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# How non-veridical perception drives actions in healthy humans: evidence from synaesthesia

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We continually perform actions that are driven by our perception and it is a commonly held view that only objectively perceived changes within the 'real' world affect behaviour. Exceptions are generally only made for mental health disorders associated with delusions and hallucinations where behaviour may be triggered by the experience of objectively non-existent percepts. Here, we demonstrate, using synaesthesia as a model condition (in $N = 19$ grapheme-colour synaesthetes), how objectively non-existent (i.e. non-veridical) but still non-pathological perceptions affect actions in healthy humans. Using electroencephalography, we determine whether early-stage perceptual processes (reflected by P1 and N1 event-related potential (ERP) components), or late-stage-integration processes (reflected by N2 component), underlie the effects of non-veridical perceptions on action control. ERP analysis suggests that even though the examined peculiarities and experimental variations are perceptual in nature, it is not early-stage perceptual processes, but rather higher-order executive control processes linking perceptions to the appropriate motor response underlying this effect. Source localization analysis implicates activation within medial frontal cortices in the effect of how irrelevant non-veridical perceptions modulate behaviour. Our results challenge common conceptions about the determinants of human behaviour but can be explained by well-established theoretical frameworks detailing the link between perception and action.

This article is part of a discussion meeting issue 'Bridging senses: novel insights from synaesthesia'.

## 1. Introduction

We continually perform actions driven by our perceptions, and it is commonly held that only objective changes of perceptual aspects in the 'real' world (that are *veridical*) can affect our behaviour. This common-sense assumption has dominated research to such a great extent that it seems counterintuitive that perceptual aspects lacking perceptual presence (that are *non-veridical*) affect our motor responses and behaviour in healthy humans. Exceptions are usually made for instances of mental illnesses, associated with delusions or hallucination. In the current study, we challenge this view by showing how sensorimotor integration is modulated by objectively non-existent but still non-pathological perceptions.

It is well established that objective perception and action are intimately intertwined and strong theoretical frameworks have been put forward focusing on this link. One of these is the theory of event coding (TEC) [1] formulating a theoretical basis for action–perception interactions central for sensorimotor integration processes and cognitive control. TEC states that to-be-produced events (i.e. actions) and perceived external events (i.e. stimuli) are coded for by their constituting feature codes within a common format—the 'event file' [2]. Stimuli,

such as letters, for example, may be coded by objective features, such as their shape (e.g. italics or bold), colour and identity (e.g. A, B, etc.) as well as subjective associations that may accompany a specific stimulus–response relation (i.e. affordances). These features are closely bound to one another (i.e. integrated) to achieve a coherent perception facilitating behavioural responses. Likewise, action or (re-)actions (i.e. to-be-produced events) are represented by features detailing a potential outcome and, for example, hand or finger movements used to execute a response. Hence, event files establish bindings between features specifying a stimulus and features specifying an action [3]. The activation of an event file follows a pattern-completion logic, meaning that the entire event file can be (re-)activated once a single feature of either a stimulus or a response is (re-)encountered. TEC proposes that whenever there is a perception of a stimulus that has previously been integrated in an event file, this can affect actions [3]. For this to happen, *all* perceived and integrated stimulus features are relevant to consider [3]. Notably, stimulus representations can be enriched by idiosyncratic, object-related associations [2] and stimulus features can get automatically bound to a response and affect it even if its presence is neither necessary nor useful for an action outcome [3]. It is therefore conceivable that actions are modulated by non-pathological, but still objectively non-existent, idiosyncratic enriched perceptions, i.e. by perceptual aspects lacking perceptual presence or real-world perceptual veridicality if they are automatically activated and integrated into an event file.

A prime example of perceptual idiosyncrasy in healthy humans is synaesthesia, a condition in which the experience of a veridical percept (i.e. the inducer) consistently and automatically elicits a vivid experience in another modality (i.e. the concurrent) [4–8]. Importantly, individuals with synaesthesia know that the inducer is objectively 'there', while the perceived synaesthetic concurrent lacks objective perceptual presence (i.e. is non-veridical) [9]. Thereby, synaesthesia can clearly be differentiated from hallucinations and delusions associated with psychopathology or drug-induced states, and can serve as a useful tool for studying the underlying neurophysiology of healthy non-veridical perceptions relevant to the higher-order cognitive control of action [10,11]. Using synaesthesia as a model condition, we show how non-pathological perceptual feature dimensions that are not objectively perceived as present in the real world (i.e. are non-veridical) and that are irrelevant for an action nevertheless modulate the control of an action. Studies within the field of synaesthesia research have shown that an additional idiosyncratic experience triggered by an inducer can have advantageous effects on cognition, for example, in the domain of memory performance [12,13]. However, it has also been shown to have adverse effects on synaesthetes' performance, for example, when a presented stimulus is incongruently coloured to their perceived non-veridical synaesthetic colour; comparable to a Stroop-like conflict (i.e. 'synaesthetic Stroop-effect') [14]. Notably, in these instances, colour acts as a task-relevant stimulus dimension and thus, directly interferes with the task at hand (i.e. colour naming) on incongruent trials and therefore contrasts with standard 'synaesthetic Stroop' tasks that are not able to clarify how non-veridical percepts affect action control.

Within the field of action selection, it has been suggested that processes operating on action-irrelevant perceptual information reflect automated processes, while processes operating on task or action-relevant perceptual information are more controlled. If non-veridical sensory content is task-irrelevant but should nevertheless affect action control, it is hypothesized that non-veridical perceptual information modulates action selection only in situations where automated processes govern action selection. No effects of non-veridical task-irrelevant perceptions should be evident under more controlled action selection processes. To examine this, we employ a novel experimental paradigm combining a Simon task with a Go/NoGo task specifically designed to measure inhibitory control performance within the context of automatic and controlled action selection modes [15,16] (refer to Material and methods for details). Participants are asked to respond to letter stimuli (the letters 'A' left key and 'E' right key: Go) and withhold responses to the same letters printed in bold-italic style ('***A***' and '***E***': NoGo). Thus, each letter stimulus is bound to a clear response. It has been shown that in spatially *corresponding* (i.e. stimulus presented at the same side as response hand) conditions where stimulus–action binding is mediated via automated processes [17], response inhibition is worse, compared to spatially *non-corresponding* (i.e. stimulus presented at opposite side of response hand) task conditions where stimulus–action binding is mediated via controlled processes [15,16,18–20].

These stimulu–response spatial congruity paradigms are referred to as Simon tasks. The current task can be completed by simply attending to the target letters' identity ('A' or 'E') or shape ('***A***' and '***E***') without taking into account the colour in which the letter is presented. However, for synaesthetes, processing of a letter is intimately bound to the experience (i.e. the activations) of a colour dimension. Crucially, a specific semantic representation of a letter stimulus (e.g. 'A') will evoke the same, consistent and automatic experience or colour (e.g. red) independent of its appearance or 'shape' (i.e. 'A', 'a', 'ɑ', '*A*' or '***A***' → red) [4,21–23]. Importantly, even though this additionally activated synaesthetic experience is task-irrelevant, it is likely to be an integral part in event files in synaesthetes. Within the group of synaesthetes, the idiosyncratically perceived non-veridical colour feature consistently accompanying the perception of a letter will, in fact, serve as an overlapping feature between different stimulus–response mappings (or event files). That is, a subjectively perceived colour (i.e. red for 'A') represents a feature that is integrated into two event files coding for *opposing* stimulus–response representations ('A': Go/'***A***': NoGo).

According to TEC, feature overlap between event codes impairs behavioural control, because the cognitive representation of the stimulus–response relationship (consisting of several feature codes) has to be continuously updated and re-constructed according to the intended action (react or withhold reaction), making the behavioural response more prone to error. Anecdotal evidence suggests that synaesthetes experience a feeling of discomfort whenever they perceive incongruence between a concurrent of certain grapheme and an actually presented colour. Thus, by precisely modifying the presented colour of the letter, we can adapt the target stimuli to be either matching or mismatching with the subjective non-veridical colour experience of the synaesthete. This causes 'idiosyncratic conflict' to arise between the subjective experience of a non-veridical colour of the individual synaesthete and the colour of the objectively present (veridical) letter stimulus. We predict that the presentation of a

mismatching colour of the target letter will negatively affect response inhibition (i.e. it will increase false alarm rates in synaesthetes). This will only be the case in automated, not controlled, action selection modes. Specifically, we predict that within the automatic condition, false alarm rate should increase, while response inhibition should improve (i.e. false alarm rate decreased) within the controlled task context.

To examine whether effects of non-veridical experience specifically affect the response selection level, we examine neurophysiological (electroencephalography—EEG) data. Response selection, conflict monitoring and adaptation processes have consistently been shown to be reflected by the N2 event-related potential (ERP) [24], reflecting processes of the anterior cingulate cortex (ACC) and more rostral regions including the supplementary motor area [24]. The medial frontal cortex has been shown to orchestrate the connection of perception and action [25] due to its hub-like structural and functional connection to sensory and motor areas [25,26]. If non-veridical experience affects cognitive control, these processes in particular are hypothesized to be differentially modulated between synesthetes and controls. In synaesthetes, we expect stronger N2 amplitudes in response to the existence of a non-veridical conflict between stimulus dimensions (i.e. mismatching non-veridical feature condition). By contrast, these differences in modulations are not expected for the controls. If the effects are specific for response control, there should be no effects in correlates of salience-based bottom-up perceptual and attentional selection processes (i.e. P1 and N1 ERP components) [27].

## 2. Material and methods

### (a) Participants

The sample size was estimated *a priori* assuming low-to-medium effect sizes ($f^2 = 0.30$), an $\alpha$ error probability of 5% and a power of 95%. We estimated a total sample size using G-Power software (http://www.gpower.hhu.de/). This estimation revealed a minimum total sample size of $n = 26$ (i.e. $N = 13$ participants for each group). However, we included $N = 22$ grapheme-colour synaesthetes (19 female/3 male) between age 19 and 43 (31 ± 8 years of age) and $N = 22$ gender-, education- and age-matched controls into the study. Importantly, and as shown in the Results section, the achieved power for the critical interaction of 'Go versus NoGo × non-veridical feature match × congruency × group' in the ERP data was $\eta_p^2 = 0.637$ ($f^2 = 1.32$) (refer to data analysis of the N2 ERP component). Thus, the effect size observed in the results is much stronger than that used to estimate necessary sample size in our *a priori* calculations. In fact, the results show that the assumption on which the effect size estimation is based actually reflects a conservative estimate of effects. The empirical data show that the obtained effect is much stronger.

Matched controls were selected from the general population and screened with a questionnaire to ensure they did not experience grapheme-colour synaesthesia. We did not control for the co-occurrence of potential other types of synaesthesia (such as sequence-space synaesthesia) in our participants, because the current task required responses to single-letter graphemes rather than sequences of graphemes or words.

All participants had normal or corrected-to-normal vision and were screened on personal health background to ensure the sample was free of individuals previously diagnosed with any psychiatric disorders or taking regular medication (except birth control). All participants gave written informed consent prior to taking part in the experiment and received payment (12.50 £ $h^{-1}$) or equivalent SONA credits (for Psychology students at the University of Sussex) after completion of the study. Three participants had to be excluded due to health reasons (epilepsy), insufficient synaesthetic consistency or low EEG data quality, resulting in a total of $N = 19$ participants (17 female/2 male; age 29.9 ± 11 years of age) for each group included in the data analyses. Synaesthetes were recruited from an existing synaesthesia database at the University of Sussex. Prior to completing the experimental task, synaesthetic consistency was checked using the Eagleman Battery [24,28]. The Eagleman Battery is a set of online tests (freely accessible on http://www.synesthete.org) to determine the genuineness of different types of synaesthesia. Synaesthetes are asked to indicate the colour concurrent they perceive for graphemes 0–10 and A–Z on a colour picker resulting in an RGB code for each grapheme for which consistency is calculated. The grapheme-colour consistency of our sample of synaesthetes was confirmed by an average score of 0.74 ± 0.12, which was significantly below the proposed cut-off value of 1.43 (28) ($t_{18} = -15.13$, $p < 0.001$).

### (b) Task and procedure

The experiments took place in a dimly lit shielded Faraday cage. Stimuli were presented on a computer running Presentation Software (neurobehavioural systems). Participants were seated in front of a 22 inch cathode ray tube monitor running at 100 Hz refresh rate. Participants executed responses via the left and the right 'CRTL button' on a low latency keyboard. The monitor was placed at eye-height, and the viewing distance was 60 cm.

Participants were asked to place their left index finger on the left CRTL key and their right index finger on the right CRTL key. A white fixation cross was continuously presented on a dark-grey background in the centre of the screen. The fixation cross was always accompanied by white frame boxes presented on the same vertical level at 1.1° visual angle left and right of the fixation cross.

The 'Simon Go/NoGo' task [15,16] requires participants to respond to single target letter stimuli presented in normal font (i.e. 'A' or 'E'; Go trials), and to withhold responses when target letters are presented in bold italics ('***A***' or '***E***'; NoGo trials). Whenever an 'A' was presented, a left-hand response was required. Whenever an 'E' was displayed, a right-hand response was required. These responses were required, irrespective of the spatial position of the letter stimulus, i.e. irrespective of whether the letter appeared in the left or right white frame box on the screen. Thus, the only task-relevant stimulus features for completing the task were the letters' identity ('A' or 'E) and shape (bold-italics style) and all participants were instructed that these are the only relevant feature dimensions to attend to. The task consisted of the following conditions: a spatially *corresponding* condition in which the letter stimuli were presented on the same side of the hand carrying out the response, and a spatially *non-corresponding* condition in which the stimuli were presented on the opposite side to the hand carrying out the response. This variation creates the Simon component of the task, which applies to both, Go and NoGo trials. Essentially, Simon conflicts (i.e. spatial non-correspondence) have been shown to compromise response execution performance (i.e. hits on Go trials), but to improve inhibitory control performance (i.e. restraint on NoGo trials) [15,16].

In order to examine the effects of non-veridical perceptual features (i.e. the synaesthete-specific subjective perception of a specific colour concurrent when perceiving a certain letter inducer), this paradigm was specifically adapted for each synaesthete by adapting the colour in which the stimuli ('A' or 'E'—Go trials, and '*A*' or '*E*'—NoGo trials) were displayed (see figure 1 for details).

For each synaesthete (and their matched control), the target letters ('A' or 'E') were either displayed in colours which were

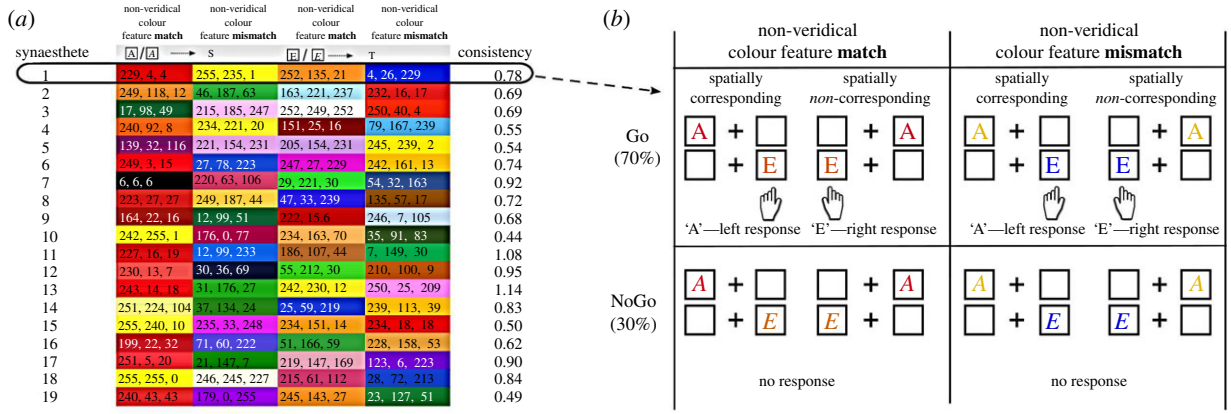


**Figure 1.** Schematic illustration of the experimental procedure. (*a*) Depiction of the stimulus colour used for each individual synaesthete ($N = 19$) and their matched controls. Shown are the precise RGB codes of the non-veridical colours associated with the letters 'A', 'E' (target), 'S' and 'T' (idiosyncratic distractor) for each synaesthete and the corresponding grapheme-colour consistency scores as obtained from the Eagleman Battery test. A colour consistency score below 1.43 indicates genuine synaesthesia. The stimuli in the Simon NoGo task were created on the basis of these individually determined colours. The stimuli used for synaesthete participant 1 in the Simon NoGo paradigm are shown. (*b*) In the 'non-veridical colour feature **match** condition', the colour of the presented target letter (Go: 'A'/'E', NoGo: '***A***'/'***E***') was adjusted using the RGB code for the letters 'A' and 'E' (i.e. for synaesthete 1, red and orange). In the 'non-veridical colour feature **mismatch** condition', the colour of the presented stimuli (Go: 'A'/'E', NoGo: '***A***'/'***E***') was adjusted using the RGB code for the target letters 'S' and 'T' (i.e. for synaesthete 1, yellow and blue) causing 'idiosyncratic interference' (note, the letters 'S' and 'T' were never presented on screen). Controls do not perceive a 'non-veridical colour'; thus, interference should only apply to individual synaesthete participants. Target letters were presented for 200 ms. For Go trials, a response was required within 800 ms. NoGo trials were considered as false alarms if any response was obtained within this time interval. (Inter-trial interval was jittered around 850–1050 ms.)

in accordance, or in conflict with the non-veridical colour this specific synaesthete perceives when being presented with the 'A' or 'E' letter. By means of this manipulation, in conditions with *matching non-veridical colour features*, the letter 'A'/'***A***' ('E'/'***E***') was presented in the *matching* synaesthete-specific RGB code (as obtained from the Eagleman Battery) of the non-veridical (automatically perceived) colour for the letter 'A'/'***A***' ('E'/'***E***'). For participant 1, for example, 'A'/'***A***'s were presented in red, and 'E'/'***E***'s in orange (see figure 5). For conditions with *mismatching non-veridical colour features*, the letter 'A'/'***A***' ('E'/'***E***') was presented in the RGB codes of the synaesthete-specific synaesthetic concurrent of the letter 'S' ('T'), hence creating interference between the subjectively perceived non-veridical colour of this specific letter and the actual colour in which the stimulus was presented. For participant 1, for example, 'A'/'***A***'s were presented in yellow instead of the synaesthetically perceived red, and 'E'/'***E***'s in blue instead of orange (see figure 5). Hence, an 'idiosyncratic conflict' between the objectively presented colour of the target and the idiosyncratically perceived non-veridical colour of the stimulus was specifically created for each synaesthete in the mismatching non-veridical conditions. This manipulation created the following eight experimental conditions: corresponding Go trials with matching or mismatching non-veridical colour features, non-corresponding Go trials with matching or mismatching non-veridical colour features and corresponding NoGo trials with matching or mismatching non-veridical colour features, non-corresponding NoGo trials with matching or mismatching non-veridical colour features.

According to the TEC, specific stimulus feature codes are connected with specific response feature codes in event files [2]. In the context of this task, for both synaesthetic participants and controls, task-relevant features are 'identity' of the letter (i.e. 'A' or 'E', relevant for Go trial execution), indicating a specific response (left or right), and 'shape' ('***A***' or '***E***', relevant for NoGo trial identification), indicating whether to execute, or to withhold a response. Stimulus 'location' (left or right frame box) and even, more importantly, the stimulus 'colour' were task-irrelevant features. For synaesthetes, however, the involuntary perception of an additional synaesthetic colour concurrent is intimately coupled to the 'identity' of the target letter [23]. Hence, a task-irrelevant stimulus feature, namely the idiosyncratically perceived 'non-veridical colour', is automatically activated in synaesthetes whenever they are processing a letter. For synaesthetes, the non-veridical colour' is thus likely to be a fundamental part of the event file. In cases where the objective colour of the presented letter does not match the non-veridical colour coupled to the 'identity' of the target letter (conditions with mismatching non-veridical colour features), there will likely be an interference between the non-veridical and the veridical (objectively presented) colour feature dimension. Therefore, non-veridical stimulus features, although not objectively presented, should impact on executive control. As 'non-veridical colour' is not perceived by controls, such interference should only apply to synaesthete participants. Furthermore, differential effects are to be expected in synaesthetic participants for Go and NoGo trials. This is based on the fact that for NoGo trials, the stimulus feature 'identity' essentially becomes task-irrelevant (A or E), as inhibition is required in response to the letters' 'shape' (bold italics versus normal font) disregarding its presented 'identity'. Therefore, the 'non-veridical colour' should differentially affect Go and NoGo trial performance. Similarly, as the feature 'identity' might be less important for task performance in corresponding than in non-corresponding trials, performance differences might be expected based on the 'location' of the trial.

Before conducting the experiment, a standardized exercise of 40 trials using white letters was conducted to familiarize participants with the task. The experiment consisted of 7 blocks of 160 trials with an equal distribution of pseudorandomized corresponding or non-corresponding, matching and mismatching non-veridical Go (70%) and NoGo (30%) trials (refer to electronic supplementary material, tables S1 and S2 for details regarding the number or trials per condition and for the entire experiment). This Go/NoGo ratio was chosen to ensure that we establish the classic characteristic of a Go/NoGo task, i.e. the induction of a pre-potent response tendency, which is based on the higher probability of Go trial in comparison to NoGo trial occurrence [19,20]. Each trial began with the presentation of a letter for 200 ms. For Go trials, a response was required within 800 ms or the trial was counted as a miss. In contrast with that, NoGo trials were considered as false alarms if any response was obtained within this time interval. The inter-trial interval was jittered between 850 and 1050 ms. The experiment consisted of 1120 trials and took around 40 min to complete depending on breaks taken by

the participants. Participants were actively encouraged to take breaks in order to avoid fatigue.

### (c) Electroencephalography recording and analysis

The EEG was recorded at a sampling rate of 256 Hz using a 64-channel Refa 8 amplifier and 64-channel Waveguard EEG caps (both from ANT Neuro, Enschede, The Netherlands). A band-pass filter from 0.5 to 20 Hz (with a slope of 48 dB/oct each) and a notch filter of 50 Hz were applied. Following that, a raw data inspection was conducted manually to reject technical artefacts from the EEG, before an independent component analysis (ICA; Infomax algorithm) was conducted. Using ICA, horizontal and vertical eye movement, blinks and pulse artefacts were corrected in the EEG data. After these pre-processing steps, cue-locked segments were formed. Only correct trials were included in the data analysis; i.e. Go trials were included whenever a correct response was given in a time window of 800 ms of stimulus onset. NoGo trials were included when there was no response within 800 ms of stimulus onset. Segments started 500 ms prior to the locking point (cue onset was set to time point 0) and ended 1000 ms thereafter, resulting in an overall segment length of 1500 ms. Afterwards, an automated artefact rejection was applied for all the segments. Activity below 0.5 µV in a 100 ms period and a maximal value difference of 200 µV in 200 ms within the epoch were used as rejection criteria. If an artefact was detected in a trial, the trial was discarded. To eliminate the reference potential from the data and to re-reference the data, we applied a current source density (CSD) transformation, which also serves as a spatial filter resulting in values for amplitudes in $\mu V\ m^{-2}$. The CSD transformation also works as a spatial filter that helps to find electrodes which best reflect neurophysiological processes during the paradigm [29]. The segmented conditions were 'non-veridical matching corresponding Go', 'non-veridical matching *non*-corresponding Go', 'non-veridical *mis*matching corresponding Go', 'non-veridical *mis*matching *non*-corresponding Go trials', 'non-veridical matching corresponding NoGo', 'non-veridical matching *non*-corresponding NoGo', 'non-veridical *mis*matching corresponding NoGo trials' and 'non-veridical *mis*matching *non*-corresponding NoGo trials'. A baseline correction from −200 ms to 0 prior to target onset was applied on the relevant ERP components: P1 (at P7 and P8: 108–118 ms after target presentation onset), N1 (at P7 and P8: 162–182 ms), N2 (at C4: 292–302 ms) and P3 (at Fcz and Pz: 511–517 ms) were identified by means of scalp topography. Within these intervals, the mean amplitude was calculated. This choice of electrode included in the data analysis was validated using a statistical approach outlined in Mückschel *et al*. [26]. Doing so, the above time intervals were taken and the mean amplitude within the defined search intervals was determined for each of the 60 electrode positions. Then, to compare each electrode against an average of all other electrodes, the Bonferroni correction for multiple comparisons (critical threshold, $p = 0.0007$) was used. Only electrodes which displayed significantly larger mean amplitudes (i.e. negative for the N-potentials and positive for the P-potentials) when compared with other electrodes were chosen. This procedure revealed the same electrodes as those chosen by visual inspection.

### (d) Standardized low-resolution brain electromagnetic tomography

For source localization, sLORETA (standardized low-resolution brain electromagnetic tomography; [30]) was applied. This algorithm provides a single linear solution for the inverse problem without localization bias [31,32]. The validity of sources estimated via sLORETA analysis has been corroborated by evidence from fMRI and EEG/TMS studies [32,33]. The computation of the standardized current density at each voxel was executed using the MNI152 template [34]. The sLORETA images (partitioned into 6239 voxels at 5 mm spatial resolution) of synaesthetes were contrasted with those of the controls. This comparison was based on statistical non-parametric mapping using the sLORETA—built-in voxel-wise randomization test with 2000 permutations ($p < 0.01$, corrected for multiple comparisons). Significant differences between voxels in contrasted conditions were located in the MNI brain (www.unizh.ch/keyinst/NewLORETA/sLORETA/sLORETA.htm).

### (e) Statistical analysis

Data analysis was organized as previously when employing a Simon GoNoGo paradigm [15,16]. Behavioural data were analysed using mixed-effects ANOVA for Go and NoGo trials separately, including the within-subject factors 'congruency' (corresponding versus non-corresponding) and 'non-veridical colour feature match' (synaesthetically matching colour versus synaesthetically mismatching colour) and 'group' (synaesthetes versus controls) as between-subject factor. For Go trials, we analysed accuracy (%) and hit reaction times (ms). For NoGo trials, we analysed false alarm rate, being the most important measure in a GoNoGo task. The small number of false alarms per condition, however, did not allow for a meaningful interpretation of false alarm reaction times. For the neurophysiological data, the factors 'condition' (Go versus NoGo) and 'electrode' were added into the model. The Greenhouse–Geisser correction was applied where appropriate and *post hoc* tests were Bonferroni-corrected. For all descriptive statistics, the standard error of the mean (s.e.m.) is given as a measure of variability. Data analysis was performed using IBM SPSS Statistics v. 25.

## 3. Results

### (a) Non-veridical stimulus features affect behavioural control during automated responses

A summary of the false alarm data, for all conditions, is shown in figure 2 (refer to supplementary figure 1*a*,*b* for plots of hit reaction time (ms) of all conditions). For the Go trials, the mixed-effects ANOVA on the hit rate revealed a main effect of 'spatial congruency' ($F_{1,36} = 10.63$, $p = 0.002$, $\eta_p^2 = 0.228$). Responses were more accurate in the spatially corresponding condition (95.13% ± 0.91) than in the spatially non-corresponding condition (93.55% ± 0.92). There were no other significant main or interaction effects (all $F \leq 3.10$, $p \geq 0.09$, $\eta_p^2 \leq 0.077$). For the reaction times (RTs), we also found a significant main effect of 'congruency' ($F_{1,36} = 17.56$, $p < 0.001$, $\eta_p^2 = 0.328$), showing that RTs were significantly shorter (faster) on corresponding Go trials (586 ms ± 14.33) compared to non-corresponding Go trials (601 ms ± 13.74). There were no other significant main or interaction effects (all $F \leq 2.08$, $p \geq 0.06$, $\eta_p^2 \leq 0.055$).

In a Go/NoGo task, false alarm rates reflecting inhibitory control performance represent the most important behavioural parameter. For the false alarm rates, we found a significant main effect of 'spatial congruency' ($F_{1,36} = 11.62$, $p = 0.002$, $\eta_p^2 = 0.913$), showing that the false alarm rate was higher in corresponding trials (7.12% ± 0.93), compared to non-corresponding trials (5.17% ± 0.85), i.e. in spatially consistent stimulus–response mappings inducing automatic response tendencies and thus, increasing false alarm rates. Importantly, there was a significant interaction of 'congruency × non-veridical feature match × group' ($F_{1,36} = 8.70$, $p = 0.006$, $\eta_p^2 = 0.195$). To further analyse the effects of non-veridical matching compared to non-veridical mismatching stimulus

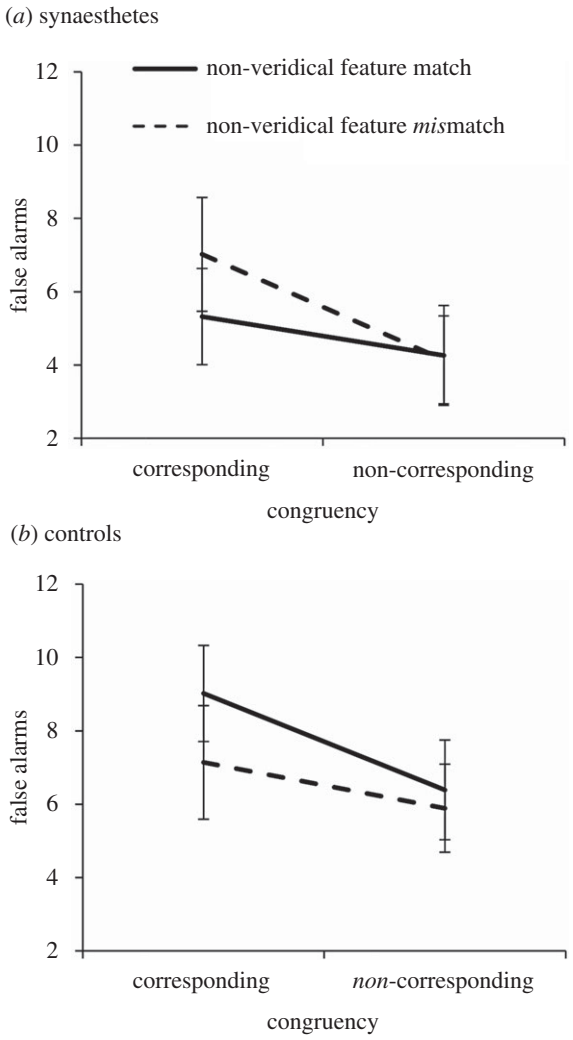


**Figure 2.** Interaction plots showing the behavioural results for both groups of participants. (*a*) Mean false alarm rate (%) data for the group of synaesthetes (mean ± s.e.m.) and (*b*) mean false alarm rate (%) data for the control group (mean ± s.e.m.). Results are shown for the spatially corresponding and spatially non-corresponding condition as well as for each non-veridical colour feature condition (matching, solid line; mismatching, dashed lines).

features on false alarm rates, we calculated the difference values for each group (i.e. 'colour feature match' minus 'colour feature mismatch') for the corresponding as well as the non-corresponding condition. The resulting difference values were compared using independent samples *t*-tests. Significant differences between the groups were revealed comparing controls (1.88% ± 4.87) and synaesthetes (−1.70% ± 5.42) on corresponding trials ($t_{36} = 2.14$, $p = 0.039$). On non-corresponding trials, differences between non-veridical feature matching and mismatching trials between controls (0.50% ± 3.87) and synaesthetes were not significant (0.13% ± 3.68) ($t_{36} = 0.31$, $p = 0.761$). This shows that, for synaesthetes, a stimulus inducing 'idiosyncratic conflict' (i.e. a stimulus with perceived mismatch between the presented and a non-veridical colour dimension on the same side as the response) acts as a distracting feature which drives up the false alarm rate specifically in this condition.

## (b) Neurophysiological data

### (i) No differential effect of non-veridical stimulus features during perceptual and attentional selection processes

The P1 and N1 ERP components are shown in figure 3*a*,*b*.

Concerning the P1-ERP component as a correlate of perceptual gating processes [27], the analysis of the amplitude data at electrodes P7 and P8 only revealed a significant interaction effect of 'electrode × spatial congruency' ($F_{1,36} = 43.66$, $p = 0.046$, $\eta_p^2 = 0.104$). To follow up this interaction, we employed independent samples *t*-test comparing P1 at electrode P7 on corresponding trials and electrode P8 on corresponding trials as well P7 on non-corresponding trials and electrode P8 on non-corresponding trials. We found that on corresponding trials, P1 was significantly greater (i.e. more positive) at electrode P8 (11.83 µV $m^{-2}$ ± 1.73) compared to electrode P7 (8.77 µV $m^{-2}$ ± 1.54) ($t_{36} = -2.24$, $p < 0.05$). For the non-corresponding condition, expression of P1 did not significantly differ between electrode P7 (10.10 µV $m^{-2}$ ± 1.43) and P8 (12.10 µV $m^{-2}$ ± 1.70) ($t_{36} = -1.70$, $p = 0.11$). Interestingly, there were no other main or interaction effects including the factor 'group' (all $F \leq 4.04$, $p \geq 0.52$, $\eta_p^2 \leq 0.101$). This shows that within the automatic task context (i.e. spatially corresponding stimulus response mappings), the P1 was more lateralized towards the right hemisphere.

Concerning the N1 ERP component as a correlate of bottom-up attentional selection processes [27], in the analysis of the amplitude data at electrodes P7 and P8, there was a significant main effect of 'electrode' ($F_{1,36} = 7.38$, $p = 0.047$, $\eta_p^2 = 0.105$), showing that N1 amplitudes were larger (i.e. more negative) at electrode P7 (−4.67 µV $m^{-2}$ ± 0.50) compared to electrode P8 (−2.85 µV $m^{-2}$ ± 0.59). There also was a significant main effect of 'Go versus NoGo' ($F_{1,36} = 8.68$, $p = 0.006$, $\eta_p^2 = 0.194$), showing that N1 was more negative in the NoGo condition (−27.36 µV $m^{-2}$ ± 2.51) compared to the Go condition (−26.00 µV $m^{-2}$ ± 2.58). We also found a significant main effect of 'group' ($F_{1,36} = 4.95$, $p = 0.32$, $\eta_p^2 = 0.121$), showing that N1 amplitude was more negative in synaesthetes (−32.32 µV $m^{-2}$ ± 3.56) compared to controls (−21.04 µV $m^{-2}$ ± 3.56).

The source localization shows that the precuneus (BA19) displayed stronger activity in synaesthetes than controls reflecting unspecific changes in perceptual/attentional processes related to synaesthesia itself. The only significant interaction was an interaction 'electrode × Go versus NoGo × congruency' ($F_{1,36} = 52.02$, $p = 0.024$, $\eta_p^2 = 0.133$). However, *post hoc* tests showed that this interaction was only evident for N1 amplitude differences between Go and NoGo trials at electrode P8 where amplitudes were greater on incongruent than congruent trials. This, however, does not explain the differential group effects observed at the behavioural level. As with the P1 data, there were no other main or interaction effects including the factor 'group' (all $F \leq 0.94$, $p \geq 0.53$, $\eta_p^2 \leq 0.026$).

The lack of modulatory effects on the P1 and N1 by the factor 'group' is corroborated by a Bayesian analysis of the data. The approach proposed by Masson [35] allows estimating the relative evidence for different statistical models from sums-of-squares data used in the ANOVA. This analysis revealed a probability for H0 hypotheses, given the data (pH0 | D) of $p = 0.96$, thus providing strong evidence for the null hypothesis according to the criteria of Raftery [36], i.e. that there were no group effects.

### (ii) Neurophysiological mechanisms of response selection are modulated by non-veridical stimulus features

The N2 ERP component is shown in figure 4*a*,*b*.

Concerning N2 ERP-component amplitudes at electrode C4, we found a significant main effect of 'condition' ($F_{1,36} = 51.22$,

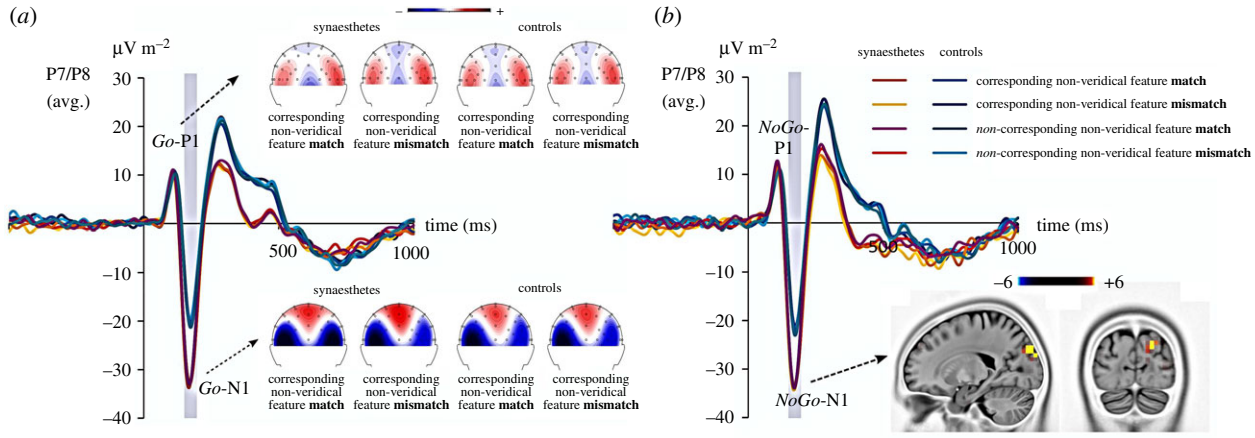


**Figure 3.** ERP P1 and N1 components averaged across electrodes P7 and P8 for each group of participants. (*a*) P1 and N1 on Go trials. (*b*) P1 and N1 on NoGo trials for all experimental conditions. Example scalp topographies are shown for non-veridical conditions since these are the most important conditions in the study. Within the topographies, red colours denote positive amplitudes and blue colour negative amplitudes. The different colours of the ERP traces represent the experimental conditions for both groups. Warm colours are used to show the experimental conditions in the group of synaesthetes; cool colours are used to show the experimental conditions in the group of controls. Time point zero denotes the point of stimulus presentation. Results from the source localization analysis using sLORETA indicate that the main effect of group for the N1 ERP component is associated with activation differences within the precuneus (BA19).

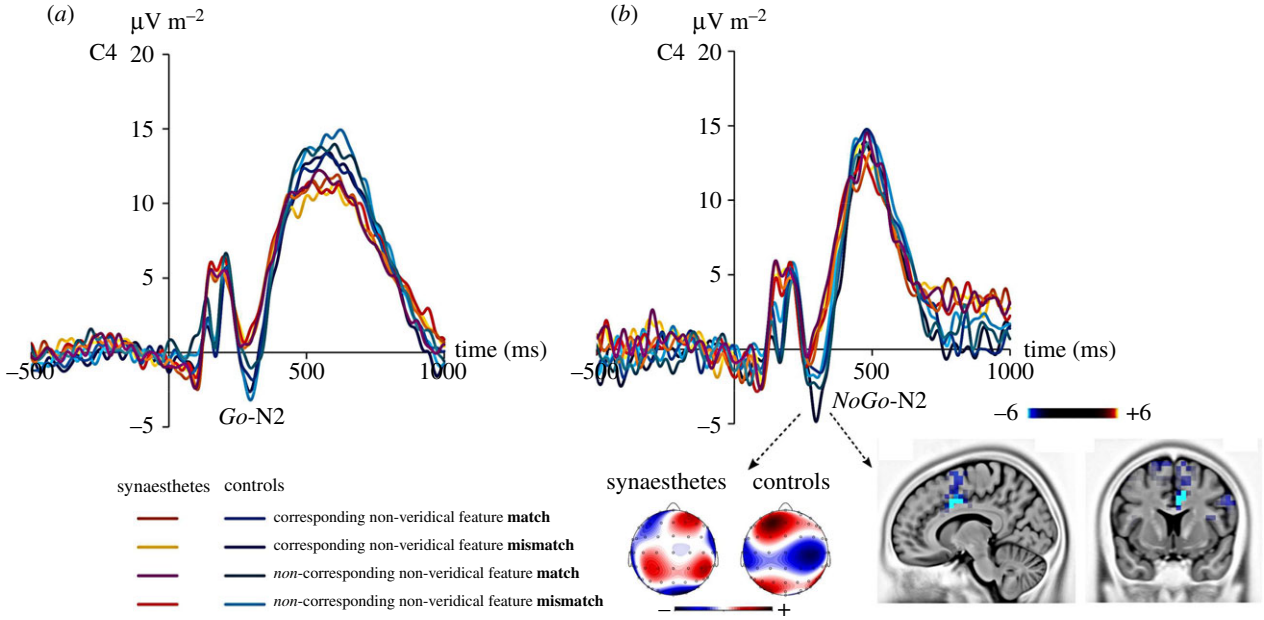


**Figure 4.** ERP N2 component at electrode C4 for both groups of participants with scalp topographies as well as a visual representation of the source localization results (sLORETA). Components are shown for (*a*) the Go-N2 and (*b*) NoGo-N2 in each experimental condition. Scalp topographies show the difference in ERP signal between the non-veridical matching colour feature condition and the non-veridical mismatching colour feature condition. Within the topographies, red colours denote positive amplitudes and blue colours negative amplitudes in the difference. The different colours of the ERP traces represent the different experimental conditions for both groups. Warm colours are used to show the experimental conditions in the group of synaesthetes; cool colours are used to show the experimental conditions in the group of controls. Time point zero denotes the point of stimulus presentation. The sLORETA results indicate the source of the differential effect between experimental conditions and groups in the NoGo-N2 in ACC (corrected for multiple comparisons using SnPM, $p < 0.01$). The colours denote critical *t*-values.

$p < 0.001$, $\eta_p^2 = 0.587$), showing that N2 amplitudes were higher (i.e. more negative) on NoGo trials (−1.28 μV m$^{-2}$ ± 1.03) compared to Go trials (17.54 μV m$^{-2}$ ± 2.39). Importantly, there was a significant interaction of 'Go versus NoGo × non-veridical feature match × congruency × group' ($F_{1,36} = 4.20$, $p = 0.023$, $\eta_p^2 = 0.637$). To analyse this interaction in more detail, we calculated mixed-effects ANOVAs for Go and the NoGo trials separately. For Go trials, there were no significant main or interaction effects (all $F \leq 0.13$, $p \geq 0.5$, $\eta_p^2 \leq 0.051$). For NoGo trials, there was a significant interaction of 'non-veridical feature match × congruency × group' ($F_{1,36} = 5.54$, $p = 0.024$, $\eta_p^2 = 0.133$). To further analyse the effects of non-veridical matching compared to non-veridical mismatching stimulus features in NoGo trials, we calculated the difference values for each group (i.e. 'non-veridical feature match' minus 'non-veridical feature mismatch') for the corresponding as well as the non-corresponding condition. The resulting difference values were compared by means of independent samples *t*-test. For corresponding trials, differences in N2 amplitudes at electrodes differed significantly between

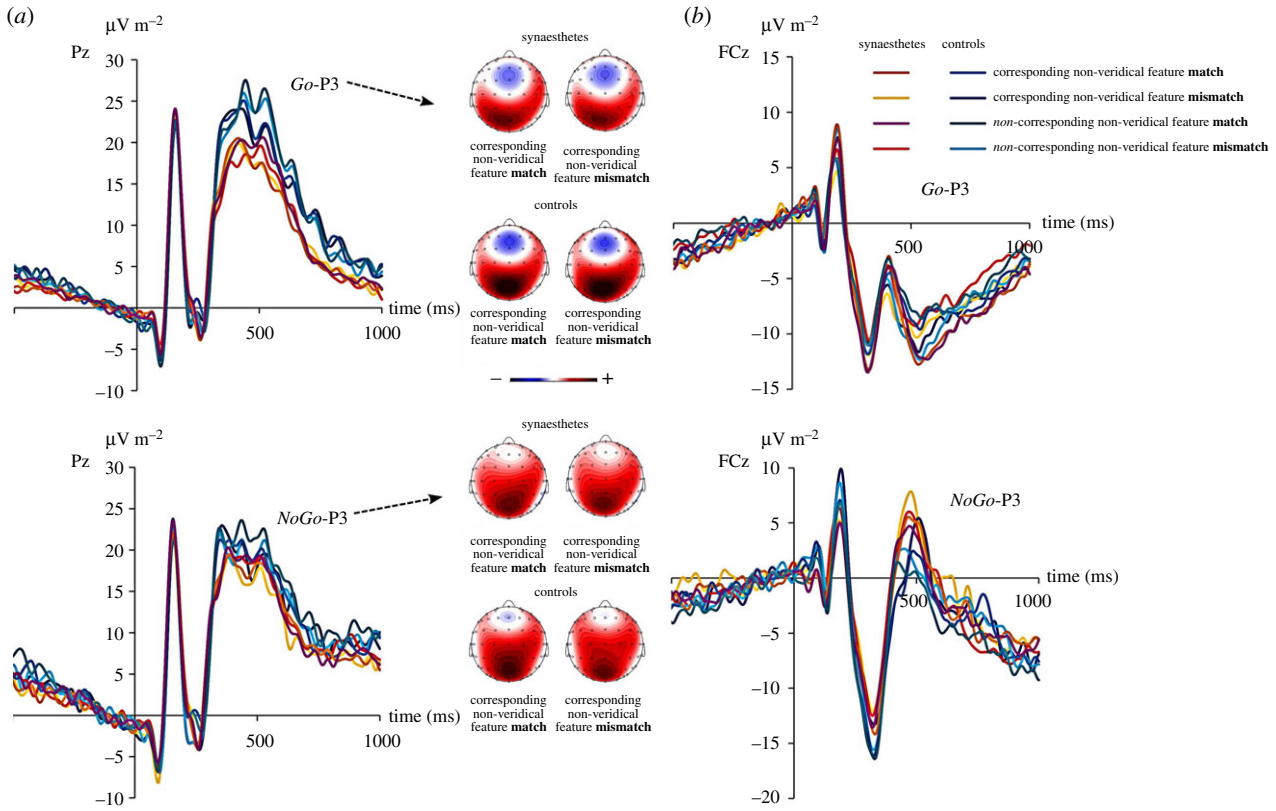


**Figure 5.** ERP P3 components at electrodes (*a*) Pz and (*b*) FCz for both groups of participants with scalp topographies. (*a*) Go and NoGo-P3 at C4 and (*b*) Go and NoGo-P3 for all experimental conditions. Scalp topographies are shown to represent scalp distribution for the relevant experimental conditions. Within the topographies, red colours denote positive amplitudes and blue colours negative amplitudes in the difference. The different colours of the ERP traces represent the different experimental conditions for both groups. Warm colours are used to show the experimental conditions in the group of synaesthetes; cool colours are used to show the experimental conditions in the group of controls.

controls (3.34 μV ± 5.64) and synaesthetes (−0.57 μV $m^{-2}$ ± 4.12) ($t_{36} = 2.44$, $p = 0.02$). For non-corresponding trials, differences of N2 amplitude between synaesthetes (0.67 μV $m^{-2}$ ± 4.91) and controls (−0.53 μV $m^{-2}$ ± 5.59) did not reach significance ($t_{36} = -0.70$, $p = 0.50$). The sLORETA analysis revealed that this differential effect in N2 amplitudes between controls and synaesthetes was associated with activation differences in the ACC. All other main effects or interactions were not significant (all $F \leq 1.41$, $p \geq 0.4$, $\eta_p^2 \leq 0.002$).

The P3 ERP component at electrode Pz, as well as FCz, is shown in figure 5*a*,*b*.

Concerning P3 at electrodes Pz and FCz, we found a significant main effect of 'electrode' ($F_{1,36} = 93.81$, $p < 0.001$, $\eta_p^2 = 0.723$), showing that P3 was larger at electrode Pz (20.58 μV $m^{-2}$ ± 2.11) compared to electrode FCz (0.25 μV $m^{-2}$ ± 0.39). There also was a significant main effect of 'congruency' ($F_{1,36} = 10.79$, $p = 0.002$, $\eta_p^2 = 0.231$), showing that P3 was significantly smaller on spatially corresponding trials (9.80 μV $m^{-2}$ ± 1.10) compared to spatially non-corresponding trials (11.03 μV $m^{-2}$ ± 1.15). However, there was no interaction of 'Go versus NoGo × non-veridical feature match × congruency × group' ($F < 0.56$, $p \geq 0.8$, $\eta_p^2 \leq 0.003$). There was a significant interaction of 'electrode × Go versus NoGo' ($F_{1,36} = 5.42$, $p = 0.026$, $\eta_p^2 = 0.131$). *Post hoc* tests showed that for Go trials, the P3 was significantly larger at electrode Pz (43.17 μV $m^{-2}$ ± 4.30) compared to electrode FCz (−0.36 μV $m^{-2}$ ± 0.99) ($t_{36} = 10.01$, $p < 0.001$). Likewise, for NoGo trials, the P3 was significantly larger at electrode Pz (39.14 μV $m^{-2}$ ± 4.40) compared to electrode FCz (1.35 μV $m^{-2}$ ± 0.98) ($t_{36} = 8.68$, $p < 0.001$). Furthermore, there was no significant interaction of 'electrode × spatial congruency' ($F_{1,36} = 4.57$, $p = 0.113$, $\eta_p^2 \leq 0.028$). This lack of modulatory effects on the P3 reflecting the interaction shown for the behavioural data is corroborated by a Bayesian analysis of the data. This analysis revealed a probability for H0 hypotheses, given the data (pH0 | D) of $p = 0.97$, thus providing strong evidence for the null hypothesis according to the criteria of Raftery [36].

## 4. Discussion

In the current study, we show that actions and cognitive control processes are modulated by non-pathological perceptions that are not objectively present, i.e. by experiences in which a perceptual presence or real-world perceptual veridicality is lacking. By examining synaesthesia, a perceptual phenomenon in healthy humans distinct from psychopathological delusions or hallucinations [10], we show behavioural effects and identify plausible neuronal correlates of how this is possible. Grapheme-colour synaesthesia is a condition in which single digits, letters and words (i.e. the inducer) consistently and automatically evoke an additional experience of colour (i.e. the concurrent) [4,5,7,8]. This experience of a synaesthetic concurrent, despite being perceptually vivid, lacks perceptual presence, i.e. it is non-veridical [9]. Previous research has shown that experiencing an additional non-veridical percept can have adverse effects on cognition [14,37]. However, so far, disadvantageous effects on performance were only evident in conflict tasks when the task-relevant colour stimulus was incongruent to the perceived non-veridical synaesthetic colour; and thus,

directly causing interference with the task at hand (i.e. with colour categorization) [37]. Notably, in our study, 'colour' (neither veridical nor non-veridical) never represented a critical task-relevant stimulus dimension clearly distinguishing the current experiment from paradigms previously used to study colour experiences in synaesthetes.

The behavioural data clearly show that such non-veridical features negatively affect performance even if there is no direct interference with task-relevant stimulus dimensions. We demonstrate this by employing a novel paradigm combining a Simon task with a Go/NoGo task to measure inhibitory control performance within the context of automatic (i.e. spatially corresponding stimulus–response mappings) and controlled action selection modes (i.e. spatially non-corresponding stimulus–response mappings) modified to match (or mismatch) the idiosyncratic perception of each individual within the group of synaesthetes [15,16]. In both groups, we found that RTs were shorter and accuracy was higher on spatially corresponding compared to spatially non-corresponding stimulus–response relations in Go trials and that erroneous responses on NoGo trials (i.e. the false alarm rate) were increased on corresponding compared to non-corresponding stimulus–response relations in line with previous findings [15,16]. In synaesthetes, false alarm rates were increased whenever the veridical colour of the presented letter stimulus was not matching the subjectively perceived non-veridical colour (i.e. synaesthetic concurrent) induced by the presentation of the letter (i.e. the inducer). Thus, a conflict between veridical and non-veridical sensory content modulates executive control processes. It seems that vulnerability to the influence of non-veridical precepts is particularly high in situations in which behaviour is mediated via more automated action-selection modes, i.e. more impulsive response tendencies.

Interestingly, these effects depend on the specific response selection mode: according to the dual process model [17], behaviour is mediated via a 'direct' route in response to spatially corresponding stimulus–response relations, in which a more automatic stimulus–response translation is evident. Opposed to this, an 'indirect' route involving a controlled stimulus–response translation mediates behaviour on incongruent trials. The increase in false alarm rate in the corresponding condition seems to suggest that non-veridical perceptions only modulate behavioural control when response selection relies on rather automated processes. It seems that, although the perceptual presence (veridicality) of the perceived stimulus colour is what segregates the examined groups, effects of perceptual idiosyncracy only become evident in higher-order cognitive control functions. Furthermore, if different degrees of perceptual saliency (of the target letters) were to underlie the false alarm rate differences, saliency effects would likely improve the synaesthetes performance to congruently coloured target letters (i.e. idiosyncratically matching trails), which was not the case. Thus, early perceptual processes (effects of colour saliency) cannot be assumed to underlie the behavioural differences. This is supported by the neurophysiological data, showing that the P1 and N1 ERP components, reflecting bottom-up perceptual gating and attentional selection processes [27], did not show interactive in line with the behavioural data. A Bayesian analysis of these data providing strong evidence for a lack of group effects for the P1 and N1 ERP components further supports this interpretation. Since the P1 and N1 ERP components are well known to be modulated by bottom-up processes, e.g. driven stimulus saliency [31,38,39], this finding also rules out that the stimulus manipulations could have led to differences in the saliency of the target letters. As shown in the examples presented in figure 5, the capital letter A presented in yellow may be considered to be less salient than when it is presented in red or orange. The electrophysiological data show that this does not confound our results.

Importantly, the interaction of 'non-veridical feature match × congruency × group' was evident for an ERP component reflecting higher-order response selection and cognitive control processes—the N2. In the context of response inhibition, the N2 is assumed to reflect pre-motor inhibition processes with the N2 being larger when these processes are fully deployed [15,40–44]. In controls, N2 amplitudes were more negative in non-veridically mismatching feature trials compared to non-veridically matching feature trials. This was not shown in the case of the synaesthetes. In fact, a mismatch between the presented colour of the letter stimulus and the non-veridical colour feature associated with the letter (i.e. concurrent) seemed to prevent pre-motor inhibition processes to be deployed, as was reflected in worsened response inhibition performance (increased false alarm rates) whenever the task context was mediated via more automatic stimulus–response translations ('direct' route). The source localization analysis suggests that these modulations of the N2 are associated with the ACC. This region, and the medial frontal cortex in general, plays a major role in inhibitory control [38,39] and has been suggested to orchestrate the connection of perception and action [25] due to its hub-like structural and functional connection to sensory and motor areas [45,46]. Corroborating this, it has been shown that the N2 reflects a concomitant coding of stimulus and response-related aspects, likely mediating the binding between stimulus and response features [16,41]. The neurophysiological data thus suggest that altered stimulus–response binding processes underlie effects of sensory aspects lacking real-world perceptual veridicality on cognitive control. The idea of binding stimulus and response features to facilitate an action is central to the TEC detailing the links between perception and action [1,44]. TEC can also explain how non-veridical perceptual aspects modulate overt response control.

According to TEC, feature codes defining a percept and an action are represented in a common representational structure called an 'event file'. Event files establish bindings between features specifying a stimulus and features specifying an action [1,18]. Importantly, the activation of an event file follows pattern completion logic, meaning that the entire event file can be (re)activated once a single feature of either a stimulus or a response is (re-)encountered. According to TEC, an event file is built activating *all* stimulus and response features, no matter whether they are relevant to the task at hand or not [3]. Moreover, once a perceptual feature dimension has been integrated into an event file, it is likely to affect action. So, if stimulus representations are enriched by idiosyncratic, stimulus-related associations, the feature dimensions are automatically bound to a response even if their presence is neither necessary nor useful for the desired outcome of the action [1,2]. Following this assumption, we hypothesized that action should be modulated by task-irrelevant perceptual feature dimensions, even if these are *not* objectively perceived to be present in the real word, i.e. strong, automatic stimulus-related associations, lacking perceptual veridicality. In our experiment, the task-relevant

feature dimensions of the target stimulus were the letters' 'identity' (A or E) and its 'shape' (normal print or bold italics). Importantly, the 'colour' dimensions never did serve as a task-relevant feature dimension. Yet, in grapheme-colour synaesthesia, the presentation of the letter A or E (i.e. the 'identity': task-relevant) inevitably and automatically triggers the experience of an additional non-veridical feature dimension (i.e. 'colour': task-irrelevant). Crucially, the consistent and automatic colour experience (e.g. red) is intimately bound to the specific semantic representation of a letter stimulus (e.g. 'A') independent of its appearance or 'shape' (i.e. 'A', 'a', 'ɑ', '*A*' or 'A'→red) [4,22]. Thus, even though this additionally activated synaesthetic experience is irrelevant to the desired action, it is likely to be an integral part of the event files of synaesthetes. According to TEC, stimulus and response features are integrated into event files and activated before the task is performed, so that simply registering a stimulus should suffice to spread activation to the related response. Thus, the same non-veridical colour is activated and integrated into Go as well as NoGo event files. Simply processing the letter (i.e. its 'identity'), without regarding whether it is printed bold or italic is enough to elicit an additional colour experience in synaesthetes but does not provide enough information on whether to execute or to withhold a response. The colour is bound to the letter's identity, but the feature conveying information about Go or NoGo trials (i.e. its 'shape'/bold or italics) does not by itself elicit a non-veridical colour experience in grapheme-colour synaesthesia. Therefore, Go and NoGo event files partially overlap in terms of their integrated non-veridical feature dimension for synaesthetes but not for controls. The same non-veridical feature is part of two opposing event files. Such a partial overlap between opposing event files will cause interference leading to performance decline [1]. In our experiment, this interference is amplified by presenting the inducer (i.e. letter) in a veridical colour incongruent with the concurrent (i.e. non-veridical colour), ultimately leading to a decline in inhibitory control performance. As a result, the synaesthetic experience leads to interference between opposing event files and modulates action selection.

## 5. Conclusion

We show using synaesthesia as a model condition, how irrelevant and non-existent but still non-pathological perceptions, i.e. perceptual aspects lacking objective perceptual presence (that are non-veridical), can affect our actions. We provide insights into the conditions in which such a modulation is possible and identify neurophysiological correlates. We show that perceptual peculiarities as examined here do not primarily influence action via perceptual processes. Rather, it is higher-order processes integrating perception with motor responses that reflect the underlying processes of how actions are modulated by non-veridical perceptions. Although the results challenge common conceptions about the determinants of human action control, the results can be explained by established theoretical frameworks detailing the link between perception and action.

Ethics. All procedures performed in this study were approved by the IRB of the University of Sussex in line with the ethical standards of the 1964 Declaration of Helsinki.

Data accessibility. The article's supporting data (behavioural and ERP datasets for participants) and the experimental code (presentation scenario file) are included as part of the electronic supplementary material. The individual results of the synaesthetes as obtained from the Eagleman Battery (https://www.synesthete.org/) cannot be shared as it contains sensitive human subject information (full names, e-mail address, age). Participants only gave permission for this information to be shared with the team of researchers.

Authors' contributions. M.L.S., W.X.C., C.B. and J.W. contributed to conception and design of the study. W.X.C. coded the experiment. M.L.S. collected the data. J.W. provided the recruitment details for grapheme-colour synaesthetes. M.L.S. and W.C. analysed the data. M.L.S., W.C., C.B. and J.W. contributed to the interpretation of the data. M.L.S., W.C. and C.B. drafted the article and J.W. critically revised the manuscript and contributed important intellectual content as well as the final approval of the version to be published.

Competing interests. The authors declare that they have no conflicts of interest.

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