centroparietal regions with comparatively smaller intensities over frontal regions in the switch task. Towards the end of our long 1200 ms cuetarget interval, the switch LPC subsided and ERP waveforms for switch and repeat grey gratings did not differ over parietal regions (Fig. 4), which suggests that proactive rule updating was fully completed by the onset of the first target trial. This could explain the absence of local switch costs in the mean RTs of correct trials (cf., Kang, Diraddo, Logan, & Woodman, 2014), and it concurs with findings about a transient and short-lived signature of anticipatory task-set reconfiguration (Barceló et al., 2008; Kang, et al., 2014; Karayanidis et al., 2011; Lavric et al., 2008). Regression analyses suggested a positive association between the amount of transmitted sensorimotor information and mean LPC₁ amplitudes over frontal and parietal regions, with grey gratings that overshot memory capacity eliciting larger LPC₁ amplitudes over frontal regions (Fig. 8). This association might explain the presence of restart costs in first

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target trials following nogo distracters and repeat cues. In sum, these findings suggest contextlocked LPCs are a mixture of functionally distinct neural operations, probably reflecting higherorder context-updating operations (i.e., proactive rule updating) necessarily more complex to those indexed by conventional P300 potentials to rare oddballs.

A Sustained Positivity (SP) Indexes Early Reactive Task Rule Implementation

A slow positivity was elicited by first targets following any grey gratings in the switch and go/nogo tasks –but not in the oddball task (Fig. 4). This slow positivity was absent from third target trials, and has received little attention in past task-cueing studies. Two sources of evidence suggest that the slow positivity to first targets may reflect carryover of residual interference from the previous grey grating. Firstly, the slow positivity was observed only in first targets ensuing highly informative grey gratings, and those which overshot the theoretical human capacity for holding information in memory (2.5 bits in Fig. 2; Miller, 1956). Secondly, task differences in the amplitude of this slow positivity mimicked the information value and P3-like activity evoked by grey gratings (cf., Figs. 2, 4, 5B).

In the switch task, the sustained positivity probably reflects additional reactive control during the first implementation of a simple visuomotor rule (Rubinstein et al., 2001). The mean amplitude of the slow positivity to first targets was significantly larger following "switch" than "repeat" grey gratings, thus providing an electrophysiological index of local switch costs at target onset (Fig. 7B), even though this did not translate into significantly longer RTs to correct first targets after a switch cue, probably owing to our long cue-to-target intervals. Instead, the larger error rates observed following switch than repeat cues, suggest this slow positivity could somehow interfere with efficient rule execution on first target trials (Rubinstein et al., 2001). Further research will be needed to clarify this dissociation between behavioral and electrophysiological indexes of local switch costs.

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Finally, a large portion of residual behavioral costs, the mixing cost, was not captured by transient ERP waveforms to third target trials. Nevertheless, one might expect this mixing cost to be reflected in indexes of enduring neural activity sensitive to the overall amount of task-set information, $\Sigma(s_i r_j)$, held in working memory during the task. This post hoc hypothesis warrants further examination using further indices of sustained neural activity, as well as through a finer-grained parametrical manipulation of the total amount of task-set information.

Limitations and Future Challenges

There are a number of limitations in our attempt to model P3-like positivities from an information theory approach. Firstly, even though the largest differences in the amplitudes of context-locked ERP positivities appeared over centroparietal regions, our model predicted gradually more frontal activations with increasing task demands (Koechlin & Summerfield, 2007). However, this frontal displacement might be partly hidden by overlapping frontal negativities in our young adults (Fig. 4, upper row), which suggests that formal models need to take into account individual differences in age and behavioral efficiency. Instead our information estimates were done for an ideal subject with 100% correct responses, which is a good approximation given the high accuracy of our young participants in all tasks. Secondly, our information metrics did not consider some sources of contextual effects that may also modulate ERP positivities such as trial-by-trial perceptual and motor priming effects, or S-R spatial compatibility (Simon) effects. More fine-grained analyses are warranted to decide the contribution from additional contextual demands to those late ERP positivities. This aim could be achieved through a systematic parametrization of low- and higher-order sensorimotor control processes, for instance by varying the number of response alternatives, the number of task rules, or the entropy of stimuli and responses (Barceló & Knight, 2007; Barceló et al., 2008; Kopp & Lange, 2013). Thirdly, our long interstimulus intervals favored a temporal

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segregation of ERP positivities. However, shorter intervals will likely result in a greater overlap between domain-general P3s and switch P3-like positivities (Karayanidis et al., 2003; Lavric et al., 2008; Nicholson et al., 2005). Moreover, time constrains are a crucial determinant of behavioral costs (Monsell, 2003), and they should be incorporated in more sophisticated formal models of cognitive control. Finally, conventional analyses of mean amplitudes at the sensor space were preferred to favor integration with the extant literature. However, the relative implication of specific nodes within the frontoparietal network will require more sophisticated procedures for identification of underlying ERP components, such as source localization, time-frequency decomposition (Cooper et al., 2016; Kappenman & Luck, 2012) and independent component analyses (Enriquez-Geppert & Barceló, in press; Makeig et al., 1999).

Conclusions

The scalp topographies of two domain-general P3s (350-400 ms) differed significantly from the scalp topography of later switch P3-like positivities (500-900 ms) during both proactive and reactive control of task-switching. A strict interpretation of this outcome points to distinct configurations of underlying sources for conventional P300 potentials elicited by infrequent oddballs (Spencer et al., 1999; Squires et al., 1975), as compared to late P3-like potentials observed in task-switching (Barceló et al., 2006; Karayanidis et al., 2003). However, direct visual inspection of scalp topographies shown in Fig. 5 suggests all those P3-like positivities are still compatible with an extended family of P300 potentials with subtly distinct configuration of sources as a function of gradually more complex cognitive demands. Importantly, the largest modulations in this family of P300 potentials were observed during context-updating in response to temporarily surprising grey gratings and in anticipation to target onset (cf., Posner & Petersen, 1990; Petersen & Posner, 2012). After all, it would be reasonable that a putative

brain index of "context updating" engaged correspondingly more complex neural machinery to update higher order representations of task-set information (cf., Barceló & Knight, 2007).

In spite of fine-grained topographic differences with domain-general P3s, the observed switch positivities showed a centroparietal scalp distribution compatible with an extended family of P3-like potentials observed across many task domains (i.e., attention, memory, language, decision-making, etc). Indeed, switch positivities evoke a late positive complex (LPC) that has long been associated with the classic P300 in terms of its latency, centroparietal scalp distribution and response to experimental variables (Kappenman & Luck, 2012; Polich, 2007). In fact, few authors attempt a fine-grained topographical analysis to verify the nature of P300 potentials recorded in a variety of task domains (Holig & Berti, 2010). From this perspective, "the P300" cannot be regarded as a single ERP component -sensu strictu it has never been such a thing. Instead, it might well correspond with the electrophysiological signature of a multiple demand system for the integration of contextually relevant information in a wide variety of cognitive domains (cf., Duncan, 2013). The fronto-parietal scalp topography and intensity of this extended family of P3-like potentials critically depends on the temporal context for goal-directed behavior (i.e., proactive versus reactive control modes; Braver, 2012), as well as on a hierarchy of low- and higher-order sensorimotor demands that can be finely operationalized with more formal models of cognitive control (Koechlin & Summerfield, 2007).

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Author Notes

Acknowledgements: Supported by grants from Fundació La Marató de TV3 (112710) and Spanish Ministry of Economy and Competitiveness (MINECO PSI2013-44760-R) (FB). We thank Javier Villacampa, Rosa Martorell, Marcelina Chamielec, and Alvaro Darriba for their contribution to task programming, recruitment, data collection, and EEG signal pre-processing.

Conflict of interest: The authors declare no conflicts of interest, financial or otherwise, related to this work.

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Footnotes

¹ As clarified in the Method section, the distinction between domain-general and switchrelated P3-like positivities relied on their sensitivity to experimental factors (i.e., switch vs. repeat trials) and on their distinct scalp topographies. However, given the large variability in the latency of P300 potentials with task complexity (Kutas, McCarthy, & Donchin, 1977), latency was not regarded as a criterion to differentiate ERP positivities (Kappenman & Luck, 2012), and switch positivities were sampled from a wider (300-900 ms) latency window, consistent with previous task-switching studies.

² A bilateral display was intended to assess hemispatial attention deficits in unilateral brain lesioned patients (cf., Barceló & Knight, 2007). A pilot study showed this bilateral display did not modulate late switch ERP positivities relative to a more conventional central display.

Figure captions

Figure 1. Task design, stimulus material and S-R mappings. All three tasks consisted of the same sequence of frequent color gratings with semi-randomly interspersed infrequent grey gratings. (A) In the switch task, vertical and horizontal grey gratings instructed participants to switch and repeat the previous S-R mapping, respectively. (B) The go/nogo task consisted of two-forced choice responses ('press button 1 for red gratings, and button 2 for blue gratings'); and (C) the oddball task involved one-forced choice responses (i.e., 'press a button to all red gratings'). Participants were explicitly instructed not to respond to the grey Gabor gratings. Hypothetical task-set information and S-R mappings for correct performance are also shown for each task. Cognitive demands were manipulated by (1) varying the amount of task-set information to be handled in working memory (oddball vs. go/nogo task); and (2) by varying the type of contextual information conveyed by the grey gratings for anticipatory updating of active S-R mappings (go/nogo vs. switch task).

Figure 2. A priori estimations of transmitted information, $I(s_i, r_i)$, between stimuli and responses as a function of the sensory entropy, $H(s_i) = -p(s_i) \cdot \log_2 p(s_i)$, of grey and color gratings in the three tasks (or input-output correlations; c.f, Miller, 1956). The dotted line marks the theoretical human capacity for holding information in working memory: 2.5 bits. Accordingly, targets conveyed the same information for response selection across all tasks. In turn, grey gratings carried varying amounts of information for response selection in the oddball, go/nogo and switch tasks. The information transmitted from stimuli to responses is derived from the notion of mutual information, I(S; R), between the sets of stimuli, $S = \{s_1, s_2, s_3, s_5, s_6\}$, and associated responses, $R = \{r_0, r_1, r_2\}$, in our three tasks (cf., Attneave, 1959; Koechlin & Summerfield, 2007; see details in the Supplementary materials).

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Figure 3. Behavioral results. Mean reaction times (RTs) to correct target trials and error rates as a function of target trial position following a grey grating in each of the three tasks. Residual restart and mixing costs were observed in both correct (left panel) and incorrect trials (right panel). Local (switch > repeat) costs were observed to the first target in incorrect trials only (right panel).

Figure 4. Grand average ERPs. Brain responses are shown from midline frontal and parietal ROIs to vertical and horizontal grey gratings and to the first and third target gratings in the switch, go/nogo and oddball tasks. The second target trial following grey gratings (not shown) also elicited a sustained positivity of lesser intensity to that of first target trials. Continuous lines: Trial runs starting with a vertical grey grating. Dashed lines: trial runs starting with a horizontal grey grating. Note, the largest differences in the intensity of domain-general P3 and switch positivities occurred in response to grey gratings, as well as to the ensuing first target trials. In sharp contrast, task differences in mean amplitudes were less apparent in third target trials. Scalp topographies of mean amplitudes (μ V) and surface Laplacian values (μ V/cm²) are shown for switch trials at three latency windows: 350-400 ms, 550-600 ms, and 750-800 ms.

Figure 5. Scalp topography of domain-general P3 and switch P3-like positivities. (A) Scalp distribution of mean voltages for context-locked P3, LPC₁ and LPC₂ positivities to vertical and horizontal grey gratings across the three task domains. (B) Scalp distribution of target-locked P3, SP₁ and SP₂ positivities to first target (target1) trials following grey gratings in the switch task. (C) Scalp distribution of domain-general target P3 and LPC₁ positivities to third target (target3) trials across the three task domains.

Figure 6. Topographic profiles of domain-general P3 and switch positivities across three task domains. (A) Mean amplitudes of context P3 and the early (LPC₁) and late (LPC₂) aspects of a

late positive complex (LPC) in response to grey gratings under different task demands. (B) Mean amplitudes of target P3 in response to third target (target3) trials under different task demands. (C) and (D) present surface Laplacian values for the same conditions as in (A) and (B).

Figure 7. Topographic profiles of domain-general P3 and switch positivities for switch and repeat trials in the switch task. (A) Mean amplitudes of context P3 and the early (LPC₁) and late (LPC₂) aspects of the late positive complex (LPC) in response to grey gratings prompting for a switch and repetition in task rules, respectively. (B) Mean amplitudes of target P3 and the early (SP₁) and late (SP₂) aspects of the slow positivity (SP) in response to first target trials following grey gratings prompting for a switch and repetition in task rules for the same conditions as in (A) and (B).

Figure 8. Linear regression of mean P3-like amplitudes against the amount of sensorimotor information transmitted by vertical and horizontal grey gratings (A) and the ensuing target3 gratings (B) across the three task contexts. Three functionally and topographically distinct P3-like components are modelled in response to the grey Gabor gratings: P3 (circles), LPC₁ (squares), and LPC₂ (triangles). Only one P3-like component is modelled in response to target Gabor gratings: P3 (black circles). In line with our model's predictions, only the switch task showed significant differences in mean P3-like amplitudes between vertical and horizontal grey gratings (i.e., Switch-repeat vs. Switch-switch cues).

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Abstract

Event-related potential (ERP) research on task-switching has revealed distinct transient and sustained positive waveforms (latency circa 300-900 ms) while shifting task rules or stimulusresponse (S-R) mappings. However, it remains unclear whether such switch-related positivities show similar scalp topography and index context-updating mechanisms akin to those posed for domain-general (i.e., classic P300) positivities in many task domains. To examine this question, ERPs were recorded from 31 young adults (18-30 yo) while they were intermittently cued to switch or repeat their perceptual categorization of Gabor gratings varying in color and thickness (switch task), or else they performed two visually identical control tasks (go/nogo and oddball). Our task cueing paradigm was designed to examine $\underline{d \ two \ temporarily \ distinct}$ stages of proactive and reactive control during task rule preparation updating and reactive rule execution stages, respectively. A simple information theoryetical model helped us gauge cognitive demands under under distinct temporal and task contexts in terms of low-level S-R pathways and higher-order rule updating operations. Task demands modulated domaingeneral (indexed by classic oddball P3) and switch-related positivities -indexed by both a cuelocked late positive complex (LPC) and a sustained positivity (SP) ensuing task transitions. Topographic scalp analyses confirmed subtle yet significant split-second changes in the configuration of neural sources for both domain-general $\underline{\texttt{P3s}}$ and switch-related positivities as a function of both the the task and temporal and task (proactive vs. reactive) context. These findings partly meet information theoretical predictions from information estimates, and are compatible with a family of P3-like potentials involved in functionally indexing functionally distinct neural operations within a common frontoparietal "multiple demand" system during the preparation and execution of simple task rules.

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21	Introduction
22	Event-related notentials (ERPs) measured during task-switching have consistently shown
23	several distinct positive waveforms present when shifting task rules/stimulus-response (S-R)
24	mappings (e.g., Karayanidis, Coltheart, Michie, & Murphy, 2003; Karayanidis, Mansfield,
25	Galloway, Smith, Provost, & Heathcote, 2009; Karayanidis, Provost, Brown, Paton, &
26	Heathcote, 2011Karayanidis et al., 2009; Rushworth, Passingham, & Nobre, 2002). These ERP
27	positivities, which typically occur 300-900 ms post switch stimulus, are often interpreted as
28	reflecting switch-specific control processes (Jamadar, Michie, & Karayanidis, 2010; Kopp &
29	Lange, 2013; Lavric, Mizon, & Monsell, 2008; Nicholson, Karayanidis et al., Poboka, Heathcote,
30	& Michie, 20052011; Swainson et al., 2003). However, some authors have suggested switch-
31	related positivities may actually have a functional relationship with the ubiquitous P300
32	component observed across many task domains (hereafter, the "domain-general" P3),
33	probably reflecting higher-order context-updating mechanisms akin to those hypothesized for
34	P3 potentials in simpler target detection tasks (Barcelo, 2003; B arcelo, Escera, Corral, &
35	Penanez, 2000, barcelo, Penanez, & Kingirt, 2002, barcelo, Penanez, & Nynus, 2008, ch.,
36	Ridderinkhof, 2007; Wyle, Javitt, & Foxe, 2003, fc, Donchin, 1981).
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38	Switch-related and P300 positivities appear to have similar scalp topographies, suggesting they
39	both recruit activity from a common cluster of frontoparietal regions (Bledowski et al., 2004);
40	J amadar et al., 2010; Kim, Cilles, Johnson, & Gold, 2012) . Given that frontoparietal networks
41	are readily associated with cognitive control across many task domains (Cole et al., 2013;
42	Petersen & Posner, 2012), common the notion of such activation of a "multiple demand"

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system by challenges across many cognitive domains (Duncan, 2013). Woolgar, Hampshire,
Thompson, & Duncan, 2011) may underpin the link between P3 and switch potentials. While
many authors have interpreted the similar scalp topographies between the canonical P300 and
switch positivities as reflecting context-updating mechanisms akin to those posited for P300
elicitation (Barceló & Knight, 2007<u>et al., 2008</u>; Donchin, 1981; Jost et al., 2008; Kieffaber &
Hetrick, 2005): Tieges et al., 2007), to date this link remains unconfirmed. Few ERP studies
have attempted <u>directly</u> to directly examined whether switch-related positivities are
comparable to the canonical P300 both in their scalp topographies and in-in-their purported
context-updating function across a variety of task domains (cf., Barceló et al., 2008; H olig &
Berti, 2010; Lavric et al., 2008).
Many practical difficulties hinder progress toward a theoretical integration of domain-general

P3 and switch-related positivities. First, one prominent issue is the temporal contingencies among task stimuli and responses (i.e., the "temporal context" of goal-directed actions; Fuster, 2001). For example, in oddball paradigms, it is widely accepted that P300 potentials can be elicited by both the targets of goal-directed behavior, and also by infrequent *oddball* distracters that are not to be responded to (Polich, 2007; Squires, Squires, & Hillyard, 1975). These targets and rare distracters elicit two anatomically and functionally distinct P300 potentials whose scalp topographies differ along a *costrofronto*-caudal <u>parietal</u> axis, with a more centroparietal scalp distribution for the former, and a more *costral_frontal* distribution for the latter (Polich & Comerchero, 2003; Spencer, Dien, & Donchin, 1999). However, most many P300 studies use *oddball targets* and thus confound the "oddballness" and "targetness" aspects of cognitive control, akin to the stages of proactive strategic preparation and reactive execution of simple sensorimotor rules, as defined in task-cueing paradigms (Braver 2012). That is, when an oddball target occurs within a sequence of repetitive standard distracters, one has to process its *oddballness* first, and then process its target or distracter features in

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19	order to select the appropriate motor response (and activate the corresponding S-R link), and
20	these two processes overlap in the summated ERP waveforms (similar to a fixed cue target
21	interval of 0 ms in task-cueing paradigms). Therefore, to clarify whether the rostral-frontal and
22	parietal aspects of P300 index strategic resolution of contextual uncertainty (oddballness), as
22	distinct from reactive execution of simple sensorimotor rules (targetness), targets need to be
20	presented at predictable intervals following within the contextually informative events in the
24	trial run. Hndeed, t <u>T</u> ask-cueing procedures have revealed distinct frontoparietal switch-related
20	positivities for these two distinct processing stages, with parietal maxima to temporally
20	predictable targets during rule execution, and more anterior maxima to infrequent
21	unpredictable task cues that anticipate a switch in rules (Barceló, 2003; Barceló et al., 2002;
28	Jost et al., 2008; Kieffaber & Hetrick, 2005). This evidence highlights the temporal dynamics of
29	two distinct modes for the control of task-switching, with proactive rule updating and reactive
30	rule implementation <u>execution</u> stages dimerentially engaging the frontopanetal control
31	network (Braver, 2012 ; Braver, Reynolds, & Donaldson, 2003). Presumably, these same
32	first target trials following an brief unavoirted interruntion has been proposed as a prime
33	determinant of residual (restart) costs under single task conditions (Alloort, Styles, & Hsieh
34	1994: Barceló et al., 2008).
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36	A second key limitation toward an integrative view of the P300 and switch positivities is a
37	reliance on the strict categoricalstrict distinctions dichotomy between the anterior P3a and
38	posterior P3b<u>two</u> sub-components of the P300, often linked to notional definitions of stimuli
39	delivered in very different task paradigms., with Such traditional views propose a strict
40	dichotomy between the frontal P3a evoked linked to by r are, novel and ignored stimuli, and
41	the centroparietal P3b evoked-linked by to attended, relevant and consciously-processed
42	stimuli (for a review, see Polich, 2007). Such a sharp and dichotomous taxonomy impedes a
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theoretical integration of P3a/P3b sub-components with modern views about the a relative	
graded_contributions from both frontal and temporo-parietal nodes of frontoparietal cortical	
networks while dealing with a continuum of gradually increasing cognitive demands	
(Bledowsky et al., 2001; Cole et al., 2013; Petersen & Posner, 2012). For example, Barceló et a	al.
(2006) used Principal Component Analysis (PCA) to demonstrate that P3-like potentials to	
irrelevant novel sounds (P3a) and relevant tones (P3b) that signaled an upcoming task switch	
both showed similar peak latencies and scalp topographies, with more frontal or parietal	
maxima depending on their task context (for P3a potentials with parietal maxima see Polich,	
2007; Friedman et al., 2001; Kopp & Lange, 2013). This finding suggests that both irrelevant	
novel stimuli and familiar task cues may potentially evoke a continuous gradient of activity	
across both anterior and posterior frontal and oparietal regions depending on their task	
context. Here we assume there likely exists a common frontoparietal network for dealing with	h
a whole gamut of cognitive demands in between beyond the traditional extreme dichotomy of	f
"ignore" vs. "attend" <u>dichotomy</u> conditions. (Barceló et al.,<u>&</u> Knight, 200 6;7_Duncan and Owe	A
2000; Duncan, 2013).	
A third limitation is the use of notional rather than formal definitions of context, which hinde	rs
examination of the prevailing "context-updating" hypothesis of P300 (Donchin 1981) across	
different task contexts, and impedes a direct comparison with switch-related positivities.	
Traditional views have considered the stimulus context (i.e., mean stimulus probability) to be	а
major determinant of P300 amplitudes (Donchin, 1981; Polich, 2007). However, the above	
examples highlight the influence of both temporal and task contexts on frontoparietal P300	
dynamics, as a function of the cognitive demands associated with similar stimuli delivered	
under different task contexts-(i.e., each with distinct motor and sensorimotor demands). This	
highlights the importance of S-R links and sensorimotor information processing-transmission	-
over and above stimulus properties alone- to completely explore the link between P3 and	
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19	switch positivities (Verleger, Baur, Metzner, Smigasiewicz, 2014; Verleger, Jaskowoski &
20	Wäscher, 2005). To this end, here we adopted a simple information theoretical model of
21	cognitive control based on information theory to compare cognitive demands associated with
22	equally infrequent grey Gabor gratings, which set the temporal context for implementing the
22	same visuomotor color-rule upon ensuing colored Gabor gratings delivered under three
23	different task contexts (Switch, Go/NoGo, and Oddball tasks). This approach helped us to
24	mathematically operationalize the hypothetical construct of "context-updating" (Donchin,
25	1981) across three task domains, and to control for the typical confound of
26	simultaneousbetween oddballness and targetness by factoring out the influence of the
27	temporal context on performance and neural activity and behavior. In doing so, we estimated
28	the sensorimotor information transmitted between contextually related task stimuli and their
29	associated motor responses (or "input-output correlations"; Miller, 1956) at both lower and
30	higher order levels in a putative hierarchy of sensorimotor control (cf., Barceló & Knight, 2007)
31	Barceló et al., 2008; Barceló et al., 2008; Koechlin & Summerfield, 2007).
32	
33	Information theory allows the ability us to assign task properties binary digit values or bits
34	(Attneave, 1959; see Cooper, Garrett, Rennie, Karayanidis, Koechlin, & Summerfield, 200715).
35	In this way, S-R contingencies can be ascribed an information value, permitting simple
36	contrasts between tasks. Information theoretical <u>theory</u> approaches allow <u>s</u> us to gauge
37	cognitive demands associated with dissimilar stimulus and response sets, and distinct S-R
38	mappings in order to predict the intensity and scalp topography of ERP positivities under
20	across different changing temporal and task contexts domains (Barcelo et al., 2006; Barcelo &
39	knight, 2007). For instance, Barcelo and Knight (2007) estimated an increase in the information
40	content of novel oddball distracters when these consistently predicted a target onset, and
41	such estimates matched con esponding induciduois or novery rs -out not target rs-
42	ampitudes, the wat, barcelo et al. (2006) relied on monimation theoretical <u>theory</u> estimates
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19	to demonstrate the distinct functional roles of cue-locked context-related (i.e., context-cue-
20	locked) P3 and target P3 potentials elicited by the same sequence of red and blue shapes
21	interspersed with infrequent black symbols, when these were administered under oddball,
22	go/nogo and task-cueing proceduresinstructions. These authors found similar frontocentral
22	scalp topographies -albeit with different magnitudes- for context-related P3s and switch-
20	related positivities to the infrequent black symbols, consistent with their information
24	estimates. In sharp contrast, target P3 amplitudes were not modulated by task demands, and
20	showed similar midparietal amplitudes and topographies across all task contexts. Thereby,
20	hereafter we will adopt the term "context P3" to describe frontoparietal positivities elicited by
27	infrequent grey Gabor gratings that are predicted to index context-updating operations
28	proactively, in anticipation to target onset <u>, and in all three task domains (and</u> -regardless of the
29	their task context rostral or posterior scalp maxima). Conversely, we will adopt the term
30	"target P3" to describe ERP positivities elicited by temporally predictable colored Gabor
31	gratings that are thought to recruit mainly mostly reactive target detection, but without the
32	temporal unpredictability of oddball targets-(see details for context-locked and target-locked
33	ERP waveforms in the Methods section). Finally, it could be argued that Barceló's et al (2008)
34	null task effects for target P3 might not be sufficiently compelling due to their between-subject
35	design and small sample sizes. Here we circumvent earlier limitations of an earlier study
36	(Barceló et al., 2008) by using a within-subject task design, larger sample sizes for reliable
30	topographical analysis of amplitudes, and include surface Laplacian estimates values to
37	minimize volume conduction of scalp recorded potentials.
38	
39	In sum, this study aimed to examine the similarities and differences in the intensities and scalp
40	distribution of domain-general P3 (300-400 ms) and switch-related (300-900 ms) ¹ ERP
41	positivities while participants were intermittently cued to switch or repeat their categorization
42	of Gabor gratings varying in color and thickness (switch task). Two perceptually identical tasks
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18	served as controls with varving cognitive and response demands (go/ongo and oddhall)	
19	Served as controls with varying cognitive and response demands (go nogo and oddban).	
20	portivities to page abiently civiliar and functionally compatible with a context undating	
21	positivities topographically similar and functionally compatible with a context-updating	
22	mechanism akin to that proposed for the canonical P3 component recorded in simpler oddbail	
23	and go/nogo tasks? This question was addressed by testing two specific hypotheses on both	From the A Fred Note
24	domain general P3 and switch related P3 like positivities: (1) if the remport context of goal	
25	directed actions (i.e., proactive strategic preparation versus reactive execution of asimple	
26	visuomotor rules/modulates the noncopanetal scalp distribution of rate cher <u>rshike</u>	
20	positivities, then more tostrai rontar positivities will be elicited during proactive preparation	
21	(e.g., higher-order rule updating) than during lower-order sensorimotor control of reactive rule	
28	execution at target onset (Barcelo et al., 2008; Braver, 2012 <u>); Looper, Darnoa, Karayanidis, F.,</u>	
29	Barcelo, 2010). [2] if the parametric increase in cognitive demands posed by three different	
30	task contexts (oddball, go/nogo, switch) modulates the frontoparietal distribution and	1 Fornatted: Fort: Talic
31	magnitude of late ERP <u>P3-like</u> positivities, then gradually more restral <u>frontal</u> positivities will be	
32	elicited with gradually higher cognitive demands, in line with predictions from an information	
33	theor <u>yetical</u> model of cognitive control (Cooper et al., 2016; Koechlin & Summerfield, 2007).	
34	These two predictions relied on the hypothetical contribution from a common frontoparietal	
35	"multiple demand" system (Duncan, 2013) to both domain-general P3 and switch-related P3-	
36	ince positivities. To test these two hypotheses, we recorded P3 potentials to oddball and	
37	go/nogo Gabor gratings and compared their scalp distributions with switch-related P3-like	
38	potentials to identical stimuli delivered under switch task conditions. To favor integration with	
20	the extant literature, we analyzed mean and normalized EKH amplitudes, and surface Laplacian	
39	values at <u>from</u> four midline regions (frontopolar, frontal, central and parietal), under the	
40	assumption that <u>distinct scalp topographies and</u> functional dissociations in response to	
41	experimental factors and distinct scalp topographies will denote characterize different distinct	
42	ERP components (Kappenman & Luck, 2012). For simplicity, we modeled sensorimotor	
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information transmission only at two levels in the putative hierarchy of cognitive control, namely, low-level sensorimotor control (i.e., changes in single s<u>S</u>+<u>R</u> pathways), and higherorder episodic control of task rule retrieval and updating (Dayan, 2007; see the Supplementary material).

Methods

Participants

Thirty-one participants (25 female, mean= 21.8, ± 2.7 years) took part in the current study and received course credit for their collaboration. All were graduate or postgraduate students at the University of the Balearic Islands with normal or corrected-to normal vision and reported no history of neurological or psychiatric disorders. Informed consent was obtained from all participants and experimental procedures and behavioral testing was performed in accordance with the Declaration of Helsinki, and with-the approval of the Ethics committee of the university.

Stimulus Materials and Procedures

Participants sat in a sound attenuated and dimly lit room at a viewing distance of 150 cm from a 27-inch video LCD monitor (800 x 600 at 75 Hz). Stimuli were displayed against a grey background (2.85 cd/m²) at a visual angle of 6.5° to the left or right of a central fixation cross with 0.5° x 0.5° of visual angle². A central fixation cross remained continuously present throughout each experimental run. Stimuli consisted of four equally probable (p = 0.21), colored Gabor gratings with horizontally oriented gratings (either red or blue, 4 or 10 cpd, 25% contrast, 1° visual angle, 3.5 cd/m²), and two infrequent (p = 0.08) grey Gabor gratings (oriented either vertically or horizontally, 2 cpd, 25% contrast, 1° visual angle, 3.5 cd/m²). Participants responded via a hand-held response pad with their left or right index fingers.

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15 16 17 18 19 20 21 22 23 24	The experimental procedures have been described elsewhere (Cooper, Darriba, Karayanidis & Barceló, 2016), and consisted of three different tasks: <i>switch, go/nogo</i> and <i>oddboll</i> , yoked for stimuli and trial sequences but involving different response and cognitive demands each (Fig. 1). A test sequence included 976 trials of colored and grey Gabor gratings that was semi-randomly generated offline, with the constraint that consecutive grey Gabors gratings were separated by four to eight colored gratings. This trial sequence was divided into eight blocks to allow for short self-paced breaks approximately every five minutes. Each trial consisted of a
25 26 27 28 29 30 31 32 33 34 35	Gabor grating presented for 100 ms in the left or the right visual hemifield. On designated target trials, participants had to respond within a maximum of 1200 ms after stimulus onset. Participants were instructed to fixete their gaze on the central cross and avoid shifting their every gaze to the lateralised Gabor stimuli-Instructions emphasized both response speed and accuracy. All error trials (i.e., incorrect, late responses and false alarms; i.e., button presente to non-target gratings) were followed by visual feedback and the following trial was delayed by 500 ms to help subjects keep on task. As a consequence/tence, stimulus onset asynchrony (SOA) was either 1900 or 2400 ms on correct and error trials, respectively. The present ERP analyses were based on correct trials only. The stimulus display and behavioral response recording were implemented using Presentation® software (Neurobehavioral Systems Inc., Albary, CA).
36 37 38 39 40 41 42 43	Each participant was presented with a unique pseudorandomly generated test sequence that was repeated three times under different task instructions for the oddball, go/nogo and switch tasks. Tasks were administered in counterbalanced order-between-participants to control for inadvertent order effects. Thus, the three tasks involved an identical stimulus context but different cognitive and response demands (Fig. 1).
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repeat the task. The colored Gabor stimuli were targets and required a left or right hand response based on either the color (blue or red grating) or the grating's spatial frequency (thick or thin grating). Hence, in this task, the orientation of the grey grating in the gr (cue) instructed participants whether to switch or repeat the task they completed on the previous set of trials run. Grey grating orientations and instructions were counterbalanced between participants. A short training session was administered to ensure that participants reached a criterion of 80% correct responses and had understood task instructions. The go/nogo task (Fig. 1B) served as a control for the switch task. It involved an identical stimulus sequence and again participants responded only to the colored Gabors. However, importantly, here the grey Gabors had no predictive significance regarding the task to be performed, but set the temporal context for the next target onset. Rather they were defined as nogo stimuli and participants were asked to withhold their response while Implementing color classifications across the entire trial block of trials essence, this task is very similar to a single-task block, except that the grey gr A. In sum, the go/nogo task involved responding sorting to the same Gaborstargets by their color an identical stimulus sequence and similar S-R mappings as the switching task The oddball task (Fig. 1C) served as a control for both switch and go/nogo tasks, having an al<u>identical-</u>stimulus context-and equivalent perceptual demands, but with different ide response demands. Specifically, a response was required only to red Gabor gratings, which were defined as oddball targets. All other stimuli did not require a motor response. This oddball task was inspired on regular novelty oddball tasks (cf., Barceló and <u>&</u> Knight, 2007; 12

The switch task (Fig. 1A) was a variant of the intermittent-instruction paradigm (Monsell, 2003;

vorth et al., 2002). The grey Gabor stimuli were cues, indicating whether to switch or

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Friedman 2011), except that all targets, standard and rare distracters included an additional irrelevant stimulus dimension (e.g., thickness of gratings).

Insert Figure 1 around here

Information Theoryetical Estimations

We adopted an information the retical theory approach to model of cognitive control as a formal tool to help us operationalize both temporal and task contexts in terms of low- and high-order sensorimotor (S-R) information transmission within a putative hierarchy of frontoparietal control processes (cf., Barceló & Knight, 2007; Barceló et al., 2008; Cooper et al., 2016). In doing so, we followed recommendations by Miller (1956) for estimating the amount of information transmitted between contextually related stimuli and responses (or inputoutput correlations). These information theoretical estimates allowed us to define the informational structure of our tasks in terms of, not only mean stimulus probabilities, but also joint and conditional probabilities among stimuli, their associated motor responses, and any relevant cognitive operations putatively involved (e.g., rule updating). Thus, the task context was modeled at two hierarchically distinct levels: (1) low-level sensorimotor control of single sr pathways, and (2) higher order episodic control of task rule updating (Dayan, 2007; Koechlin & Summerfield, 2007). The temporal context was separately modeled for infrequent grey Gabors and for the relatively more frequent colored Gabors. Thus, while infrequent grey Gabors were visually identical in all tasks, and appeared with identical probability, the type of information provided varied. Oddball grey Gabors transmitted the lowest sensorimotor information for response selection (as they did not anticipate target onset on the following trial), and no episodic information given that the same task rule was used for all Oddball targets and non-target distractors. Alternatively, increased sensorimotor information was conveyed by nogo grey Gabors as these stimuli were associated with less frequent nogo 13

responses (r_0) compared to the Oddball task, and they did anticipate target onset on the next
trial. As with grey Gabors in the oddball task, no episodic information can be assumed for nog
grey Gabors given that the same task rule was consistently used across all trials. Finally, similar
sensorimotor information was transmitted by all grey Gabors in the Switch task, plus an
additional amount of episodic information was transmitted only by 'switch' grey Gabors, as
these served as cues requiring anticipatory updating of episodic task rules. Note that these
information estimates can be seen as a more formal and accurate way to translate into bits the
mean probabilities of task events,- <u>that are as is common practice in most experimental</u>
psychology studies. Yet they bits provide a common metric to compare our manipulation of
context across different task domains. For instance, instead of saying that a grey Gabor
distractor occurs with an overall mean probability of p = 0.08 throughout our Oddball task, we
chose to quantify this in bits by saying that the sensory entropy of this distractor is: $H(s_1)$ =
-0.08 · log ₂ 0.08 = 0.29 bits (cf., x-axis of Fig. 2). A similar formalism was used to quantify in bits
the relative probabilities of specific sensorimotor processes, such as the joint probability of
specific $s_i \cdot r_j$ mappings using the concept of transmitted information: $l(s_i, r_j) = \log_2 p(s_i, r_j) - \log_2 p(s_i, r_j)$
$p(s_i) = \log_2 p(r_2)$. For simplicity, additional sources of contextual information (i.e., stimulus-
response congruency effects, stimulus repetition effects, etc.) were randomized and not
modeled in these estimates. Fig. 2 presents a summary of these information-theoretic
estimations, in line with the two specific predictions of our study; for a detailed technical
technical description see the Supplementary material (cf.,and Cooper et al., (2016).

Insert Figure 2 around here

Psychophysiology

Behavioral Analyses

Psychophysiology

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19	At the beginning of the switch task, subjects were instructed to start sorting by color up to the			
20	onset of the first grey grating in the trial run. These trials were removed from the analyses.			
21	Reaction times (RTs) are reported from correct trial runs only, while trial runs containing any			
21	false alarm, omission, or any other errors were discarded. Errors were used to compute			
22	accuracy indexes. Only the first three target trials following a grey grating entered the			
23	analyses, since behavioral costs typically reach an asymptote in later trials (Monsell, 2003;			
24	Rushworth et al., 2002)]. Following previous studies, steat costs were defined as the	= 1	Formatte	ed: Font: Italic
25	difference in mean RTs and errors between the first and second target responses following any	٦	Formatte	d: Font: Italic
26	grey grating. Equivalent indices were obtained for the two control tasks. Mixing costs were			
27	estimated for the switch task only as the difference in mean RTs and errors between third			
28	target responses in the switch vs. go/nogo tasks. Third targets provided a relatively pure index			
29	of mixing costs independent from restart costs. Finally, although we did not expect to find			
30	switch-specific behavioral costs due to our long cue-to-target intervals (cf., Foxe, Murphy, &			
31	De Sanctis, 2014), local switch costs were also computed as the difference in mean RTs and			
32	errors between first target responses after switch versus repeat cues. Only color-rule trials			
33	were considered in the behavioral analyses of switch trials, to limit any task rule switch			
34	asymmetries-relative to the control tasks. Equivalent behavioral indexes were obtained in the			
35	two control tasks. The mMean RTs and percentage correct error target trials were subjected to			
20	repeated-measures analysis of variance (ANOVA) with the following factors: Grey grating			
30	(vertical vs. horizontal), Target trial (1st, 2nd, 3rd target in the trial run), and Task context			
37	(oddball, go/nogo, switch). All participants had an overall hit rate better than 89% in the switch			
38	task, with at least 60% correct trial runs to the initial three targets following any grey Gabor			
39	(see Stimuli and Procedurescf., Cooper et al., 2016). These strict selection criteria were meant			
40	to avoid any posterror slowing effects (Barceló et al., 2008) , and ensured that the final sample			
41	consisted of highly efficient participants had that complied with task instructions.			
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EEG Recordings and ERP Analyses

below 10 kΩ, as in Cooper et al. (2016).

Continuous EEG data (0.05–100 Hz bandpass) were collected using SynAmps RT amplifiers (NeuroScan, TX, USA) from 60 scalp sites using tin electrodes mounted on an elastic cap (Synamp2 Quikcap, Compumedics, TX) at a sampling rate of 500 Hz. EEG electrodes were placed following the extended 10–20 position system (Fp1, Fp2, AF7, AF3, AF2, AF4, AF8, F7, F5, F3, F1, F2, F2, F4, F6, F8, FT7, FC5, FC2, FC1, FC2, FC2, FC4, FC6, FT8, T7, C5, C3, C1, C2, C2, C4, C6, T8, TP7, CF5, CP3, CP1, CP2, CP4, CP6, TP8, P7, P5, P3, P1, P2, P3, P4, P6, P8, P07, P03, P04, P08, O1, O2, O2)with and were referenced to theal left mastoid reference, and -The electrodes were-later re-referenced offline to the algebraic average of the right and left mastoids. Four additional electrodes were placed above and below the left eye and on the outer canthi of both eyes to monitor blinks and eye movements. Sensor impedances were kept

riteria were used to select trials for EEG and behavioral analyses (e.g., only

ontrol, analyses were restricted to grey g

red or blue Gabor gra

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for the oddball task, nogo trials for the go/nogo task and

k while blue gratings were an additional type of distractor. Additionally noisy trials

EEG data were processed using MATLAB (Mathworks, Navick, MA) through a pipeline utilizing EEGLab (Delorme & Makeig, 2004), CSD Toolbox (Kayser & Tenke, 2003), and in-house

functions. Preprocessing was performed in EEGLab as follows. EEG data were re-referenced
offline to linked mastoids and band-pass filtered (0.1 – 30 Hz). Epochs for each stimulus type
were extracted from -200 ms to +1200 ms relative to stimulus onset, with a 200 ms pre-
stimulus baseline. Trials were inspected for with non-stereotyped artifacts (e.g., cable
movement, swallowing) and were removed if present., Stereotyped and stereotyped artifacts
(including-e.g., blinks, eye movements and muscle artifacts) were deleted using independent
components analysis (extended infomax algorithm; Bell & Sejnowski, 1995) , and the remainir
components were then projected back into electrode space. Note, only color-rule trials were
considered for analysis of switch trials (to limit any influence of task asymmetries relative to
the control tasks), which resulted in an average of 142.8 (± 9.6.SD) grey distractor, 73.5 (± 4.9
target 1, and 75.3 (± 5.4) target 3 trials for oddball; 126 (± 16 50) nogo, 130 (± 16) target 1 an
122.2 (± 15.6) target 3 go trials for go/nogo; and 28.4 (± 4.6) repeat cues, 30.7 (± 4.8) repeat
arget 1 and 30.9 (± 4.8) repeat target 3 trials; 31.4 (± 3.7) switch cues, 31.1 (± 3.7) switch
target 1 and 31.2 (± 3.6) switch target 3 trials for the switch task. This same dataset was
employed to examine EEG oscillatory dynamics during proactive and reactive control of task-
switching in the same sample of young participants (cf., Cooper et al., 2016).
veighboring electrodes were combined into topographical ROIs (frontopolar: including Fp1,
Fpz, Fp2; frontal: F1, Fz, F2; central: C1, Cz, C2; and parietal: P1, Pz, P2) to preserve statistical
ower (Picton et al., 2000). Time windows for ERP analyses were selected based on visual
nspection of the corresponding grand mean waveforms. Two groups of ERP measures were
obtained: context-locked and target-locked; based on the assumption that the grey gratings
provide <u>d</u> the temporal context for subsequent target detection (Posner & Petersen, 1990), ar
that they require proactive control mostly in the switch task. Thus, five distinct ERP
components were measured and analyzed in the context-locked waveforms: P3 (350-400 ms)
two windows of a late positive complex (LPC1: 550-600 ms, LPC2: 750-850 ms), and a frontally

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19	distributed slow negativity towards the end of the recording epoch (contingent negative
20	variation, CNV; 1000-1200 ms). In the target-locked waveforms, maximal signal amplitudes
21	were observed at one latency window: P3 (350-400 ms), and only for the first target following
22	any grey grating, two more latency windows captured a sustained positivity starting around
23	300 ms post-target onset and lasting to the end of the epoch (SP ₁ : 550-600 ms and SP ₂ : 750-
24	sourns; see Figure 4). The latency of P300 potentials is known to vary weeky with task complexity (Kappenman & Luck. 2012: Kutas et al., 1977), and hence, switch-related
25	positivities were examined using a wider (300-900 ms) latency window in line with previous
26	s tudies (Barceló et al., 2002; Jost et al., 2008; Karayanidis et al., 2003; Karayanidis et al., 2009;
27	Kieffaber & Hetrick, 2005; Rushworth et al., 2002). Accordingly, our distinction between
28	domain-general P3_and switch-related positivities relied on their distinct scalp topographies
29	and sensitivity to experimental factors (i.e., switch vs. repeat trials), and on distinct scalp
30	topographies, rather than on any unreferices in peak latencies.
31	Mean ERP amplitudes were analyzed using repeated-measures analysis of variance (ANOVA) to
১८ २२	examine our manipulation of Temporal temporal and Test task contexts on domain-general
34	P3s –common to all tasks while uninfluenced by task switching demands- and switch-related
35	positivities. Firstly, a Temporal context (grey grating, target_target3) factor examined
36	differences in P3-like amplitudes between infrequent and temporally unpredictable grey
37	Secondly, and given the highly different P3-like task effects observed for grey gratings (i.e.,
37 38	Secondly, and given the highly different P3-like task effects observed for grey gratings (i.e., context P3) and third targets trads (i.e., target P3), the Task context factor was tested
37 38 39	Secondly, and given the highly different P3-like task effects observed for grey gratings (i.e., context P3) and third targets the second secon
37 38 39 40	Secondly, and given the kinghold protocol and an according and a group protocol and a secondly, and given the highly different P3-like task effects observed for grey gratings (i.e., context P3) and third targets track-(i.e., target P3), the Task context factor was tested separately for context-locked and target-locked ERP waveforms. Thus, context-locked ERP waveforms were analyzed considering the following within-subject factors: Task context
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19	Task context (switch, go/nogo, oddball), Grey grating (vertical, horizontal), Target trial
20	(target,target1, target,target3), and ROI (frontopolar, frontal, central, parietal). The
21	Greenhouse-Geisser sphericity correction was applied as needed. Corrected p values are
21	reported, but original degrees of freedom are kept for easier reading. A significance level of ρ <
22	0.05 was adopted for all main statistical analyses, and a Bonferroni-corrected threshold
23	(0.05/4 = n < 0.0125) was used for multiple tests at the four midline regions
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20	Analyses of ERP Scalp Topographies
20	As in many past studies (Polich & Comerchero, 2003; Squires et al., 1975), to assess the effects
27	of temporal and task contexts on ERP positivities, we examined the scalp distribution of mean
28	and normalized amplitudes across four midline regions (frontopolar, frontal, central, parietal),
29	two temporal contexts (grey grating, target, target3) and three task contexts (switch, go/nogo,
20	oddball). Further, to identify switch-related P3-like positivities as distinct from domain-general
30	D2 we leaked for significant interactions with the Crew grating factor /switch us repeat) in the
31	rs, we looked for significant interactions with the drey grating factor (switch vs. repeat) in the
32	switch task only. Next, to address our first and second hypotheses, we examined changes in
33	the scalp distribution of domain-general P3 across the three task contexts, as well as for the
24	two temporal contexts, namely, for proactive (grey gratings) and reactive (target_target3)
34	processing modes, respectively. Accordingly, answers to our first and second hypotheses were
35	addressed by looking for significant ANOVA interactions between the ROI factor and the
36	Temporal and Task context factors, respectively. Further, we specifically tested the null
37	hunothoric of civiliar scale distributions for quitch related CDD particulties and domain general
38	hypothesis of similar scalp distributions for switch reaces care positivities and domain-general
30	P3 by examining the interaction between ROI x ERP component in the switch task only. To
39	minimize the effects of volume conduction on the analyses of scalp topographies and favor
40	integration with past studies, data were also compared by using a surface Laplacian filter
41	(smoothing = 10-5, number of iterations = 10, spherical spline order = 4; Kayser & Tenke, 2006;
42	Urbach & Kutas, 2002). Likewise, to help capture scalp topographies more robustly and favor
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Behavioral Results

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integration with many past studies, mean ERP amplitudes were normalized using the vector length transform to examine changes in topography independent of source strength. Vector length was computed as the square root of the sum of squared amplitudes over all location and was calculated separately for each task and trial condition (McCarthy & Wood, 1985).

Results

All three tasks were performed very efficiently, with an average of only 6.3% incorrect trials in the switch task (95% CI [5.1, 7.4]), 4.5% in the go/nogo (95% CI [3.5, 5.5]), and 0.4% in the oddball (95% CI [0.3, 0.5]). A main effect of Task (*F*[2, 60] = 47.6, *p*< 0.0001; *G*C= 0.83; η^2 = 0.61), confirmed differences in overall error rates among all three tasks (all *p*'s< 0.001; Fig. 3<u>6</u>). Accuracy did not vary across target trials in the oddball, but larger error rates were observed in first relative to second target trials following any grey gratings in both switch and go/nogo tasks (all *p*'s< 0.001), with no further differences between second and third target trials, as revealed by a 2-way interaction between Task and Target trial (*F*[2, 120] = 5.1, *p*< 0.003; *G*G= 0.73; η^2 = 0.15). The 3-way interaction with Grey gratings in the switch task only (<u>P5% vs. 6.5%</u> errors respectively, *p*< 0.02]. No other effects reached significance for accuracy data, which thus confirmed the presence of <u>local</u>, restart and mixing costs <u>for accuracy data</u> in the switch tasks (see Fig. 3). No other effects reached significance.

The speed of correct target responses differed among all tasks (p's< 0.001; Fig 3B), as revealed by a main Task context effect (f(2, 60) = 99.9, p< 0.0001; GG 0.76; η ² 0.77). A 2-way interaction between Task context and Target trial (F(4, 120) = 17.8, p< 0.0001; GG 0.59; η ² =

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19	0.37) revealed the presence of restart costs in the switch and go/nogo tasks, both showing slower responses to the first than the second or third targets (all p's< 0.001), without any
20	further slowing observed between the two latter trials. In contrast, the oddball task did not
21	show any first trial slowing. Mixing costs were inferred from the larger mean RTs to third
22	target trials in the switch compared to both control tasks (all p's< 0.001; Fig. 3B). The third
20	order interaction with Grey grating failed to reach significance, suggesting the absence of local
24	switch costs in the mean RTs to correct first target trials in the switch task, an expected
20	outcome given our long <u>1900 ms</u> cue- to -target intervals (cf., Foxe et al., 2014).
20 27 28	Insert Figure 3 around here
29	Electrophysiological Results
30	Figs. 4 and 5-summarizes the grand ERP waveforms over midfrontal and midparietal regions to
31	grey gratings, and to the first (target_target1) and third (target_target3) target trials across all
32	tasks. Since ERPs waveforms to second target trials (not shown) present an intermediate stage
33	between those to target, and target, suggesting they were partly affected by residual
34	carryover interference from contextual processing. To maximize differences along the trial
35	sequence, the present analyses compared focused on f irst and third <u>target target</u> trials <u>to</u>
36	maximize trial differences. Scalp topographies for mean amplitudes and surface Laplacian
37	values are also shown for the task-switch condition only Inrough visual inspection, three distinct FRP positivities could be readily identified in the context-locked FRP waveforms of the
38	switch task, showing maximal amplitudes over centroparietal regions: P3 (350-400 ms), LPC.
39	(550-600 ms), and LPC ₂ (750-850 ms). These two aspects of the late positive complex <u>LPC</u> best
40	captured switch-related contextual effects. Finally, a sustained frontally distributed CNV-like
41	negativity extended from circa 800 ms until the onset of the first target stimulus. A target P3
42	(350-400 ms) was present in the target-locked waveforms, which showed with relatively-similar
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amplitudes and centroparietal scalp distribution across all three task contexts, <u>as shown in</u> Figs. 4 and 5. In addition, a sustained positivity (SP) starting 300 ms post-target onset and lasting until the end of the recording epoch was observed to <u>first targets (target, target)</u> in the switch and -to a lesser extent- also the go/nogo tasks. Modulations of these context- and target-locked ERP waveforms by task demands and switch-related processes are described below. The visual P1 and N1 were not modulated by task conditions, and therefore will not be discussed further.

Two Context Effects on Domain-General P3s

Two domain-general P3s with 350-400 ms peak latencies were present across all three tasks $\!$
domains(labeled as "context P3" and "target P3" in Figs. 4 & 5), given and that their mean
amplitudes were not modulated by the Grey grating factor in the switch task nor, indeed, in
any of the two control<u>three</u> tasks (labeled as context P3 and target P3 in Figs. 4 & 5). As
reported belowinstead, as reported below, these two domain general-P3s showed distinct
scalp topographies and were differently differently modulated by temporal and task contexts7
and each showed a distinct scalp topography, which justifies their consideration as two distinct
ERP-P3_components_ (and also justifies our descriptive labels as "context P3" and "target P3").
As predicted by our model, both the temporal and task contexts modulated the intensity and
scalp topography of domain-general P3s, as reflected by significant Temporal context x Task
context (F(2, 60)= 17.6, p < 0.0001; GG= 0.86; η^2 = 0.37) and Temporal context x Task context x
ROI interactions (F(6, 180)= 35.5, $p < 0.0001$; GG= 0.53; $\eta^2 = 0.54$). Given the very different P3-
like modulations elicited by grey gratings and colored targets, Table 1 presents the relevant
ANOVA results separately for context P3 and target3 P3. Firstly, increasing task demands
elicited larger context P3 amplitudes, as revealed by a main Task effect. Follow-up contrasts
revealed a larger context P3 for the switch as compared to the other two tasks (all p's< 0.005),
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19	with no such differences between oddball and go/nogo tasks (Figs. 4, 5A). A Task context x ROI
20	interaction revealed that these larger context P3 amplitudes in the switch compared to the
21	other two tasks occurred only at central and parietal regions (all p's< 0.01; Figs. 4, 5A & 6A,C
22	Left panels). In sharp contrast, mean targets P3 amplitudes were larger in the oddball
23	significant Task context x ROI interaction (see Table 1: Figs. 4, 5C & 6B.D).
24	and the second
25	Secondly, the significant interaction between Temporal context and Task context was further
26	examined by comparing mean amplitudes of context P3 and target3 P3 in each task domain
27	separately. Significantly larger target3 P3 than context P3 mean amplitudes were observed in
28	the oddball and go/nogo tasks (main Temporal context effect: $F(1, 30)=46.1$, $p<0.0001$; $q^2=$
29	0.61, and $F(1, 30)=7.7$, $p<0.01$; $\eta^2=0.20$, respectively), with differences at central and parietal
30	regions (Temporal context x ROI: F's(3, 90)> 30.4, p's< 0.0001; η ²ⁱ s> 0.52). In contrast, the
31	Temporal context x ROI interaction failed significance in the switch task (F(3, 90)= 1.4, p= 0.24),
32	suggesting no differences in mean P3 amplitudes elicited by grey gratings and third targets
33	trials in the switch task (Figs. 6B, A left panel). This pattern of results was confirmed with
34	surface Laplacian values (Table 1; Figs. 6C, D left panel), which attest to different topographies with uppling tack demonds for both contout D2 and taxaet2 D2. Thus, whereas taxaet2 D2
35	with varying task demands for both context P3 and targets P3. Thus, whereas targets P3 so the server showed a centronarietal maximum under the simplest oddhall task - context P3 to the grey
36	gratings showed maximal frontal intensities under the most difficult switch task (Fig. 4).
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38	Of note, mean target P3 amplitudes differed for first-target1 versus third targettarget3 trials,
39	as suggested by a main Trial effect ($F(1, 30) = 10.4$, $p < 0.003$; $\eta^2 = 0.26$), and these sequential
40	effects for target P3 differed across tasks but this was true only in the switch task, as revealed
41	by a 2-way Task context x Target trial interaction (F(2, 60) = 6.8, p < 0.003; GG= 0.86; η^2 = 0.18).
42	Simple tests of effects revealed that neither oddball nor go/nogo target P3 amplitudes
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t<u>starget1</u> P3 amplitudes in the switch task were increased was larger than targetatarget3 P3 across all midline regions (all p's< 0.005), owing to an overlapping slow positivity as described below. nain-general P3s were identified: one context P3 (35 ; being di e that these with the traditional P3a and P3b sub-components of P300, except that their function ny of "ignore" vs. "at d by a strict dicho ent task design allowed us to temporarily segregate oddbollr cc from as related to proactive and reactive modes of cognit ent that the lare st P3-like cts are elicited by the relatively surprisi ing grey

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changed $\frac{\text{significantly}}{\text{from first to third target trials (see Figs. 4 and 5C)}. In contrast,$

Context Effects on Switch-Related P3-like Positivities

The Grey grating factor yielded significant main effects and 3-way interactions with Task context and ROI for context-locked LPC₁ ($F(6, 180) = 9.5, p < 0.0001; GG = 0.39; \eta^2 = 0.24$) and LPC₂ positivities ($F(6, 180) = 24.3, p < 0.0001; GG = 0.38; \eta 2 = 0.45$), as well as for the sustained positivity (SP) to the first target following a switch cue (Fs(1, 30) > 10.7, $p's < 0.003; \eta^2 s > 0.26$). In all cases, LPC₁ and LPC₂ amplitudes in the switch task were larger for switch than for repeat grey gratings over midcentral and midparietal regions (all p's < 0.01; Fig. 7A), whereas only LPC₁ also differed among grey gratings over frontopolar and frontal regions (all p's < 0.02; Figs. 4.%, 5.%, 7A). Mean amplitudes for the sustained positivity (SP₁ and SP₂) to target_target1

below (see Figs. 4 and 5).

were largest for switch prev	y gratings across all midline regions (Figs. 4 .&. 5B & 7B). This effect		
was present already in the	latency window of target.target1 P3 (Grev grating main effect: <i>F</i> /1		
$30) = 11.5, p < 0.002; n^2 = 0.5$	28), with differences at frontal, central and narietal regions (all n's	<	
0.005; interaction Grev prat	ting x ROI: $F(3, 90) = 3.5$, $p < 0.04$; $\eta^2 = 0.11$).		
citer, included of erey gra			
In sum, two distinct switch-	related positivities were apparent: a context-locked late positive		
complex (500-850 ms: desc	ribed as a "switch positivity" by Karavanidis et al. (2009) and a		
sustained slow positivity (3)	00-1200 ms) elicited by the first target (target target1) following a		
switch cue (cf., Lavric Barce	eló et al., 2008 : Nessier et al., 2012).		
	Insert Table 1 around here		
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Context Effects on Domain	- General P3s		
As predicted from our infor	mation-theoretic model, both the temporal and task contexts		
modulated the intensity an	d scalp topography of domain-general P3s, as reflected by		
significant Temporal contex	در x Task context (<i>F</i>(2, 60)= 17.6, p< 0.0001; GG= 0.86; n²= 0.37) an	4	
Temporal context x Task co	ntext x ROI interactions (F(6, 180)= 35.5, p< 0.0001; GG= 0.53; n ² =		
0.54). Given the very differ	ent P2-like modulations elicited by grey gratings and colored		
targets, Table 1 presents th	e relevant ANOVA results separately for context P3 and target_ P3		
Firstly, increasing task dem	ands elicited larger context P3 amplitudes, as revealed by a main		
Task effect. Follow-up cont	rasts revealed larger context P3 amplitudes for the switch as		
compared to the other two	tasks (all p's< 0.005), with no such differences between oddball		
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and go/nogo tasks (Figs. 4, 5A). A Task context x ROI interaction revealed that these larger
context P3 amplitudes in the switch compared to the other two tasks occurred only at central
and parietal regions (all p's< 0.01; Figs. 4, 5A & 6A,C,E left panels). In sharp contrast, mean
target_P3 amplitudes to third targets were larger in the oddball compared to the other two
tasks, and only at the parietal region (p's<0.005), as revealed by a significant Task context x
ROI interaction (see Table 1; Figs. 4, SC & 6B,D,F).
Secondly, the significant interaction between Temporal context and Task context was further
examined by comparing differences in mean amplitude between context P3 and target, P3 in
each task domain. Significantly larger target _a P3 than context P3 mean amplitudes were
observed in the oddball and go/nogo tasks (main Temporal context effect: $f(1, 30) = 46.1, \rho <$
0.0001; $\eta^2 = 0.61$, and $F(1, 30) = 7.7$, $\rho < 0.01$; $\eta^2 = 0.20$, respectively), with differences at central
and parietal regions (Temporal context x ROI: - Ε's(3, 90)> 30.4, p's< 0.0001; η ² 's> 0.52). In
contrast, the Temporal context x ROI interaction failed significance in the switch task (F(3, 90)=
1.4, p= 0.24), suggesting no differences in mean P3 amplitudes elicited by grey gratings and
third targets trials in the switch task (Figs. 6B, A left panel). This outcome confirmed the
different scalp topographies in response to contextual demands for context P3 and target, P3.
Thus, whereas target, P3 showed a centroparietal maximum under the simplest oddball task,
context P3 to the grey gratings showed a relatively more frontocentral scalp distribution with
maximal intensity under the most difficult switch task. This pattern of results was confirmed
with surface Laplacian values (Table 1 and Figs. 6F, E left panel). In contrast, normalized P3
amplitudes did not yield any significant 3-way interactions, suggestive of similar configurations
of neural generators for domain general P3 across all temporal and task contexts (Figs. 6D, C
left panel). In sum, opposite modulations of context P3 and target, P3 with increasing task
demands -as revealed by surface Laplacian and mean amplitudes - confirm their distinct
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19	functional roles during proactive and reactive control of task switching, as has been suggested	
20	in previous studies (Barceló et al., 2002, 2006, 2008; cf., Polich, 2007).	
21	See Tenership of Demain Conserved D2a up Culture Destitution	
22	The main question of this study specifically required testing the null hypothesis of similar scale.	
23	distributions of switch-related ERP positivities and domain-general P3s, as indicated by the	
24	absence of an interaction between ROI x ERP component. Thus, differences in the midline	
25	scalp distributionany switch specific changes in the configuration of sources were offirst	
26	identified by comparing scalp distributions of P3-like amplitudes and Laplacian values switch-	
27	related and repeat-related positivities were examined in response to "switch" grey gratings	
28	(Table 2, Figs. 7A,C) and first switch target target-trials (Table 3, Figs. 7B,Dusing mean and	
29	normalized amplitudes, and Laplacian values (see Fig. 7). Then scalp topographies of domain-	
30	general P3 and switch related positivities were compared on switch trials (e.g., trials initiated	
31	with a service Bird Birding) in the survey cash only.	
32	Firstly, the scalp topographies of normalized amplitudes for context-locked LPC2 and the	Formatted: Highlight
33	sustained positivity to first targets did not differ significantly between switch and repeat trials	
34	In the switch task (cf., Figs. 7C,D central panels). In contrast, a significant Grey grating x ROI	
36	interaction (F(3, 90)= 10.9, p < 0.0001; GG= .63; η^2 = 0.27), revealed larger normalized LPC ₂	
37	amplitudes for switch than for repeat trials at the midparietal region, whereas the reverse was	
38	true at the trontopolar region (i.e., larger amplitudes for repeat vs. switch trials; Fig. 7C, right	
39	panely, and these differences were replicated with surface capitalian values (Fig. 7.2, Fight	
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41	SecondlyFirstly, significant differences in midline scalp-topographies of context P3 and the	
42	early and latetwo aspects of a late positive complex (LPC) to the switch cues were revealed by	
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19	2-way interactions between ERP and ROI for mean and normalized amplitudes, as well as
20	forand surface Laplacian values (Table 2; Figs. 7A,C). Follow-up tests of effects showed
21	$\underline{revealed}_{\mbox{significant}} differences \underline{t} \mbox{ in the topographies } \underline{offor} P3 \mbox{ and } LPC_1 \mbox{ (amplitudes: P3< LPC_1)} \\$
21	at all sites, all p's <0.002 <u>, Fig. 7A</u> ; vector: non significant; Laplacian: P3> LPC ₁ at frontal; P3<
22	LPC ₁ at central and parietal, all p's <0.005; Fig. 7C). Likewise, there were significant differences
23	scalp in-topographyies differed between P3 and LPC ₂ (amplitudes: P3> LPC ₂ at all ROIs; all p 's
24	<0.004. Fig. 7A; vector: P3> LPC ₂ at frontal and frontopolar; all p's <0.03; Laplacian: P3> LPC ₂ at
25	frontal, <i>p</i> <0.002 <mark>, Fig. 7C</mark>).
26	
27	ThirdlySecondly, significant differences in the scalp topographies topography of target_target1
28	P3 and the early SP1 and late SP2 aspects of a slow positivity to first switch targets also differed
29	as following a switch cue were revealed by 2-way interactions between ERP and ROI for mean
30	and normalized -amplitudes , as well as for<u>and</u> surface Laplacian values (see Table 3<u>; Figs.</u>
31	7B,D). Simple tests of effects showed significant differencest in topographyies between
32	target_target1 P3 and SP1 (amplitudes: P3> SP1 at all ROIs; all p's <0.02, Fig. 7B; vector: non
33	significant; Laplacian: P3→ <sp1 and="" at="" frontopolar="" p3="">SP1 at frontal; p's <0.001, Fig. 7D).</sp1>
24	Likewise, the scalp topography Topographies of of target_target1 P3 and SP ₂ also differed $\frac{4}{2}$ for
34 25	mean amplitudes: P3> SP ₂ at frontal, central and parietal, (all p's <0.002, Fig. 7B;-), but not for
30	<pre>vector: non significant; Laplacian: values non significant(Table 3; Fig. 7D; Table 3).</pre>
30	
31	In sum, statistical <u>these</u> analyses of scalp topographies <u>analyses of scalp topographies</u> for
38	mean and normalized voltages and surface Laplacian values (Figs. 7A-F) showed resulted in
39	significant ERP x ROI interactions when comparing domain-general P3s in the switch task with
40	for the two switch-related P3-like positivities identified in the preceding analyses, namely, a
41	context-locked late positive complex and a target-locked sustained positivity to first target
42	trials (Tables 2 and 3). These analyses spoke againstfailed to support the our null hypothesis,
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19	thus discontirming our original visual impression of apparently similar scalp topographies for switch-related P3-like and domain-general P3 potentials in the switch task (cf., Figs. 4 & 5). On	
20	the contrary, these scalp profile analyses lent support to the alternative hypothesis	
∠ i 22	ofsuggested significant -albeit subtle- split-second changes in the disposition of frontoparietal	
23	sources with varying contextual and task demands (see Fig. 7 ,: cf., K appenman & Luck, 2012;	
24	urbach & Kutas, 2002).	
25	Insert Tables 2 and 3 around here	
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27	Insert Figure 6 around here	
20 29	Insert Figure 7 around here	
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31	Linear Regression Analyses	
32	Finally, Ho further assess the reliability of our model's predictions, we performed linear regression analyses using the mean P3 and P3-like amplitudes from mid-frontal and mid-	
33	parietal ROIs as criteria; predictors were the values of transmitted sensorimotor (S-R)	
34 35	information estimated for all-the six Gabor gratings in used in each the three task contexts (Fig.	
36	2; see Table s7 in the Supplementary material; cf., <u>Cooper</u> , <u>Garrett, Rennie, Karayanidis, 2015</u>).	(Formatted: Strikethrough
37	regression analyses were performed separately for either temporal context. For a more	
38	sensitive analysis of this linear association, the same regression analyses were run separately	
39	for each subject, and t-tests were used to examine whether the standardized (beta) regression	
40 41	weights averaged across all participants differed significantly from zero. The significance of mean beta regression weights across subjects is provided in brackets next to R ² coefficients for	
41	the grand ERP averages. For the grey gratings, a direct <u>association</u> relationship was found	
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between increasing sensorimotor information and larger midparietal amplitudes for context P3 (R²= .664, p= .05; Fig. 8A) [beta= .49, t(30)= 6.12; p= .0001)], and context LPC₁ (R²= .881, p= .008; Fig. 8A) [beta= .73, t(30)= 11.8; p= .0001)], and larger-midfrontal amplitudes for context LPC₁ (R²= .920, p= .002; not shown) [beta= .40, t(30)= 3.8; p= .01)]. Of note, mean context LPC₂ amplitudes were not predicted by sensorimotor information neither at parietal (R^2 = .473, p= .13; Fig. 8A) [although this reached significance across subjects: beta= .34, t(30)= 3.7; p= .01)], nor frontal regions (R²= .524, p= .104) [beta= -.14, t(30)= -1.39; p= .096)], reflecting that this switch-specific ERP-P3-like component was present in the switch task only (cf., Figs. 2 and 8A). For the targets, an inverse relationship was was found apparent between increasing sensorimotor information and smaller target P3 amplitudes, although this did not reach significance neither at parietal (R^2 = .284, p= .28; Fig. 8B) [beta= -.09, t(30)= -.82; p= .42)], nor frontal regions (R2= .445, p= .14) [beta= .09, t(30)= .83; p= .41)]. This is consistent with model's of similar sensorimotor information for targets delivered under all three task contexts (see Fig. 2). Critically, these results concur with our model's predictions that the of ERP : cross different task contexts were mostly linked to porarily unexpected grey gratings rather than to Braver & Barch, 2002; Posner & Petersen, 1990). This is consistent with our model's predictions (Fig. 2) in that the strongest modulations of P3-like positivities across tasks were linked to the processing of unexpected grey gratings rather than to target detection per se (cf., Posner & Petersen, 1990). Insert Figure 8 around here Formatted: Centered

Discussion

This study address	ed one important que	stion for a theoreti	ical integration of I	oast P300
research on the hy	pothesis of context-up	odating (Donchin, 1	1981) with newer E	RP studies on the
cognitive control o	f high-order rule upda	i <mark>ting in t</mark> ask-switch	ing, as hypothetica	lly regulated by a
common frontopa	rietal network of corti	cal regions. Our res	sults provide new e	vidence about
our main research	question, and toward	s-two ancillary hyp	otheses about the	purported
relationship betwe	en domain-general P3	Is and switch-relate	<mark>ed</mark> P3-like positivit	es. Firstly, the
results clearly supp	port that switch-relate	<mark>d</mark> positivities are fu	unctionally distinct	from the two
aspects of domain	general P3s recorded	in simple oddball a	and go/nogo tasks,	including subtle
-albeit significant-	- changes in scalp topo	graphy -relative to	domain-general P	s. Secondly, our
results support the	hypothesis that the t	emporal context (i	.e., the -proactive p	reparation versu
reactive execution	of a simple v isuomoto	or rule <u>s</u>) was a cruc	ial determinant of	the scalp
distribution of both	h domain-general P3s	and switch-related	positivities (Brave	r, 2012; Fuster,
2001). Finally, resu	ilts also lent support to	o our second hypot	thesis that gradual	ly more rostral
larger frontopariet	al P3-like positivities a	ire <u>were</u>elicited wi	ith <u>under</u> higher co	gnitive demands
but only <u>for fortho</u>	<u>se -those </u> P3-like posit	ivities potentials el	licited to by tempo	rarily_surprising
grey gratings<u>event</u>	s that proactively pro	npted prompted f e	or proactive cognit	ive <u>for future</u>
control<u>rule</u> executi	ion , in accord with ou	r information theo	retic estimates of	sensorimotor
information under	different task context	<mark>s (</mark> Cooper et al., 20)16; Koechlin & Su	nmerfield, 2007;
cf., Kopp & Lange,	2013; Verleger et al., :	2014).		
These findings sug	gest that the present s	witch- related posi	tivities are compa	ible with two
types of context-up	pdating mechanisms a	s defined from by	a n information the	oretical model of
cognitive control <u>b</u>	ased on information t	heory: the updatin	g of low-level sens	orimotor S-R
pathways (a doma	in-general mechanism	common to many	tasks), and the up	dating of higher-
order task rules fro	om episodic memory.	When considered a	alongside domain-g	eneral P3s, the
current results are	compatible with the h	hypothesis of switc	hpositivities as pa	art of an
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19	extended P300 family of late positive potentials, and also as plausible neural indexes of a
20	multiple demand system (Duncan, 2013) of frontoparietal generators being differently rapidly
21	engaged under varying contextual demands (Kappenman & Luck, 2012; Urbach & Kutas, 2002).
27	These findings carry far-reaching implications for a redefinition of "the P300" component in
22	terms of an extended family of late ERP-P3-like positivities involved in both low- and high-
23	order-cognitive control-operations.
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25	Two Domain-General P3s Index Distinct Proactive and Reactive Control Modes
26	The present analyses identified two functionally distinct domain-general P3s: one context-
27	locked P3 (350-400 ms) and one target-locked P3 (350-400 ms). These two ERP positivities
28	were examined in its simplest form in response to the infrequent grey gratings and target
29	gratings in the oddball task, respectively; although they were also clearly apparent in the
30	go/nogo and switch tasks. Target _s P3 was most neatly defined in the simplest oddball task,
31	although it was partly overlapped by a slow positivity to first targets in the switch and go/nogo
32	tasks, probably reflecting carry over effects from the additional demands deployed for
33	processing the highly informative grey gratings in those more complex tasks. These two
34	domain-general P3s fit well with the two aspects of conventional P300 potentials, namely, an
35	anterior P3a to rare distracters, and a target P3b with its characteristic midparietal scalp
36	distribution (Polich, 2007). However, these P3-like modulations cannot be explained by the
37	updating of stimulus features alone, but are better accounted for in terms of sensorimotor S-R
38	inks and amount of task-set information field in memory while upnotding, preparing, or
30	executing goar-precised actions (veneger et al., 2014). <u>Vector normalization failed to reveal</u>
10	any uncreases in the monopanetal distribution of these two positivities (rigs, bo)c left
40	B200 component instead mMean amplitudes and surface Lanlacian values of context P3 and
41	target 3 P3 portraved them as two functionally distinct components, since context P3 and
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19	target, P3 were differently modulated very differently by increasing task demands (Fig. 4, 5,
20	6A,B }). This is consistent These results agree w ith the extant literature that describes two
21	functionally and topographically distinct P300 aspects, namely, novelty P3a and target P3b
22	(Debener, Makeig, Delorme, & Engel, 2005; Spencer et al., 1999; Squires et al., 1975), only that
22	our formal operationalization of both temporal and task contexts allows allowed us a much
23	richer and complex-finer-grained functional characterization beyond the conventional "ignore"
24	vs. "attend" dichotomy.
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26	Critically, third target trials elicited very similar ERP waveforms across all tasks, a paradoxical
27	outcome given the intuitive differences in task difficulty also supported by behavioral results.
28	However, this outcome concurs with our model's prediction that, on average, target gratings
29	transmitted similar amounts of sensorimotor information for response selection in all three
30	tasks (Fig. 2). The only reliable difference affected mean target_target3 P3 amplitudes
31	parietally, which were largest for in the simplest oddball task, and smaller in more difficult
32	tasks. This effect is consistent with the reduced target P3b observed in relatively more
33	complex tasks (Donchin, 1981), and is also compatible with carryover interference from
34	competing S-R mappings that <u>may result in lead to diminished</u> reduced target P3b mean P3b
35	amplitude <u>s</u> several trials after a task transition (Barcelo et al., 2002 ; Karayanidis et al., 2003).
36	Thus, it seems plausible that target P3 indexes fundamentally equivalent cognitive resources
37	that are transiently deployed to implement a simple visuomotor rule (i.e., press a button to designated colored taxaets), regardless of additional contextually related and more ordiving
38	designated control targets), regaristess or addictional contextually related and more endoring
39	ouerall tack set information, probability of rule alternations, carryouer of interference, etc.)
40	Hance, target, P2 amplitude: seemed to index transient reactive control operations while
40 //1	implementing single sensorimotor s-r-pathways (cf., Verleger et al., 2014), in agreement with
41	model predictions. This These findings also suggests that target P3b -when disentangled from
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temporal unpredictability (oddballness) and additional overlapping processes- reflects one
type of reactive control-operation largely shared across different many task domains, such as
the execution of simple s _i -r _i pathways (i.e., press a button to designated targets; cf., Verleger
et al., 2014). This is consistent with the definition of a domain-general ERP component once
additional perceptual and motor factors have been adequately controlled for (cf., Barceló &
Knight, 2007; Barceló et al., 2008).
The model accurately predicted contextual effects upon mean P3 amplitudes to the grey
gratings (henceforth-hence described as "context P3") that were mostly sensitive to task
differences in cognitive demands. Overall, context P3 showed a relatively more frontal scalp
distribution for oddball grey gratings, and a relatively more parietal distribution for the most
informative switch grey gratings. A stronger frontalization of context P3 with larger cognitive
demands has been observed in elderly adults using a similar task design (Barceló et al., 2014).
One critical aspect that might account for the functional dissociation between context P3 and
target_target3 P3 is the need to uphold a motor response to the unpredictable onset of grey
gratings within a context of relatively infrequent 'nogo' responses in the go/nogo and switch
tasks, which confer those stimuli \underline{with} higher order sensorimotor information relative to \underline{the}
grey gratings in the oddball task (cf., Verleger et al., 2014; see Supplementary material).
Importantly, stimulus oddballness alone (i.e., the temporal unpredictability of grey gratings
relative to the more predictable occurrence of third-colored target gratings-within the trial
sequence) cannot explain the present results. Instead, context P3 amplitudes captured the
oddballness of specific S-R links involved in the strategic resolution of contextual uncertainty,
as can be formally estimated in terms of low-level and high-level sensorimotor control
(Verleger et al., 2014). This contextual predictability hypothesis would agree with evidence
that infrequent and unexpected distracters convey large amounts of information that may
overshoot working memory capacity, and hence, they thus typically eliciting novelty P3a
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10	potentials with a more rostral anterior scalp distribution (Barceló et al., 2006; cf., Kopp &
19	Lange, 2013).
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21	In sum, target_target3 P3 potentials suggest similar reactive control processes across all task
22	domains, whereas switch-related positivities overlaying context P3 and target_target1 P3
23	potentials hint at distinct proactive and early reactive control operations for across each tasks
24	(Rubinstein, Meyer, & Evans, 2001). This functional dissociation is consistent with the model's
25	predictions, and with carry over effects due to the temporal contiguity between the highly
26	informative grey gratings and the subsequent first targets, not only in the switch task (Monsell,
27	2003), but also in the the cognitively simpler go/nogo task (Allport et al., 1994; Barceló et al.,
28	2008).
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30	A Late Positive Complex (LPC) Indexes Proactive Task Rule Updating
31	A late positive complex (LPC, circa 500-900 ms) with a centroparietal scalp distribution was
32	elicited by grey gratings both in the go/nogo and switch tasks, and was sensitive to the spatial
33	vertical orientation of grey gratings (i.e., switch cues) in the switch task. Both the early LPC1
34	and late LPC_2 aspects showed larger mean amplitudes for switch than repeat cues over
35	centroparietal regions (Figs. 7A, EC, central and right panels). In line with previous results from
36	task-cueing paradigms, this effect may reflect higher-order context-updating operations, such
37	as memory uploading of new S-R mappings in preparation for upcoming targets that need to
38	be classified with new rules (Jost et al., 2008). This could be seen as one type of proactive
20	control operation, presumably one requiring episodic memory retrieval of designated task
39 39	rules (Uayan, 2007), as predicted byconsistent with our our model's of cognitive
4U 44	contropyreauctions (Koechina & Summerikeia, 2007, see Table S5). Topographic profiles of early
41	ereliers (Fig. 6474, control and right earels). Further, subtle differences in the scale
42	regions (Fig. 6427), central and fight panels). Full their, subtle differences in the scalp
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topography of early LPC ₁ and late LPC ₂ pointed to their distinct roles in proactive <u>rule</u> updating
of task rules. The early LPC ₁ was maximal showed maximal frontal intensities in response to
switch cues, with lesser <u>centroparietal</u> intensities for repeat and nogo grey gratings— all with
similar topographies: a centroparietal maximum and larger involvement from frontal regions
for switch cues. In contrast, the late LPC_2 was elicited only by switch cues with a distinctly
larger intensity over parietal regions, and a comparatively lesser frontal involvement (Figs. 4 &
6A7A, C, right panels). This functional and topographical dissociation portrays LPC1 as a lower-
order control process shared by all both task cues and nogo distracters (e.g., the stopping or
inhibition of active $s_i \cdot r_j$ mappings; Robbins 2007), which is a prerequisite for subsequent rule
updating, specifically indexed by the late LPC_2 aspect. Hence, LPC_1 cannot be regarded as a
pure switch-specific positivity (Karayanidis et al., 2009), given that it partly encoded lower-
level sensorimotor control processes also shared by nogo and repeat grey gratings. All in all,
LPC modulations matched well our information estimates for grey gratings in the switch and
go/nogo tasks (Figs. 2 and 8; Table s7 in the Supplementary material), with an early LPC_1
aspect indexing a mixture of both low-level sensorimotor control and high-order task rule
updating, followed by a late \mbox{LPC}_2 more specifically related to rule updating.
In spite of apparently similar centroparietal topographies to that of context P3, sSwitch-related
LPC1 and LPC2 showed distinct scalp topographies, indicative of significant –albeit subtle–
changes in the configuration of underlying sources relative to classic P3 potentials. In general,
LPC amplitudes were larger over centroparietal regions with comparatively smaller intensities
over frontal regions relative to context P3-in the switch task. Towards the end of our long 1200
ms cue-target interval, the switch-related LPC subsided and ERP waveforms for switch and
repeat grey gratings did not differ over parietal regions (Fig. 4), which suggests that proactive
rule updating was <u>fully</u> completed by the onset of the first target trial. This could explain the
absence of local switch costs in the mean RTs of correct trials (cf., Kang, Diraddo, Logan, &

	man, 2014), and it concurs with findings about a transient and short-lived signatur
anticip	atory task-set reconfiguration (Barceló et al., 2002; Barceló et al., 2008 <u>; Kang, et a</u>
<u>2014;</u>	; Jost et al., 2008; Karayanidis , Provost, Brown, Paton, & Heathcote<u>et al.</u>, 2011; La
al., 20	08) , as this operation can be fully completed in less than one second, at least for s
task ru	iles (Kang, Diraddo, Logan, & Woodman, 2014) . Regression analyses suggested a p
associ	ation between the amount of transmitted sensorimotor information and mean LP
amplit	udes over frontal and parietal regions, with grey gratings that overshot memory c
elicitir	g gradually larger <u>LPC_L intensities amplitudes</u> over frontal regions (see Figs. 4 , 6A,
7A <u>8</u> ,8	. This association might explain the presence of restart costs in first target <u>trials</u> tr
follow	ing the nogo distracters and repeat go/nogo and switch tasks <u>cues</u> . In sum, these f
sugge	st context-locked LPCs are a mixture of functionally distinct neural operations, inve
in pro	active rule updating (task-set reconfiguration), probably reflecting higher-order co
updat	ng operations (i.e., proactive rule updating) necessarily more complex to those in
by cor	ventional P300 potentials to rare oddballs-during simple perceptual discrimination
A Sust	ained Positivity (SP) Indexes Early Reactive Task Rule Implementation
A targ	et-locked-slow positivity was elicited by first targets trials following any grey gratin
the sw	ritch and go/nogo tasks—but not in the oddball task (Fig. 4). A- <u>This</u> slow positivity (
lesser	magnitude was also observed to second target trials (not shown), but was absent
third t	arget trials, and has received little attention in past task-cueing studies. Three Two
	s of evidence suggest that the slow positivity to first targets may reflect carryover
source	
source residu	al interference from the previous highly informative grey gratings. Firstly, the slow
source residu positiv	al interference from the previous highly informative grey gratings. First <u>ly</u> , the slow ity was observed only to in those first targets ensuing highly informative grey grat
source residu positiv <u>and th</u>	al interference from the previous highly informative grey gratings. First <u>ly</u> , the slow ity was observed only to in those f irst targets ensuing highly informative grey grat o <u>se</u> and precisely only those that <u>which</u> overshot the theoretical <u>human</u> capacity e
source residu positiv <u>and th</u> huma	al interference from the previous highly informative grey gratings. First <u>ly</u> , the slow ity was observed only 4-in those fi rst targets ensuing highly informative grey grat o <u>se</u> and precisely only those that <u>which</u> overshot the theoretical <u>human</u> capacity e 4- for holding information <u>in memory</u> in working memory (2.5 bits in Fig. 2; Miller,

	value of and P3-like activity evoked by grey gratings (cf., Figs. 2, 4, <u>58)</u> and 8), as well as
	corresponding differences in amplitude of the context-locked late positive complex (Figs. 4,
	5A,B). Finally, in the oddball task, where grey gratings were comparatively uninformative
	events, target P3 amplitudes were similar for first and third target trials suggesting similar
	reactive control across all target trials in the simplest oddball task (Fig. 4).
	In the switch task, the sustained positivity probably reflects additional reactive control during
1	the initial first implementation of a simple visuomotor rule (Rubinstein et al., 2001). These
	carryover effects may persist over several trials following task transition points, presumably
	depending on various task parameters such as task complexity (Allport et al., 1994). However,
	the sustained positivity to first target trials was also present in repeat and nogo trials,
	suggesting differential early reactive control ensuing any grey gratings that overshot the
	theoretical limit for holding information in working memory (2.5 bits in Fig. 2; Miller, 1956).
	The mean amplitude of the slow positivity to first targets was significantly larger following
	"switch" than "repeat" grey gratings, thus providing an electrophysiological index of local
	switch costs at target onset (Fig. 7B), even though this did not translate into significantly
1	longer RTs to correct first targets after a switch cue, probably owing to our long cue-to-target
	intervals. Instead, the marginally larger error rates were observed following switch than repeat
	cues ₂ (9.5% vs. 6.5% respectively, p= 0.08), which suggests this slow positivity could somehow
	interferged with efficient rule execution on first target trials (Rubinstein et al., 2001). Further
	research will be needed to clarify this dissociation between behavioral and
	electrophysiological indexes of local switch costs.
	Finally, a large portion of residual behavioral costs, the mixing cost, was not captured by
	transient ERP waveforms to third target trials. Nevertheless, one might expect this mixing cost
	to be reflected on otherin indexes of more enduring or sustained neural activity, perhaps one
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19	sensitive to the overall amount of task-set information, $\boldsymbol{\Sigma}(s_{\textit{f}})$, that needs to be continuously
20	held in working memory during a <u>the whole trial taskblock</u> . This post hoc hypothesis warrants
21	further examination using further indices of sustained neural activity, as well as through a
22	finer-grained parametrical manipulation of the total amount of task-set information.
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20	Limitations and Future Challenges
24	There are a number of limitations in our attempt to model ERP_P3-like positivities from an
20	information theoretical theory approach. Firstly, even though the largest differences in the
20	amplitudes of context-locked ERP positivities appeared over centroparietal regions, our model
27	predicted gradually more rostral-frontal activations with increasing task demands (Koechlin &
28	Summerfield, 2007). Such a frontalization effect with larger cognitive demands has been
29	observed in elderly adults using a similar paradigm (Barceló et al., 2014). However, this rostral
30	frontal displacement might be partly hidden by overlapping frontal negativities in our young
31	adults (Fig. 4, upper row), which suggests that formal models need to take into account
32	individual differences in age and behavioral efficiency. Instead our information estimates were
33	done for an ideal subject with 100% correct responses, which can be regardedis a good
34	approximation given the high accuracy attained of by our young participants in all tasks.
35	Secondly, our information metrics did not consider some sources of contextual effects that
36	may also modulate ERP positivities such as trial-by-trial perceptual and motor priming effects,
37	or S-R spatial compatibility (Simon) effects. More fine-grained information theoretical analyses
38	are warranted to decide the potential contribution from additional contextual demands to
20	those late EKP positivities. This aim could be achieved through a systematic parametrization of
39	low- and nigher-order sensorimotor control processes, for instance by varying overall task-set
40	information through the number of response alternatives, the number of potential task rules,
41	or the entropy of task-stimuli and responses (Barcelo & Knight, 2007; Barcelo et al., 2008; Kopp
42	& Lange, 2013). I hirdly, our long interstimulus intervals favored a temporal segregation of EKP
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positivities. However, shorter intervals will likely result in a greater overlap between domain-

general <u>P3s</u> and switch-related <u>P3-like</u> positivities (Karayanidis et al., 2003; Lavric et al., 2008;

Nicholson et al., 2005), which explains why they may be easily mistaken (Barceló et al., 2006;

Jost et al., 2008; Tieges et al., 2007]. Moreover, time constrains are a crucial determinant of

more sophisticated formal models of cognitive control. Finally, conventional analyses of mean

ERP amplitudes at the sensor space were preferred to favor integration with the extant ERP

literature. However, the relative implication of specific nodes within the frontoparietal

network will require more sophisticated procedures for identification of underlying ERP

Kappenman & Luck, 2012]; Mansfield, Karayanidis, & Cohen, 2012) and independent

component analyses (ICA; Debener et al., 2005; Makeig et al., 1999Enriquez-Geppert &

Barceló, in press; Makeig et al., 1999).

Conclusions

components, such as source localization, time-frequency decomposition (Cooper et al., 2016;

The scalp topographies of two domain-general P3s (350-400 ms) differed significantly from the

scalp topography of later switch-related P3-like positivities (500-900 ms) during both proactive

and reactive control of task-switching. A strict interpretation of this outcome points to distinct

configurations of underlying sources for conventional P300 potentials elicited by infrequent

positivities potentials observed in task-switching (Barceló et al., 2006; Karayanidis et al., 2003;

Whitson et al., 2014). However, direct visual inspection of scalp topographies shown in Fig. 5

suggests all those ERP_P3-like positivities are still compatible with an extended family of P300

potentials with subtly distinct configuration of sources as a function of gradually more complex

cognitive demands. Importantly, the largest modulations in this family of P300 potentials were

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oddballs (Spencer et al., 1999; Squires et al., 1975), as compared to the late ERP-P3-like

arietal network. Therefore, temporal constraintsthey should be incorporated in

behavioral costs (Monsell, 2003), and will likely pose additional demands on the

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10	observed during context-updating in response to the relatively temporarily surprising grey
20	gratings and in anticipation to target onset onset (cf., Braver & Barch, 2002; Posner &
20	Petersen, 1990; Petersen & Posner, 2012). After all, it would be reasonable that a putative
21	brain index of "context updating" engaged correspondingly more complex neural machinery to
22	update sensorimotor representations during simple visual oddball discriminations as
23	compared to higher order representations of updating of task-set information (cf., Barceló &
24	Knight, 2007).
25	
26	In spite of fine-grained topographic differences with domain-general P3s, the observed switch-
27	related ERP positivities showed a centroparietal scalp distribution compatible with an
28	extended family of P3-like potentials observed across a large variety of many task domains (i.e.,
29	attention, memory, language, decision-making, etc). Indeed, many authors would readily
30	identify the present switch-related positivities with evoke a late positive complex (LPC) that
31	has long been traditionally associated with conventional the classic P300 potentials in terms of
32	its latency, centroparietal scalp distribution and response to experimental variables
33	(Kappenman & Luck, 2012; Polich, 2007). In fact, few authors attempt a fine-grained
34	topographical analysis like the one accomplished here to substantiate verify the nature of
35	P300 potentials recorded in a variety of task domains (Holig & Berti, 2010). More sophisticated
36	source localization studies are needed to specify whether these subtle changes in scalp
27	topography owe to different weighting of sources within a common frontoparietal network, or
37	to overlapping activity from additional sources, and how all these are modulated by varying
38	contextual demands. From this perspective, "the P300" cannot be regarded as a single ERP
39	component -sensu strictu it has never been such a thing. Instead, it might well correspond
40	with the electrophysiological signature of a multiple demand system (Duncan, 2013). for the
41	integration of contextually relevant information in a wide variety of cognitive domains (cf.,
42	Duncan, 2013) (Braver & Barch, 2002; Duncan & Owen, 2000; Woolgar et al., 2011). The
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2 3 4 5 6 7 8 9 10 11 23 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 32 4 25 26 27 28 29 30 31 32 33 4 35 36 37 37 37 37 37 37 37 37 37 37	rostrefronto esudal parietal scalp topography and intensity of the this extended family of P300 P3-like potentials critically depends on the temporal context for goal-directed behavior (i.e., proactive versus reactive control modes; Braver, 2012), as well as on <u>a hierarchy of</u> Jow- and higher-order sensorimotor demands that can be finely operationalized with more formal models of cognitive control (Cooper et al., 20016; Koechlin & Summerfield, 2007).
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19 20	Footnotes
21	¹ As clarified in the Method section, the distinction between domain-general and switch- related ERP-P3-like positivities relied on their sensitivity to experimental factors (i.e., switch vs.
22 23	repeat trials) and on their distinct scalp topographies. However, given the large variability in
24	the latency of P300 potentials with task complexity (Kutas, McCarthy, & Donchin, 1977), latency was not regarded as a criterion to differentiate ERP components positivities
25 26	(Kappenman & Luck, 2012), and _Hence, switch positivities were sampled from a wider (300-
27	900 ms Jiatency window, consistent with previous task-switching studies.
28 29	² A bilateral display was intended for <u>to</u> assess ment of h emispatial attention deficits in
30	unilateral brain lesioned patients (cf., Barceló & Knight, 2007). A pilot study showed this
31 32	bilateral display did not significantly modulate late switch ERP positivities relative to a more conventional central display.
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Figure captions

Figure 1. Task design, stimulus material and S-R mappings. All three tasks consisted of the
same sequence of frequent color gratings with semi-randomly interspersed infrequent grey
gratings. (A) In the switch task, vertical and horizontal grey gratings instructed participants to
switch and repeat the previous S-R mapping, respectively. (B) The go/nogo task consisted of
two-forced choice responses ('press button 1 for red gratings, and button 2 for blue gratings');
and (C) the oddball task involved one-forced choice responses (i.e., 'press a button to all red
gratings'). Participants were explicitly instructed not to respond to the grey Gabor gratings.
Hypothetical task-set information and S-R mappings for correct performance are also shown
for each task. Cognitive demands were manipulated by (1) varying the amount of task-set
information to be handled in working memory (oddball vs. go/nogo task); and (2) by varying
the type of contextual information conveyed by the grey gratings for anticipatory updating of
active S-R mappings (go/nogo vs. switch task).
Figure 2. A priori estimations of transmitted information, I(si, rj), between stimuli and
responses as a function of the sensory entropy, $H(s_i) = -p(s_i) \cdot \log_2 p(s_i)$, of grey and color
gratings in the three tasks (or input-output correlations; c.f, Miller, 1956). The dotted line
marks the theoretical human capacity for holding information in working memory: 2.5 bits.
Accordingly, targets conveyed the same information for response selection across all tasks. In
turn, grey gratings carried varying amounts of information for response selection in the
oddball, go/nogo and switch tasks. The information transmitted from stimuli to responses is
derived from the notion of mutual information, $l(S; R)$, between the sets of stimuli, $S = \{s_1, s_2, \dots, s_n\}$
$s_{3r},s_{5r},s_{6}\},$ and associated responses, R= {r_0, r_1, r_2}, in our three tasks (cf., Attneave, 1959;
Koechlin & Summerfield, 2007; see details in the Supplementary materials).

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18	Flower & Debuilded and the Management of the Management
19	Figure 3. Behavioral results. Mean reaction times (RTs) to correct target trials and error rates
20	as a runction of target trial position following a grey grating in each of the three tasks. Residual
21	restart and mixing costs were observed in both correct (left panel) and incorrect trials (right
22	paneny. Local (switch > repeat) costs were observed to the first target in incorrect trials only
23	(ngiri panei).
24	Figure 4. Grand average FRDs. Brain responses are shown from midling fronted and ender
25	Rols to vertical and horizontal grey gratings and to the first and third target grations in the
26	where we were treat and intercontent grey gradings and to the first and third target gradings in the
27	also elicited a sustained positivity of lesser intensity to that of first target trials. Continuous
28	lines: Trial runs starting with a vertical grav grating. Dashed lines: trial runs starting with a
20	horizontal grey grating. Note, the largest differences in the intensity of domain-general D2 and
29	switch-related positivities occurred in resonance to grev gratings as well as to the ensuing first
30	l Target trials. In sharn contrast, task differences in mean amplitude were less annarent in third
31	target trials. Scalp tonorganhies of mean amplitudes (JVD and surface Lanlacian values
32	$(u_{\mu})_{\nu}$ could share to possible on mean amplitudes (μ) and sufface Laplacian Values
33	(pryshin yoke shown for switch class at three latency windows of interest. 350-400 mS, 550-600 [ms, and 750-800 ms.
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35	Figure 5. Scalp topography of domain-general P3 and switch-related ERP-P3-like positivities
36	(A) Scalp distribution of mean voltages for context-locked P3. I PC+ and I PC+ nositivities to
37	vertical and horizontal grey gratings across the three task domains. (B) Scalo distribution of
38	target-locked P3, SP1 and SP2 positivities to first target (target_target1) trials following grev
39	gratings in the switch task. (C) Scalp distribution of domain-general target P3 and LPC.
40	positivities to third target (target_target3) trials across the three task domains.
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-⊤- //2	Figure 6. Topographic profiles of domain-general P3 and switch-related positivities across
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three task domains. (A) Mean amplitudes of context P3 and the early (LPC_1) and late (LPC_2) cts of the alate positive complex (LPC) in response to grey gratings under different tas demands. (B) Mean amplitudes of target P3 and two aspects of the late po in response to third target (target, target3) trials under different task demands. (C) and (D) and (F) present surface Laplacian values for the same conditions as in (A) and (B). Figure 7. Topographic profiles of domain-general P3 and switch-related positivities for switch and repeat trials in the switch task. (A) Mean amplitudes of context P3 and the early (LPC1) and late (LPC₂) aspects of the late positive complex (LPC) in response to grey gratings prompting for a switch and repetition in task rules, respectively. (B) Mean amplitudes of target P3 and the early (SP1) and late (SP2) aspects of the slow positivity (SP) in response to first target trials following grey gratings prompting for a switch and repetition in task rules. (C) and (D) present in (A) and (B). (E) and (F) litudes for the s present surface Laplacian values for the same conditions as in (A) and (B). Figure 8. Linear regression of mean P3-like amplitudes against the amount of sensorimotor information transmitted by vertical and horizontal grey gratings (A) and the ensuing target_target3 gratings (B) across the three task contexts. Three functionally and topographically distinct P3-like components are modelled in response to the grey Gabor gratings: P3 (circles), LPC1 (squares), and LPC2 (triangles). Only one P3-like component is modelled in response to target Gabor gratings: P3 (black circles). In line with our model's predictions, only the switch task showed significant differences in mean P3-like amplitudes between vertical and horizontal grey gratings (eff.i.e., Switch-repeat vs. Switch-switch cues). 54

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Table 1. ANOVAs showing task effects for two measures of context P3 and target3 P3

Context P3

		Amplitudes		Surface Laplacian		
	df	F	η2	F	η2	
Task	2,60	6.2**	0.17	22.1***	0.42	
Task x ROI	6, 180	15.5***	0.34	13.9***	0.32	

Tai	rget3	P3
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		Amplitudes		Surface Laplacian		
	df	F	η2	F	η2	
Task	2, 60	2.48 ns	0.08	0.60 ns	0.02	
Task x ROI	6, 180	9.8***	0.25	4.2**	0.12	

* *p* < 0.05; ** *p* < 0.01; *** *p* < 0.0001

Table 2. ANOVAs comparing the scalp topographies of context P3 and two aspects of the late positive complex (LPC) in the switch task

Context P3 vs. LPC

		Amplitudes				Surface Laplacian				
		LPC ₁		LPC ₂		LF	LPC ₁		LPC ₂	
	df	F	η2	F	η2	F	η2	F	η2	
ERP (<i>P3 vs. LPC</i>)	1, 30	13.4**	0.30	17.3***	0.37	10.8***	0.27	35.7***	0.54	
ERP x ROI	3, 90	4.8*	0.13	9.3***	0.24	12.4***	0.29	8.6***	0.22	

* *p* < 0.05; ** *p* < 0.01; *** *p* < 0.001

Psychophysiology

Table 3. ANOVAs comparing the scalp topographies of target1 P3 and two aspects of the sustained positivity (SP) in the switch task

Target1 P3 vs. Slow Positivity (SP)

		Amplitudes				Surface Laplacian			
		SP ₁		SP ₂		SP_1		SP ₂	
	df	F	η2	F	η2	F	η2	F	η2
ERP (P3 vs. SP)	1, 30	13.2***	0.31	22.1***	0.42	0.01 <i>ns</i>	0.000	0.33 ns	0.011
ERP x ROI	3, 90	13.1***	0.30	21.1***	0.41	8.2***	0.22	2.65 ns	0.08

* *p* < 0.05; ** *p* < 0.01; *** *p* < 0.0001























Figure 6 Figure 6






Supplementary material

Information theoretic estimations of sensory, motor, and sensorimotor control at two levels of a putative hierarchy of cognitive control for the switch, go/nogo and oddball tasks (cf., Attneave, 1959; Barceló et al., 2008; Koechlin & Summerfield, 2007; Miller, 1956).

Stimulus Entropy: $H(s_i) = -\sum_{i=1}^6 p(s_i) \cdot \log_2 p(s_i)$

Table s1. All tasks. The same set and sequence of stimuli were used in all three tasks, and therefore, the same stimulus entropy can be assumed for all tasks:

$\begin{array}{c ccccccccccccccccccccccccccccccccccc$	Gabors	S	H(s)	p(s)	$-\log_2 \cdot p(s)$
$\begin{array}{c ccccccccccccccccccccccccccccccccccc$		<i>S</i> ₁	0.29	0.08	3.64
$\begin{array}{c ccccccccccccccccccccccccccccccccccc$	=	<i>S</i> ₂	0.29	0.08	3.64
$\begin{array}{c ccccccccccccccccccccccccccccccccccc$	-	S 3	0.47	0.21	2.25
$\begin{array}{c ccccccccccccccccccccccccccccccccccc$	-	<i>S</i> ₄	0.47	0.21	2.25
$\frac{s_6}{\Sigma H(s_i)} = \frac{0.47}{2.46}$	-	S ₅	0.47	0.21	2.25
Σ H(<i>s</i> _{<i>i</i>})= 2.46	=	<i>S</i> ₆	0.47	0.21	2.25
		$\Sigma H(s_i) =$	2.46		

Response Entropy: $H(r_j) = -\Sigma_0^j p(r_j) \cdot \log_2 p(r_j)$

Table s2. Oddball task. This task required one-button responses (r_1) and the absence of response (r_0) to all non-targets. The response set can be defined as $\mathbf{R} = \{r_0, r_1\}$

R	<i>H</i> (r)	<i>p</i> (r)	-log₂· <i>p</i> (r)
r ₀	0.45	0.58	0.78
<i>r</i> ₁	0.53	0.42	1.26
ΣH(<i>r</i> _i)=	0.98		

Table s3. Go/nogo and switch tasks. These two tasks required two-button responses (r_1, r_2) and the absence of response (r_0) to the grey gratings. Hence, the response set is $\mathbf{R} = \{r_0, r_1, r_2\}$

R	<i>H</i> (r)	<i>p</i> (r)	$-\log_2 \cdot p(r)$
r _o	0.43	0.16	2.60
<i>r</i> ₁	0.53	0.42	1.26
<i>r</i> ₂	0.53	0.42	1.26
ΣH(<i>r_j</i>)=	1.49		

Sensorimotor Information: $I(s_i, r_j) = \log_2 p(s_i, r_j) - \log_2 p(s_i) - \log_2 p(r_j)$

¹ For simplicity, these estimates assume a stimulus set $\{S\}$ with only six stimuli, regardless of the fact that each Gabor grating was randomly displayed either to the left or the right visual hemifields.

The information transmitted from stimuli to responses, $I(s_i, r_j)$, is derived from the notion of mutual information between sets of stimuli {*S*} and responses {*R*} (Attneave, 1959):

$$I(S;R) = \sum_{i} \sum_{j} p(s_i, r_j) \log \frac{p(s_i, r_j)}{p(s_i)p(r_j)}$$

Table s4. Oddball task. This task required one-button responses (r_1) only to the red Gabor gratings (s_5 , s_6), and hence, low-level sensorimotor control for the relevant task-set units (s_i - r_j) in the oddball task can be estimated as follows:

S-R	$p(s_i)$	$p(r_j)$	$p(s_i, r_j)$	$I(s_i, r_j)$
<i>s</i> ₁ - <i>r</i> ₀	0.08	0.58	0.08	0.78
<i>s</i> ₂ - <i>r</i> ₀	0.08	0.58	0.08	0.78
<i>s</i> ₃ - <i>r</i> ₀	0.21	0.58	0.21	0.78
<i>s</i> ₄ - <i>r</i> ₀	0.21	0.58	0.21	0.78
<i>s</i> ₅ - <i>r</i> ₁	0.21	0.42	0.21	1.26
<i>s</i> ₆ - <i>r</i> ₁	0.21	0.42	0.21	1.26
				$\Sigma(s_i r_i) = 5.64$

Table s5. Go/nogo and switch² tasks. These two tasks required two-button responses (r_1 , r_2) to classify blue and red Gabor gratings (s_3 , s_4 , s_5 , s_6), and hence, low-level sensorimotor control for the relevant task-set units (s_i - r_i) when sorting by color can be estimated as follows:

S-R	$p(s_i)$	$p(r_j)$	$p(s_i, r_j)$	$I(s_i, r_j)$
<i>s</i> ₁ - <i>r</i> ₀	0.08	0.16	0.08	2.61
<i>s</i> ₂ - <i>r</i> ₀	0.08	0.16	0.08	2.61
<i>s</i> ₃ - <i>r</i> ₁	0.21	0.42	0.21	1.26
<i>s</i> ₄ - <i>r</i> ₁	0.21	0.42	0.21	1.26
<i>s</i> ₅ - <i>r</i> ₂	0.21	0.42	0.21	1.26
<i>s</i> ₆ - <i>r</i> ₂	0.21	0.42	0.21	1.26
				5/) 10.00

 $\Sigma(s_i r_j) = 10.26$

Episodic Information: $I(s_i, ts_k) = \log_2 p(s_i, ts_k) - \log_2 p(s_i) - \log_2 p(ts_k)$

Table s6. Switch task. Only the Switch task required access to episodic task-set (ts_1) information on just 8% of all trials (s_1 - ts_1), while no task-set access (ts_0) was required in the

² Sensorimotor information in the switch task was slightly (~ 1 bit) larger for those color gratings that afforded bivalent responses (i.e., different buttons for either rule). For simplicity this additional source of contextual information was not included here.

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remaining trials. The transmitted information between sensory stimuli and access to episodic memories in this task can be estimated as follows:

S-TS	$p(s_i)$	$p(ts_k)$	$p(s_i, ts_k)$	$I(s_i, ts_k)$
<i>s</i> ₁ - <i>ts</i> ₁	0.08	0.08	0.08	3.61
<i>s</i> ₂ - <i>ts</i> ₀	0.21	0.92	0.21	0.12
<i>s</i> ₃ - <i>ts</i> ₀	0.21	0.92	0.21	0.12
s_4 - ts_0	0.21	0.92	0.21	0.12
<i>s</i> ₅ - <i>ts</i> ₀	0.21	0.92	0.21	0.12
<i>s</i> ₆ - <i>ts</i> ₀	0.21	0.92	0.21	0.12
				$\Sigma(a+a) = 1.21$

 $\Sigma(s_i t s_k) = 4.21$

Table s7. Summary of numerical values plotted in Figure 2. Transmitted S-R information for each task stimulus was estimated as summated information across two levels in the putative hierarchy of sensorimotor information processing (i.e., s_1 in the switch task= 2.61 + 3.61= 6.22 bits; s_1 in the NoGo task= 2.61 + 0= 2.61 bits, and in the Oddball task= 0.78 + 0= 0.78 bits).

	<i>S</i> ₁	S ₂	S ₃	S 4	S 5	S ₆
Switch	6.22	2.73	1.38	1.38	1.38	1.38
Go/NoGo	2.61	2.61	1.26	1.26	1.26	1.26
Oddball	0.78	0.78	0.78	0.78	1.26	1.26

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