

The dynamics of statistical learning in visual search and its interaction with salience processing: An EEG study

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ABSTRACT

Visual attention can be guided by statistical regularities in the environment, that people implicitly learn from past experiences (statistical learning, SL). Moreover, a perceptually salient element can automatically capture attention, gaining processing priority through a bottom-up attentional control mechanism. The aim of our study was to investigate the dynamics of SL and if it shapes attentional target selection additively with salience processing, or whether these mechanisms interact, e.g. one gates the other. In a visual search task, we therefore manipulated target frequency (high vs. low) across locations while, in some trials, the target was salient in terms of colour. Additionally, halfway through the experiment, the high-frequency location changed to the opposite hemifield. EEG activity was simultaneously recorded, with a specific interest in two markers related to target selection and post-selection processing, respectively: N2pc and SPCN. Our results revealed that both SL and saliency significantly enhanced behavioural performance, but also interacted with each other, with an attenuated saliency effect at the high-frequency target location, and a smaller SL effect for salient targets. Concerning processing dynamics, the benefit of salience processing was more evident during the early stage of target selection and processing, as indexed by a larger N2pc and early-SPCN, whereas SL modulated the underlying neural activity particularly later on, as revealed by larger late-SPCN. Furthermore, we showed that SL was rapidly acquired and adjusted when the spatial imbalance changed. Overall, our findings suggest that SL is flexible to changes and, combined with salience processing, jointly contributes to establishing attentional priority.

1. Introduction

In the visual domain, the relevance of an item can vary based on different attentional control (AC) mechanisms. According to the *Biased-Competition model of Attention*, within a visual scene all the available stimuli automatically compete with each other for our limited cognitive resources in order to gain access for further processing (Desimone and Duncan, 1995). It is therefore important to focus our attentional resources towards the stimulus most relevant for our goals, while ignoring irrelevant ones (Carrasco, 2011). Even looking for a pair of scissors on a crowded desk would not be an easy task, as other stimuli such as surrounding objects, people in the office, an email notification on the computer etc., will interfere. The competition among stimuli can be

biased by the interplay between *experience-independent* and *experience-dependent* mechanisms, which can steer attentional deployment toward one (or a few) relevant stimulus, while filtering out the irrelevant ones.

Within the *experience-independent* category, bottom-up and top-down control mechanisms are distinguished. The first mechanism is at play when an element is salient based on its physical properties (e.g., colour, luminance, shape) and can automatically capture our attention (Theeuwes, 2010; Yantis and Egeth, 1999). Conversely, top-down control acts when attention is voluntarily allocated toward a certain stimulus depending on instructions, internal guidance, or current goals (Egeth and Yantis, 1997; Posner, 1980; Reynolds and Heeger, 2009).

In contrast, experience-dependent mechanisms refer to a series of

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computations that, through the accumulation of statistical information over time, allow for the extraction of regularities in the environment and to use them to process the present state and construct (explicitly or implicitly) expectations about the future (Awh et al., 2012; Chelazzi & Santandrea, 2018; Failing and Theeuwes, 2018; Saffran et al., 1996). Statistical learning (SL), for instance, keeps track of the frequency with which a given element occurs across locations (Aslin and Newport, 2012; Druker and Anderson, 2010; Geng and Behrmann, 2005; Walthew and Gilchrist, 2006; for evidence also in animals see e.g., Newport et al., 2004; Rosa-Salva et al., 2018; Santolin et al., 2016). Nevertheless, the mechanisms underlying SL are not as well understood yet as the experience-independent mechanisms. As better described below, one of the purposes of the present study is to contribute to a better understanding of how target selection (as opposed to distractor suppression) and processing of visual information is affected by SL.

In the past, these various AC mechanisms have been usually studied in isolation; however, recently, increasing interest has been devoted to how they interact with each other. An important model assumes that attentional selection is the result of the activity of multiple AC mechanisms that all converge in the *spatial priority map* (e.g., Fecteau and Munoz, 2006; Itti and Koch, 2001), which is a topographic representation of visual space. Depending on the amount of attentional resources allocated to a spatial location, each point in the map will have a specific level of neural activation. The point having the highest activation peak represents the spatial location with the highest attentional priority, where stimulus selection will occur following a winner-take-all process (Chelazzi et al., 2014; Macaluso and Doricchi, 2013).

Nevertheless, it is still not clear how exactly the activity of different AC mechanisms is integrated in order to establish the final attentional choice. One possibility is that the highest peak is determined by the joint contribution of multiple AC mechanisms that act independently of each other, such that their activity is simply added up. Yet, another possibility is that, depending on the context, one mechanism may have precedence and prevails over the others. In this case, the final attentional choice would be the result of just one mechanism, which would block the activity of all the others.

While in the past a lot of effort has been made to study the interplay between top-down and bottom-up control (e.g., Corbetta and Shulman, 2002; Van der Stigchel et al., 2009; Luck et al., 2021), only in the last few years did researchers start to test the interaction between SL and the other AC mechanisms, such as top-down control (Dolci et al., 2023; Gao and Theeuwes 2020). However, to our knowledge, there are no published studies yet that integrated SL with bottom-up control on target selection (but see below where we report some studies that assess the processing of salient distractors in relation to SL), in addition to only a few studies addressing SL in visual search to begin with.

The main purpose of the present work is to address this gap by investigating the combined effects of the experience-dependent SL mechanism and experience-independent, bottom-up control. However, since in the literature, the term “bottom-up control” usually refers to a salient, but task-irrelevant, item, here we will use the term “salience processing” to indicate the attentional capture by a salient target. Specifically, by using the same visual search task already validated to induce a reliable effect of each AC mechanism taken individually (see Beffara et al., 2022; Dolci et al., 2023; Rashal et al., 2022), here we manipulated target salience (salient target vs. homogeneous display) and the target frequency across locations (high-frequency target location vs. low-frequency target location) to assess how they simultaneously operate to assign attentional priority to a specific spatial location. Behavioural measures and EEG activity, with a specific interest in two ERP markers related to attentional selection and post-selection processing, were considered.

The first component is the N2pc, which consists in an enhanced negativity over posterior electrodes contralateral to the covertly attended stimulus (typically studied in visual search tasks), usually emerging around 200 ms after the stimulus onset, which is commonly believed to

reflect attentional selection (e.g., Eimer, 1996; Hickey et al., 2009; Hopf et al., 2000; Luck and Hillyard, 1994).

The second ERP component of interest is the SPCN, which is a sustained posterior contralateral negativity usually observed after the N2pc. It emerges around 350 ms until around 700 ms (with the end of the time-window also depending on when the behavioural response is given, clearly signifying the end of response-relevant processing), and is believed to reflect post-selection processes and, in particular, the maintenance and discrimination of visual information in visual short-term memory (VSTM, e.g., Drisdelle and Jolicoeur, 2018; Jolicoeur et al., 2008; Towler et al., 2016; Vogel and Machizawa, 2004).

1.1. Salience processing and SL effects when taken individually

Concerning salience processing, EEG evidence has consistently revealed that the behavioural modulation due to salience processing is associated with an enhancement of the N2pc and SPCN (Rashal et al., 2023) in favour of the salient element, both when it is the target (e.g., Li et al., 2018) or a distractor (e.g., Hickey et al., 2006), that could automatically capture attention irrespective of the individual’s goals.

Similarly concerning SL, a recent study of Duncan et al. (2023) also investigated attentional selection by means of the N2pc elicited by targets at a high-frequency location, which showed a larger mean amplitude compared to the N2pc elicited by targets at low-frequency locations. Importantly, this difference emerged especially in the first half of N2pc time-window. Yet, apart from this study, little research has been done regarding the underlying ERP markers of SL effects on target selection (as opposed to distractor suppression), as well as on their downstream consequences on further processing.

In one further example, Dolci and colleagues (2023) combined SL and top-down control. While there was evidence for an interaction between top-down attention and SL, including concerning the N2pc, this earlier work did not observe a main effect of SL, which could be indicative of SL developing the bulk of its influence at a later processing stage, but could have also been related to an issue of sensitivity based on the analysis logic of the N2pc. Indeed, as in previous studies that investigated SL, also in the experiment of Dolci and colleagues (2023), the high and/or low-frequency locations were associated to one hemifield, such that it was only possible to collapse across the left and right hemisphere data at the group level (e.g., Ferrante et al., 2018; Theeuwes et al., 2022). This might have introduced the detrimental influence of inter-individual differences in the asymmetry of the activity between left and right hemisphere, which could relate to basic anatomical differences, and is usually counteracted by collapsing across them (i.e., averaging a condition with attention to the left at PO8 with a condition with attention to the right at PO7 etc.; see e.g., Wu et al., 2011).

To overcome this issue, one key point of the present work is that, after the first experimental half, we changed the hemifield of the high-frequency target location (see also Duncan et al., 2023). This is important because it allowed us to measure each ERP marker of interest (both of which represent lateralized activity) elicited in each experimental condition over both hemispheres and to then average over these within each participant, the same way typical N2pc/SPCN studies do. Simultaneously, the switch of high-frequency target location (HFTL) enables us to behaviourally test the lingering effect of SL and the ability for new SL to occur in the face of a previous, no-longer relevant imbalance, by also exploring the temporal characteristics of the learning process.

1.2. Salience processing and SL effects when active together

As said above, even if salience processing and SL have been mostly studied separately, their individual priority signals are integrated into a single topographic representation of the environment that determines the selection priority (Theeuwes and Failing, 2020). Nonetheless, it is worth noting that certain studies have already integrated these two AC mechanisms within the same paradigm, albeit focussed on distractors.

For instance, it is established that an uneven frequency of salient distractors across locations induces spatial suppression at the frequent-distractor locations, such that it is better filtered out when presented at that location (Di Caro et al., 2019; Zhang et al., 2022). However, given the lower attentional priority allocated to the frequent distractor location, the suppression seems to hamper the detection of all the stimuli presented within it, including the target stimulus (Ferrante et al., 2018). Recent research by Liesefeld and Müller (2021) provides further robust evidence supporting this indirect effect of SL, showing that spatial suppression to a specific distractor feature is not possible (Liesefeld and Müller, 2021).

However, in addition to being focused on distractors (whereas here we study SL effects on targets), in all these experiments the effect of salience processing and SL overlap with each other, making it difficult to disentangle their individual contributions during the target selection process, when active together. Specifically, when there is a frequency imbalance of the salient element, it is impossible to specifically dissociate the contribution of SL and salience to the observed spatial suppression (or prioritization, in case of salient target). To address this question, our study combines SL and salience in a visual search task, aiming to distinctly discern the impact of each AC mechanism. A crucial distinction between our study compared to previous researches lies in the equal frequency of the salient element, when present, across all locations on the display. This deliberate choice aimed to untangle the effects of SL and salience processing, even when they occur simultaneously.

Based on the evidence discussed earlier, if salience processing and SL mechanisms independently act to assign attentional priorities to visual stimuli, each mechanism should act regardless of the presence (or absence) of the other mechanism. In this case, we should find better performance and a larger N2pc for salient targets (vs. non salient targets, i.e., homogeneous display) and, at the same time, for targets presented in the high- (vs. low-) frequency location. These effects should happen independently of each other, and therefore add up if simultaneously present. Conversely, if the two mechanisms interact with one another, we should find a prevalence of one mechanism, which can override the effect of the other. Interestingly, it has been shown that the dynamics of the N2pc can be separated into an early and a late phase (Duncan et al., 2023; Eimer and Kiss, 2007), where the early part seems to index an initial attentional capture (Holmes et al., 2009). Therefore, we also investigated the N2pc here, split into two halves, in order to better explore the temporal dynamics of the interplay between salience processing and SL.

Turning to the SPCN component, little research has investigated it in relation to salience processing and even less so to SL; therefore, no specific predictions were made. However, similarly to the N2pc, studies revealed differential effects during a relatively early vs. late SPCN time-window (Luria and Vogel, 2011; Salahub and Emrich, 2018). Therefore, here, we will separately investigate the two halves of the SPCN in order to explore and better describe the progression of processes underlying target selection and processing in the presence of multiple AC signals.

2. Materials and methods

The present study was conducted in accordance with the Declaration of Helsinki and approved by the ethical committee of the Faculty of Psychology and Educational Sciences of Ghent University (code 2021/32).

Data will be made available on EBRAINS repository. Other materials for the experiment reported here are available upon request. The experiment was not preregistered.

2.1. Participants

Twenty-four healthy volunteers (7 males; mean age \pm SD, 22.15 \pm 2.84) with normal or corrected-to-normal visual acuity participated in

this experiment. One of them was excluded from the analysis due to low accuracy (62.7 %, which was more than two SDs below the average participants' accuracy). They were all naïve as to the purpose of the study and none of them had previously taken part in similar or related studies. They gave their informed consent before participation and received monetary compensation for participating in the study (€32.5).

2.2. Apparatus and stimuli

Participants sat in a dimly lit, quiet room, facing a 24" Benq XL2411Z LED monitor controlled by a Dell Optiplex 9020 tower with Intel Core i5-4590 processor, at a 60-Hz refresh-rate. The viewing distance was held constant at 60 cm by using an adjustable cushioned chin rest. The experiment was run with the PsychoPy (v1.84.2) software (Peirce, 2007). The experimenter was sitting in a different room and, by using the camera of an Eyelink 1000 plus (SR Research, Canada), eye movements were monitored. During breaks, participants were warned in case eye-movements were observed in the preceding block, to allow correction.

Here we adopted the same general visual search task, including the exact spatial lay-out, as was implemented in our previous experiments that investigated the interaction among multiple attentional control mechanisms, in order to maintain comparability across these related studies (see Beffara et al., 2022; Dolci et al., 2023; Rashal et al., 2022). Specifically, the search display comprised six rectangular bars of 2.0° x 0.5° in size, either in green (RGB coordinates: 0, 75, 0; luminance: 29.4 cd/m²) or red (RGB values: 130, 0, 0; luminance: 29.9 cd/m²), presented on grey background (RGB: 40, 40, 40; luminance: 10.3 cd/m²) and centred equidistantly 7° away from a white fixation cross (0.5° x 0.5°; RGB: 255, 255, 255; luminance: 190.2 cd/m²). Two stimuli were presented in the upper visual field, two on the horizontal midline and two in the lower visual field. Within each stimulus, there was a small gap (diameter of 0.25°) of the same grey colour as the background and positioned at the upper or lower part. The target was the bar tilted $\pm 25^\circ$ across the vertical axis, whereas all the other stimuli, that had to be ignored (distractors), were bars tilted $\pm 25^\circ$ across the horizontal axis.

As in our previous work, the target never appeared in the two upper locations, which were hence just filler items (Dolci et al., 2023). This choice relates to evidence indicating that the N2pc is usually smaller in the upper visual field, compared to the lower visual field (Bacigalupo and Luck, 2019; Luck et al., 1997).

2.3. Experimental design

The experiment included a total of 2090 trials, divided into 8 blocks. Before starting the actual experiment, a practice phase of 64 trials was used to allow participants to familiarize themselves with the task. The task was to discriminate the position of the gap within the target item (up vs down) by pressing the letter "M" on the keyboard with their right index finger if the gap was in the lower part, or the letter "Z" with their left index finger if it was in the upper part.

Unbeknownst to the participants, the spatial location of the target followed an unbalanced probability distribution. Specifically, the target stimulus was presented with high probability at one location (HFTL: 45 % of the total trials) and with low probability at all the remaining three locations (LFTL: 18.3 % each). Participants were randomly assigned to one of four groups (Fig. 1a), each with a different spatial configuration of target-location probabilities. However, as laid out in the introduction section, in typical studies that investigate the N2pc, each of the experimental condition is presented both in the right and left visual field, in order to collapse the recorded neural activity across hemispheres (e.g., Wu et al., 2011), and by extension this is also useful for other lateralized components like the SPCN. Therefore, in the first half of the present study, the high frequency target location was associated to a location in one hemifield (e.g., bottom-right spatial location), whereas in the second half it was associated with the corresponding opposite-hemifield

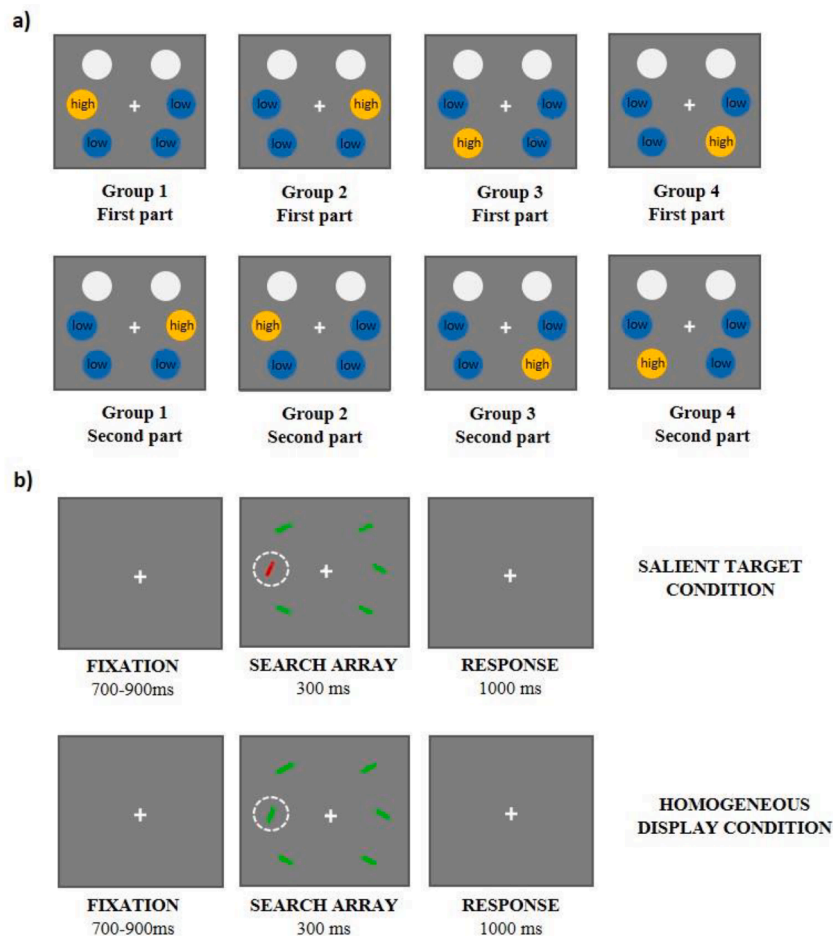


Fig. 1. (a) Target frequency distribution across groups during the first part of the experiment (first row) and during the second part (second row). In the two upper locations the target never appeared. Note that the manipulation of target location frequency was applied to homogeneous display trials only. (b) Examples of a trial sequence for the salient target condition (first row) and homogeneous display condition (second row). The target is circled for visualization purposes only (not present in the experiment) and was defined as the bar tilted $\pm 25^\circ$ across the vertical axis, while the non-targets were tilted $\pm 25^\circ$ across the horizontal axis (see text).

location (e.g., bottom-left spatial location). This assumes that asymmetries based on statistical learning can be adjusted quite quickly, with the simple collapsing of the two experimental halves only being possible if the SL effect switches quickly. We established this based on the behavioural data, as reported in the Results section.

Furthermore, to assess the interaction between SL and salience processing during target selection, in some trials the target was salient concerning colour. In particular, in some trials all the stimuli had the same colour (e.g., green: homogeneous display condition), whereas in some other trials, one of the elements, in this case the target stimulus, had a different (pop-out) colour (e.g., red among green bars: salient target condition). Importantly, when salient, the target appeared with equal frequency in all four possible locations (96 trials in each location during both the first and second half of the experiment), in order to clearly dissociate the benefit due to SL and salience processing AC signals.

2.4. Procedure

A fixation cross was constantly visible throughout the experiment. Each experimental trial (Fig. 1b) started with a display only containing the fixation cross, lasting for a random interval between 700 and 900 ms, followed by the search display that remained visible for 300 ms, followed by a 1000-ms interval with just the fixation cross again. Responses were recorded from the onset of the search display until the end of this 1000-ms interval, yielding a total of 1300 ms. Afterwards, a new

trial sequence started automatically. Within each block, all the conditions previously described were presented in a fully randomized order. Participants were instructed to maintain their eyes on the fixation cross and fixation quality was monitored by the experimenter by means of the online eye-position display of the eye-tracker.

In order to evaluate if participants were aware of the frequency manipulation, an explicit/implicit survey was conducted at the end of the experiment (see Dolci et al., 2023; Ferrante et al., 2018). Participants were first asked to report whether they noticed something about the spatial distribution of target stimuli and, in case they responded “yes”, they had to report (or guess) the location(s) where the target were presented most frequently.

2.5. Electrophysiological recording and pre-processing

EEG data were recorded using a Brain Products actiCHamp 64-channel system (Brain Products, Gilching, Germany) with 64 active scalp electrodes positioned according to the standard international 10–10 system and analysed using EEGLAB (Delorme & Makeig, 2004) and ERPLAB (Lopez-Calderon and Luck, 2014) software. Signals were recorded at a 500-Hz sampling rate, using Fz as the online reference and then re-referenced offline to the average of TP9 and TP10, corresponding to the left and right mastoids, at which point Fz was restored to the dataset. Afterwards, the data was down-sampled to 150 Hz, and a high-pass filter of 0.1 Hz was applied. During manual inspection, we excluded segments of the continuous data with clearly identifiable

artefacts. Afterwards, blinks and residual eye movements were removed by independent component analysis (ICA). We then shifted the triggers related to the search array onset for an observed delay in our set-up (16 ms) between when the digital trigger was saved in the EEG data vs. when a given stimulus appeared on the screen (Boudewyn et al., 2023). Subsequently, data were segmented into epochs from -200 ms to 800 ms relative to the stimuli array onset and we baseline-corrected with regard to the 200 ms pre-stimuli period. Then, a second artefact rejection was performed to flag and remove epochs containing an absolute amplitude exceeding ± 60 μV in the analysed channels (PO7/8). Lastly, data were visually inspected, and epochs containing any recognizable residual artefact (e.g., residual eye movement, excessive muscle noise, skin potentials) were manually removed. On average, we excluded 4.1% (standard deviation: 6.6) of total trials; all epoch exclusions were done in a fashion that was blind to the different conditions.

In order to study the different attentional distribution elicited by the exposure to a statistical regularity and how it interacts with a salience processing mechanism, our components of interest were the N2pc and SPCN, examined by averaging the activity of PO7/PO8, i.e. the electrodes where these components are usually largest (e.g., Liebrand et al., 2017; Kappenman et al., 2021; Rashal et al., 2022, 2023). The time windows we selected comprised the canonical values used in literature, i.e. from 200 to 300 ms for the N2pc (e.g., Eimer, 1996; Kiss et al., 2008) and from 350 to 650 ms for the SPCN, after the search-display onset (e.g., Rashal et al., 2023; Salahub and Emrich, 2018). As mentioned above we further divided the N2pc and SPCN time-window into early part (N2pc: 200 – 250 ; SPCN: 350 – 500) and late part (N2pc: 250 – 300 ; SPCN: 500 – 650), in order to better study the temporal dynamics of target selection.

All subsequent data analyses were performed using R 3.6.2 (R Core Team, 2016) with *ez* (Lawrence, 2011/2015) and *effectsize* (Ben-Shacharet al., 2020) packages. All EEG data analyses were based on correct trials only. To analyse the N2pc/SPCN we first calculated the mean amplitude of the *ipsi* and *contra* channels relative to the location where the target appeared, collapsing it across the two halves of the experiment (see above). Then we performed repeated-measures ANOVAs to compare the difference waves resulting from the subtraction *contra-minus-ipsi* channels, between different conditions. The p values were corrected with Greenhouse-Geisser epsilon in cases of significant sphericity violation. Because of the clear hypotheses in terms of behaviour and N2pc, one-tailed t -tests were used. Furthermore, note that, unless stated otherwise, in the described analyses the low-frequency target condition was the average of the three low-frequency target locations.

3. Results

3.1. Behavioural: interaction between SL and saliency: behavioural data

To assess the integrated effects of statistical learning and salience processing AC mechanisms, we performed 2×2 repeated-measures ANOVA with Target Frequency (high, low) and Display Type (homogeneous, salient target) for accuracy and RTs (see Fig. 2). This analysis showed significant main effects of both Target Frequency [ACC: $F(1, 22) = 8.14$, $p < 0.01$, $\eta_p^2 = 0.27$; RTs: $F(1, 22) = 19.60$, $p < 0.01$, $\eta_p^2 = 0.47$] and Display-type [ACC: $F(1, 22) = 34.94$, $p < 0.01$, $\eta_p^2 = 0.61$; RTs: $F(1, 22) = 76.17$, $p < 0.01$, $\eta_p^2 = 0.77$]. Interestingly, a significant interaction was observed, even if only in terms of RTs [ACC: $F(1, 22) = 0.47$, $p = 0.49$, $\eta_p^2 = 0.02$; RTs: $F(1, 22) = 37.83$, $p < 0.01$, $\eta_p^2 = 0.63$]. Post-hoc paired t -tests (one-tailed) on RTs revealed a strong significant Target Frequency facilitation in the high (vs. low) target frequency locations when the display was homogeneous, i.e., all the stimuli had the same colour [44 ms : $t(22) = -5.31$; $p < 0.01$, Cohen's $d = -0.64$], and a weaker one when the target was salient [20 ms : $t(22) = -3.00$; $p < 0.01$, Cohen's $d = -0.27$]. In turn, a benefit of Display Type was observed when the target appeared in the high-frequency location [41 ms : $t(22) =$

7.23 ; $p < 0.01$, Cohen's $d = 0.57$], which was stronger when the target appeared in the low-frequency location [66 ms : $t(22) = 9.23$; $p < 0.01$, Cohen's $d = 0.98$]. As such, the interaction between target frequency and Display type is explained by the SL effect being larger in the homogeneous display condition compared to when the target was salient (44 ms vs. 20 ms) and, at the same time, saliency facilitated target detection more when it was presented in the low- compared to the high- (66 ms vs. 41 ms) frequency location (Fig. 2a).

Furthermore, in a second analysis we investigated the temporal dynamics of SL and the ability of participants to adjust to new regularities after having switched the high frequency location to the opposite hemisphere at the midpoint of the experiment. We thus divided the experiment into 8 blocks, of which blocks 1–4 represented the first experimental half (before the HFTL switch), and blocks 5–8 correspond the second experimental half (after the HFTL switch). A rm-ANOVA was performed with Blocks (1–8) and Target Frequency (high, low) considering only the homogeneous display condition trials in order to purely describe the effect of SL, irrespective of saliency. Results showed a main effect of both Block [ACC: $F(7, 154) = 0.49$, $p = 0.01$, $\eta_p^2 = 0.26$; RTs: $F(7, 154) = 0.27$, $p < 0.01$, $\eta_p^2 = 0.52$] and Target Frequency [ACC: $F(1, 22) = 7.17$, $p = 0.01$, $\eta_p^2 = 0.24$; RTs: $F(1, 22) = 24.17$, $p < 0.01$, $\eta_p^2 = 0.52$], but no significant interaction [ACC: $F(7, 154) = 0.47$, $p = 0.76$; RTs: $F(7, 154) = 0.26$, $p = 0.61$], indicating that the SL effect did not significantly vary across the duration of the experiment, and hence was rapidly re-established after the switch (results remains mostly the same if we include all the trials).

Further following up this dynamic with higher temporal resolution, for each block we performed a t -tests to assess the Target Frequency effect (high- vs. low-target frequency locations). The analysis confirmed, at least for RTs, the main effect of Target Frequency in each block ($p < 0.05$; Fig. 2, panel b), suggesting that participants rapidly learned the SL bias at the beginning of the experiment and, at the same time, SL was quickly adapted to changes in the regularities.

Finally, in the survey used at the end of the experimental session we assessed if participants noticed something peculiar regarding the target frequency imbalance. Five subjects named the correct two high-frequency spatial locations (the one in the first half of the experiment and the one in the second), as the locations where the target was more likely to appear. However, excluding these participants from the

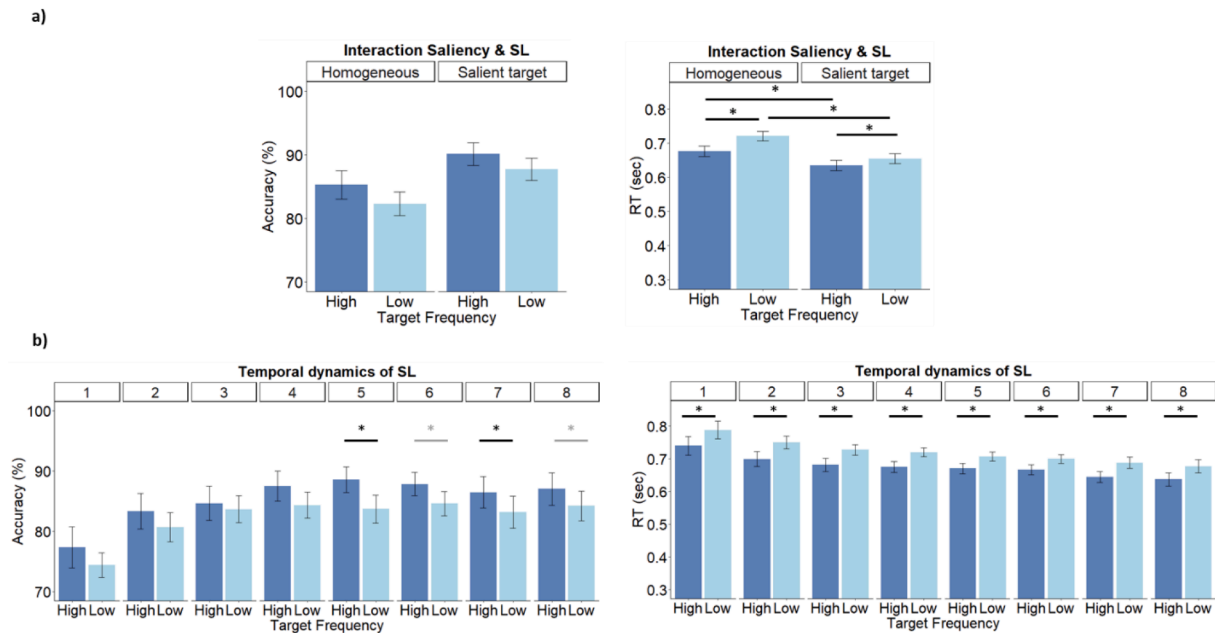


Fig. 2. In panel (a) plots show mean accuracies (left) and reaction times (right) as a function of Display-Type (homogeneous display, salient target display) and Target Frequency (high, low) conditions. In panel (b) plots show mean accuracies (left) and reaction times (right) for targets presented in the high vs. low frequency location, exclusively for the homogeneous display condition, in each of the eight experimental blocks. Note that the high-frequency target location was switched between block 4 and 5. Error bars represent the standard error of the means, whereas black asterisks index significance between conditions, with p value below 0.05, and grey asterisks trend to significance ($p < 0.1$).

analysis did not change the main results, corroborating the effect of an implicit learning process,^{1, 2}

3.2. Behavioural: SL effect is independent of inter-trial priming

Because of the higher number of trials in which the target appeared in the HFTL (vs. LFTL), it is possible that the difference between high- and low-frequency target locations was the consequence of inter-trial priming effects, rather than a more stable SL effect. Such an

¹ A 2x2 rm-ANOVA with Display-type (homogeneous, salient target) and Target Frequency (high, low) was also performed without the participants who reported to have noticed the target frequency imbalance and correctly indicated the two HFTL locations. For reaction times, the analysis confirmed the two main effects [Display-type: $F(1,17) = 61.70$, $p < 0.01$, $\eta_p^2 = 0.78$; Target frequency: $F(1,17) = 16.46$, $p < 0.01$, $\eta_p^2 = 0.49$] and a significant interaction [$F(1,17) = 35.18$, $p < 0.01$, $\eta_p^2 = 0.67$]. Post-hoc t -tests also confirmed the Target Frequency effect in favour of the HFTL both when the display was homogeneous [47 ms: $t(17) = -4.85$, $p < 0.01$, Cohen's $d = -0.77$] and when the target was salient: [19 ms: $t(17) = -2.71$, $p = 0.01$, Cohen's $d = -0.33$]. Furthermore, the salient target speeded up the responses both when it appeared in the high [42 ms: $t(17) = 6.27$, $p < 0.01$, Cohen's $d = 0.69$] and low [70 ms: $t(17) = 8.51$, $p < 0.01$, Cohen's $d = 1.19$] frequency location. Also in terms of accuracy we confirmed the previous results, i.e. a main effect of both the two factors [Target Frequency: $F(1,17) = 7.72$, $p < 0.01$, $\eta_p^2 = 0.31$; Display-type: $F(1,17) = 23.49$, $p < 0.01$, $\eta_p^2 = 0.58$] and no significant interaction [$F(1,17) = 0.03$, $p = 0.85$, $\eta_p^2 = 0.002$].

² It is important to note that, in order to avoid influencing participants' responses, the survey did not provide any information about the target frequency imbalance or the shift of the high-frequency location halfway through the experimental session. Consequently, we cannot determine whether participants, when indicating one (or two) locations as the high-frequency spot, were referring to the first, second, or both parts of the experiment. As such, it is conceivable that more participants partly figured out the manipulation. Still, the extra analysis in footnote 1, the stability of the SL effect and fast switch thereof after the switch of the HFTL, seem to still speak against a strong influence of conscious awareness on the observed SL effects.

alternative explanation would potentially also be in line with the rapid changing of the observed behavioural effects after switching the HFTL location (since such inter-trial priming effects develop by definition rather quickly). To investigate this alternative explanation, we replicated the previous 2×2 rm-ANOVA with factors Display Type (homogeneous, salient target) and Target Frequency (high, low), while excluding trials where the target occurred in the same spatial position on the immediately previous trial (30 % of total trials). The results corroborated the previous findings, showing a main effect of both Display Type, with better performance when the target was salient (vs. homogeneous display) [ACC: $F(1, 22) = 42.49$, $p < 0.01$, $\eta_p^2 = 0.65$; RTs: $F(1, 22) = 83.08$, $p < 0.01$, $\eta_p^2 = 0.79$], and Target Frequency [ACC: $F(1, 22) = 4.06$, $p = 0.05$, $\eta_p^2 = 0.15$; RTs: $F(1, 22) = 10.38$, $p < 0.01$, $\eta_p^2 = 0.32$], with a facilitation at the high- (vs. low-) frequency location. In terms of RTs, the significant interaction between the two factors was also confirmed [ACC: $F(1, 22) = 0.28$, $p = 0.60$, $\eta_p^2 = 0.01$; RTs: $F(1, 22) = 29.43$, $p < 0.01$, $\eta_p^2 = 0.57$]. Post-hoc t -tests (two-tailed) on RTs supported the previous pattern, in which the effect of one AC mechanism was reduced, but still efficient, in the presence of the other mechanism: Display Type revealed a significant benefit for the salient (vs. non-salient) target when it appeared at low-frequency location [68.9 ms; $t(22) = 9.81$, $p < 0.01$, Cohen's $d = 1.02$], and at high-frequency location [45.5 ms; $t(22) = 7.30$, $p < 0.01$, Cohen's $d = 0.63$]. Similarly, Target Frequency induced the advantage of HFTL when the display was homogeneous [36.7 ms; $t(22) = 4.17$, $p < 0.01$, Cohen's $d = -0.53$] and, marginally, when the target was salient [13.3 ms; $t(22) = -1.83$, $p = 0.07$, Cohen's $d = -0.19$].

3.3. EEG: N2pc

To assess how the N2pc was modulated by salience processing and SL, we conducted a rm-ANOVA with Display-type (homogeneous, salient target) and Target Frequency location (high, low). This was first done on the full time-window of 200–300 ms after stimulus onset, and then followed up by separate analyses of the first and second half thereof.

The analysis of the full 200–300 ms window showed a significant

main effect of Display Type [$F(1,22) = 9.56, p < 0.01, \eta_p^2 = 0.30$] with higher N2pc amplitudes for salient targets, and a trend-level interaction [$F(1,22) = 3.46, p = 0.07, \eta_p^2 = 0.13$]. No main effect of Target Frequency was observed [$F(1,22) = 0.10, p = 0.74$]. Planned post-hoc t -tests (one-tailed) revealed that Display Type produced a significantly larger N2pc for salient targets (vs. no salient) in the low-frequency location [$72 \mu\text{V}; t(22) = 3.37, p < 0.01, \text{Cohen's } d = 0.40$] and a trend-level effect for the high-frequency location [$31 \mu\text{V}; t(22) = 1.70, p = 0.05, \text{Cohen's } d = 0.22$]. Furthermore, Target Frequency produced a trend-level difference in N2pc amplitude in favour of HFTL (vs. LFTL) only when the display was homogeneous [$26 \mu\text{V}; t(22) = -1.63, p = 0.06, \text{Cohen's } d = -0.30$], whereas no difference was found when the target was salient [$14 \mu\text{V}; t(22) = 0.54, p = 0.70$] (Fig. 3, panel e).

To further investigate the temporal dynamics of attentional selection, we repeated the rm-ANOVA separately for the early and late part of N2pc time-window. Regarding the early part of N2pc time-window (200–250 ms), we confirmed a main effect of Display Type [$F(1,22) = 12.30, p < 0.01, \eta_p^2 = 0.35$] and now observed a fully significant interaction [$F(1,22) = 4.76, p = 0.03, \eta_p^2 = 0.17$]. No effect of Target Frequency emerged [$F(1,22) < 0.01, p = 0.94$]. Paired post-hoc t -tests (one-tailed) also confirmed that Display Type produced a significantly larger N2pc for salient (vs. non-salient) targets both in the low-frequency location [$89 \mu\text{V}; t(22) = 3.65, p < 0.01, \text{Cohen's } d = 0.52$] and in the high-frequency location [$41 \mu\text{V}; t(22) = 2.26, p = 0.01, \text{Cohen's } d = 0.27$]. No significant difference in the early-N2pc amplitude was found for Target Frequency neither when the display was homogeneous [$22 \mu\text{V}; t(22) = -1.30, p = 0.10$], nor when the target was salient [$25 \mu\text{V}; t(22) = 0.95, p = 0.82$].

Regarding the second part of the N2pc (250–300 ms), the results revealed a trend-level significance for Display Type [$F(1,22) = 3.60, p = 0.07, \eta_p^2 = 0.14$], and no effect of Target Frequency [$F(1,22) = 0.34, p = 0.56$] or interaction [$F(1,22) = 2.72, p = 0.11$] (Fig. 4, panel a).

In summary, the N2pc was clearly affected by salience with larger amplitudes for salient targets, especially in the early portion of the time-window. Furthermore, we observed an interaction between the different factors, which seemed to originate from the fact that SL only increased the N2pc amplitude for non-salient targets. These effects generally appeared to be stronger in the first half of the N2pc time-window.

3.4. EEG: SPCN

Similar to the analysis of the N2pc, we tested if salience processing and SL modulated post-selection processing, as indexed by the SPCN. We ran a rm-ANOVA with Display-type (homogeneous, salient target) and Target Frequency location (high, low), initially for the full time-window of the SPCN, then followed again by a separate analysis of its early and late part. Results for the full time window showed a main effect of Display type [$F(1,22) = 9.22, p < 0.01, \eta_p^2 = 0.29$], stemming from a larger SPCN amplitude for salient targets; and a trend-level main effect of Target Frequency [$F(1,22) = 3.60, p = 0.07, \eta_p^2 = 0.14$] with a larger SPCN amplitude in favour of low-frequency locations, as well as a trend-level significant interaction [$F(1,22) = 3.11, p = 0.09$]. Paired post-hoc t -tests (two-tailed) revealed that Display Type produced a significantly larger SPCN for salient (vs. non-salient) targets in the low-frequency location [$43 \mu\text{V}; t(22) = 4.79, p < 0.01, \text{Cohen's } d = 0.49$], but not in high-frequency location [$13 \mu\text{V}; t(22) = 0.91, p = 0.36$]. Furthermore, Target Frequency produced a significantly larger SPCN in favour of low-frequency locations, but only when target was salient [$43 \mu\text{V}; t(22) = 2.58, p = 0.01, \text{Cohen's } d = 0.40$] and not when the display was homogeneous [$14 \mu\text{V}; t(22) = 0.80, p = 0.43$] (Fig. 3, panel f).

Regarding the early part of the SPCN (350–500 ms), results revealed a significant main effect of Display Type [$F(1,22) = 16.39, p < 0.01, \eta_p^2 = 0.42$] and a significant interaction [$F(1,22) = 5.74, p = 0.02, \eta_p^2 = 0.20$], but again no main effect of Target Frequency [$F(1,22) = 0.43, p = 0.51$]. Again, post-hoc t -tests (two-tailed) confirmed that Display Type produced a significantly larger SPCN for salient (vs. non-salient) targets

in the low-frequency location [$81 \mu\text{V}; t(22) = 5.14, p < 0.01, \text{Cohen's } d = 0.76$] and a trend-level effect for high-frequency location [$37 \mu\text{V}; t(22) = 2.03, p = 0.05, \text{Cohen's } d = 0.28$]. Furthermore, a trend-level significant for Target Frequency showed a significant difference in SPCN amplitude in favour of low- (vs. high-) frequency location, but only when the target was salient [$32 \mu\text{V}; t(22) = 1.83, p = 0.08$] and not when the display was homogeneous [$10 \mu\text{V}; t(22) = -0.50, p = 0.61$].

In contrast, the late part of SPCN data (500–650 ms) showed a significant main effect of Target Frequency [$F(1,22) = 9.64, p < 0.01, \eta_p^2 = 0.30$] with an SPCN mean amplitude enhancement for low- (vs. high-) frequency location. No main effect of Display Type [$F(1,22) = 0.02, p = 0.86$] or interaction [$F(1,22) = 0.92, p = 0.34$] was found (Fig. 4, panel b).

Together these results suggest that early and late part of the SPCN are modulated in a different way by the two AC mechanisms of interest, with mainly salience processing acting earlier and SL acting later on.

Error bars represent the standard error of the means, whereas black asterisks index significance between conditions (results from one-tailed t -tests for N2pc and two-tailed t -tests from SPCN), with p values below 0.05 and grey asterisks trend to significance ($p < 0.1$).

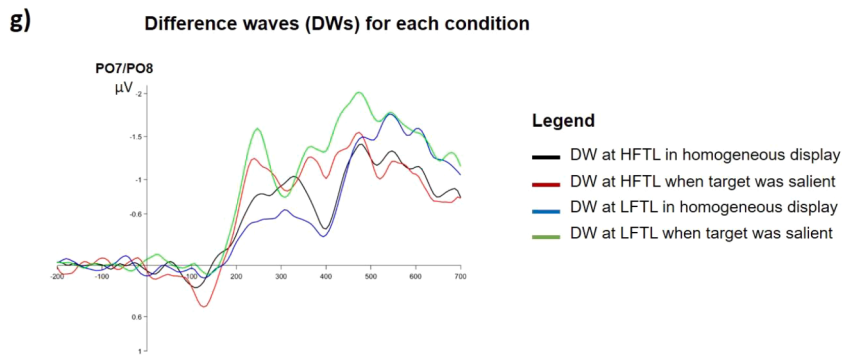
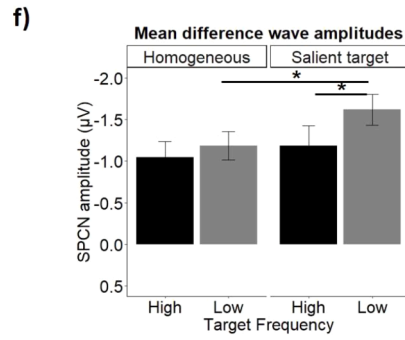
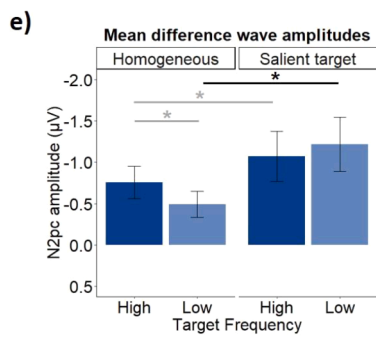
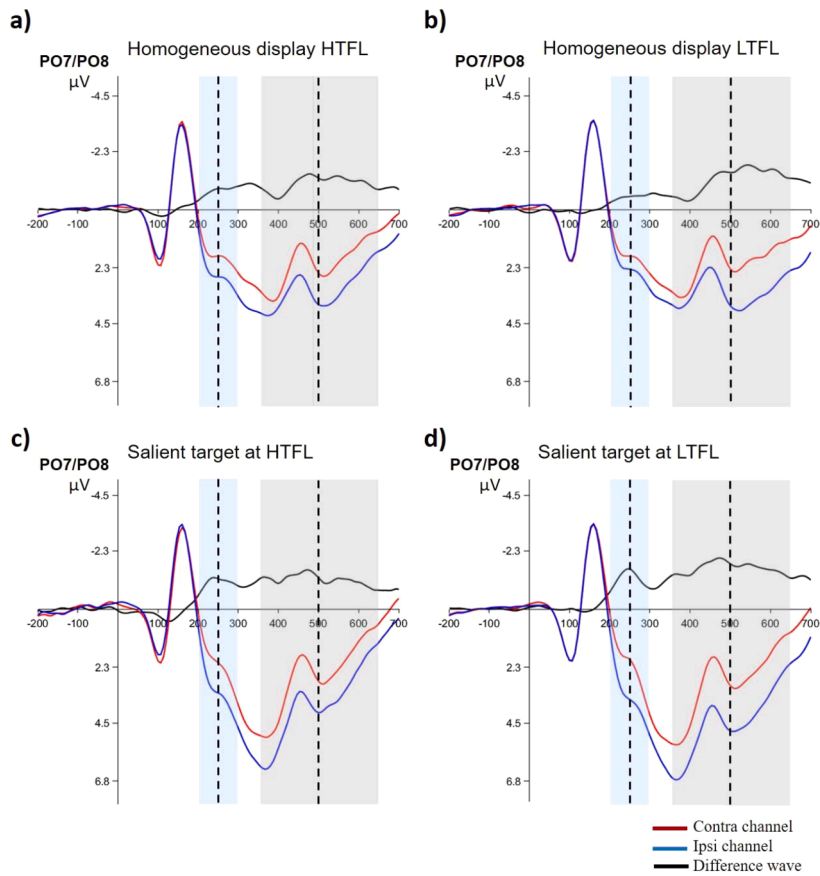
Error bars represent the standard error of the means, and black asterisks index significance between conditions (results from one-tailed t -tests for N2pc and two-tailed t -tests from SPCN) with p values below 0.05, and grey asterisks trend to significance ($p < 0.1$).

4. Discussion

The main purpose of the present study was to investigate how the effects of multiple AC mechanisms, namely salience processing and SL, are integrated in order to solve stimulus competition, and jointly define which stimulus should be selected. By using the same visual search task as implemented in some of our previous work (Beffara et al., 2022; Dolci et al., 2023; Rashal et al., 2022, 2023), here we tested the combined effects of salience processing, modulated by using a colour singleton target (vs. a non-salient target), and SL, induced by introducing an imbalance in target frequency across locations. Simultaneously, we recorded EEG activity to uncover the time course of target selection and further processing by focusing on the N2pc and SPCN. In particular, the N2pc is believed to reflect early target selection processing (Eimer, 1996; Luck and Hillyard, 1994), when focal attention is allocated toward the spatial location/item that has a higher attentional priority. The SPCN, in turn, indexes post selection processing, i.e. when visual information are maintained and discriminated in VSTM (e.g., Jolicoeur et al., 2008).

Considering our behavioural results, the data showed an overall benefit of both saliency and SL, with faster responses for salient compared with non-salient targets, and for targets in the HFTL compared with the LFTL. Critically, a significant interaction between the two factors revealed that the benefit of saliency was smaller, but still present, in the HFTL, i.e., the spatial location that should already have a higher attentional priority due to SL. Similarly, the benefit of SL was larger when the target was not salient (homogeneous display), i.e. when salience processing was not at a play.

In line with these behavioural results, our EEG data suggest that both salience processing and SL jointly contribute to solving stimulus competition, each with a different weight depending on different stages of target processing. As expected, salience processing seems to modulate the underlying neural activity specifically in the early stage of target selection, when a salient (vs. non-salient) target could automatically capture attention, as indexed by an N2pc enhancement. By separately analysing the early and late part of the N2pc time-window, we found that the impact of saliency was present especially in the initial phases of attentional selection (early part of the N2pc). Moreover, this effect was greater in the LFTL, likely compensating for the fact that fewer attentional resources were deployed at this location due to SL. At the same time, no clear main effect of SL was found at this stage of attentional



(caption on next page)

Fig. 3. Sensor plots showing the signal at the contra- (red line), ipsi-lateral (blue line) with regard to the target, and the difference waves (contra-minus-ipsi; black line) when all stimuli had the same colour, i.e., homogeneous display (a and b), or when the target was the salient element (c and d). Panels a and c depict activity in the HFTL condition, and Panels b and d depict activity in the LFTL condition. Time-point zero indicates the search-display onset. The blue area is the time-window where the mean amplitude of the N2pc time-range was quantified (early part on the left, late part on the right), whereas the grey area represents the quantified time-window of the SPCN (early part on the left, late part on the right). Panel e shows the mean amplitude of the N2pc, calculated by subtracting the *contra-minus-ipsi* channels, in the two Target Location Frequency conditions as a function of Display Type (homogeneous display vs. salient target display), considering the entire time-window (200–300). Similarly, panel f shows the mean amplitude of the SPCN (entire time-window: 350–650), calculated by subtracting the *contra-minus-ipsi* channels, in the two Target Location Frequency conditions as a function of the Display Type (homogeneous display vs. salient target display). Panel g represents the difference waves for each of the considered conditions.

selection. SL seemed to affect the N2pc, producing a larger mean amplitude for HFTL (vs. LFTL), but only in the homogeneous display, i.e. again in the absence of salience processing. This suggests that SL and salience processing interacted, potentially in a way in which salience processing dominated in the present experiment, and SL only played an additional modulatory role.

This relatively weak effect of SL on the N2pc could have various explanations. In particular, one aspect that can potentially explain the discrepancy between our results and the findings of Duncan et al. (2023) is the fact that in our experiment the differences manipulation, in terms of number of trials for the high vs. low location was smaller compared to the difference used by Duncan and colleagues. In addition, in our design, the additional salient targets (which were completely randomly distributed across locations) may have further interfered with learning. At the same time, it is worth noting that also in Duncan et al. (2023), the effect of SL on the N2pc seemed to emerge in an earlier part of their overall N2pc time window, dovetailing with the present results. Finally, the relatively weak SL effect on the N2pc in our data could have had to do with between-subject variation in the exact HFTL, which was in the lower visual field for some participants and on the horizontal meridian for others. Given that it is known that the N2pc is generally observed to

be larger in the lower visual field, such differences could have added between-subject variability to our data. These different array arrangements might also be the cause of the different pattern between high- and low-target frequency locations when the display was homogeneous versus when there was a salient target. Indeed, one can observe a (only numerical) difference in favour of the low- (vs. high-) frequency location when there was a salient target and vice versa in the homogeneous display (Fig. 3, panel e).

Regarding the comparison with earlier work, it seems that the impact of SL on the N2pc varies depending on the stimulus dimension to which SL is applied. Indeed, in a recent experiment, Wang and colleagues (2023), found that statistical learning of target colours (i.e. feature target dimension) did not bias the deployment of attentional selection as indexed by the N2pc but, instead, it affected post-selection decision-making processes, as indexed by the late positive complex, i.e. LPC (Wang et al., 2023). This could point to a prominence of an attentional-selection benefit of SL, when applied directly to a spatial configuration.

Going forward, after the attentional selection, in the present experiment, an SL effect also emerged after a candidate target has been located. Specifically, as indexed by the SPCN results, during the post-

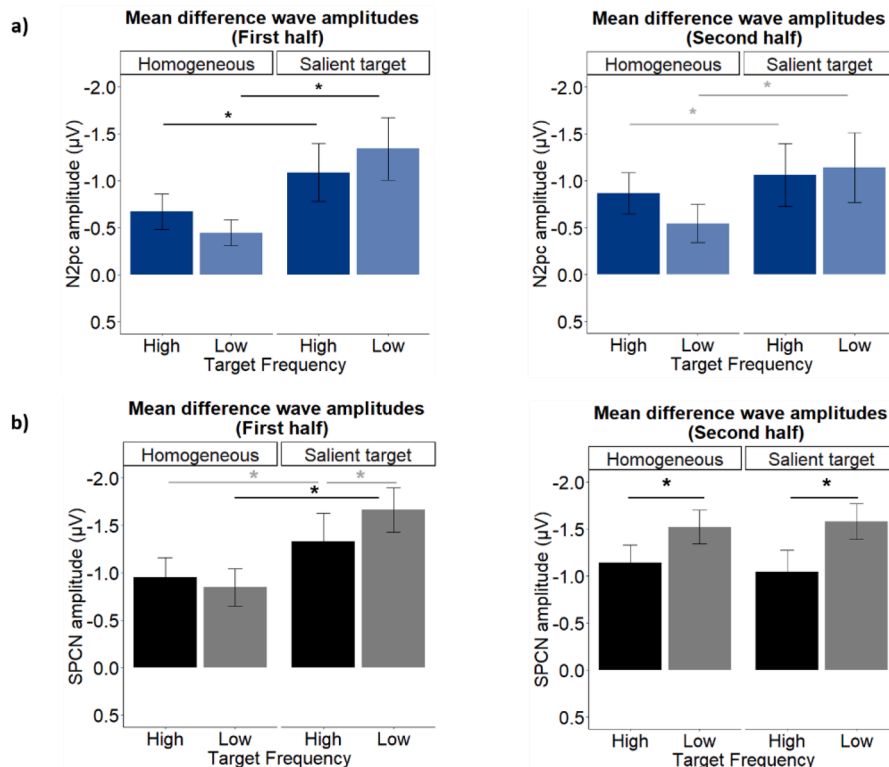


Fig. 4. Panel a shows the mean amplitude of the N2pc, calculated by subtracting the *contra-minus-ipsi* channels, in the two Target Location Frequency conditions as a function of Display Type (homogeneous display vs. salient target display), respectively for the early part (200–250, left plot) and late part (250–300, right plot) of the overall N2pc time-window. Similarly, Panel b shows the mean amplitude of the SPCN for the early part (350–500, left plot) and late part (500–650, right plot) of the overall SPCN time-window, calculated by subtracting the *contra-minus-ipsi* channels, in the two Target Location Frequency conditions as a function of the Display Type (homogeneous display vs. salient target display).

selection target processing, both salience processing and SL contributed, allowing selected visual information (i.e. the target) to move to VSTM for deeper processing and discrimination, albeit with differential dynamics. Specifically, salience processing produced an overall enhancement of the SPCN in favour of the salient (vs. non-salient) target, in particular during its early part. As such, the condition in which target selection had presumably occurred earlier, the early SPCN was also more clearly expressed, whereas SL elicited a larger SPCN toward the LFTL (vs. HFTL), i.e. the condition in which the target selection was likely more difficult, in the later part of the SPCN.

This set of results for the SPCN raises a couple of interesting points, relating to the dynamics of further processing relying on earlier selection and the need for further discrimination, as well as a temporal distinction across the two halves we investigated here. Specifically, the early SPCN showed a pattern of results that was very reminiscent of the N2pc results that directly preceded it, although with a stronger resemblance with its earlier part (which suggests that it is not a simple continuation, given that 100 ms pass between the end of the early N2pc time-window and the start of the early SPCN window). Indeed, as in that earlier window of N2pc, also in the earlier part of SPCN, a main effect of salience was observed, which interacted with SL, which itself did not produce a main effect. This resemblance with the N2pc pattern may suggest that early selection simply leads to early discrimination, and that conditions in which targets were selected early, were also transferred to a discrimination stage more quickly, a process reflected by the early SPCN. For salient targets, this stage may be subsiding during the late SPCN time window, in which SL dominated, but in the sense that larger amplitudes were observed for LFTL, hence for the condition in which targets were likely selected last. Yet, what is interesting about this interpretation is that the observed SL effect entailed a clear main effect in this later time-window, and that the SL effect was also present for salient targets.

According to the episodic theory of priming in visual search (Huang et al., 2004), it is possible that when a stimulus is identified as a possible target, the system compares it against previously encountered examples stored in episodic memory in order to confirm it is the correct target before proceeding to make the appropriate response. The verification process happens more quickly if the current target location matches with high-probability target location retrieved from episodic memory. In contrast, if the target appeared in the rare location, the system may require more time to recall enough matching trial instances to confirm it (Wang et al., 2023). As such, the late main effect of SL could reflect this process, indexing a mechanism that is largely independent of saliency, and not a pure reflection of processing dynamics derived solely from the dynamics of target selection.

Recently, a new view of the competition among different AC mechanisms assigns a major role in the attentional selection to the lingering biases of SL (Failing and Theeuwes, 2018), affecting the first feed-forward sweep of information (likely through synaptic mechanisms) into the spatial priority map before the search array onset (Kong et al., 2020; Huang et al., 2021) and adds an additional mechanism creating the overall landscape in which different AC signals (inter-)act (Gao and Theeuwes 2020). Such a synaptic mechanism of SL is strongly suggested by the earlier work of Duncan et al. (2023), including the observation that pre-stimulus alpha power is not lateralized with regard to the HFTL, which would suggest explicit anticipatory top-down control (but see also Wang et al., 2019 for a conflicting observation).

Within the priority map, Liesefeld and Müller (2021) argued that, when combined with salience processing, the modulatory impact of SL can operate at distinct levels of priority computation. In particular, in their study, they described the supradimensional and subordinate levels. Specifically, they showed that SL exerts a supradimensional influence when associated with a salient element defined by task-relevant features (in their study, a distractor defined by the same feature dimension as the target). This induced a purely space-based modulation (e.g., a location suppression in their case), within the map, without specific constraints to a particular feature of the salient element. As a consequence, all the

elements that appeared in that location were affected by the SL modulation (e.g., worst detection in the suppressed location). In contrast, if SL was linked to a salient element defined by a different, task-irrelevant feature dimension, the SL modulation (e.g., location suppression) operated at a subordinate level. In this scenario, the effect was constrained to a specific feature, precisely the feature that defines the salient element.

All these observations are in line with what we found in our study. Because SL was related to the task-relevant item, i.e. the target, a purely space-based modulation at the supradimensional level was a valid strategy for participants in this task, since no other feature of the target could help participants to make predictions about the future trial. Therefore SL might have created the landscape, described by Gao and Theeuwes (2020), within the priority map, giving a higher attentional priority to the location where target was more likely to appear, at the expense of the location where it appeared rarely. Under this scenario, salience processing could operate such that its impact was more visible in the low-frequency target location, i.e. where it could compensate for the lower attentional resources allocated at that location.

However, an alternative perspective suggests that when the target is salient, its processing takes temporal precedence over SL, aligning with the idea that it represents a stronger and more automatic AC mechanism (Theeuwes, 1991, 1992; Van der Stigchel et al., 2009). Nevertheless, our results only partially support this hypothesis. While the larger N2pc for salient targets could indicate this temporal precedence, our data revealed that a sort of influence of SL was present even in the early target selection processing. As stated above, in terms of N2pc the benefit of salience processing was evident in the LFTL, and only slightly in the HFTL, suggesting that SL was already at a play.

4.1. Flexibility of statistical learning bias

Importantly, in the present study, we also further examined the dynamics of SL by investigating how quickly it is acquired, and by further probing its flexibility in adapting to changes. Specifically, we tested the ability of participants to learn regularities about imbalances in target frequency and then adjust them with new statistical regularities, without having explicit instructions about it. Furthermore, we also assessed the role that inter-trial priming might have on SL effect.

Regarding learning speed, our data showed that the effect of SL emerged quite fast, such that a performance enhancement for targets in the HFTL (vs. LFTL) was visible even in the very first block of the experiment. This indicates that even a short exposure to a statistical imbalance of target frequency across locations allowed participants to modulate their attentional priorities within the spatial priority map, by giving a higher weight to the location where the target was more likely to appear (Wang and Theeuwes, 2020). Once acquired, to test how flexible this mechanism is (as well as in order to allow for a balanced analysis of the N2pc and SPCN; see Methods), after the first experimental half, we switched the high-frequency target location from one hemifield (e.g., right) to the other (e.g., left). This enabled us to test whether our participants could adapt their behaviour and change their attentional priorities in favour of the new HFTL; or, instead, if they would keep their preference toward the old HFTL, indicating, in this case, that SL would be an inflexible mechanism, resistant to changes.

What we found is that even in the block right after the switch, participants could efficiently learn a new target frequency distribution, i.e., they showed better performance in the new high-frequency location compared to when the target appeared in the low-frequency locations, supporting the hypothesis that SL is a fast and flexible mechanism that can be adjusted to environmental modifications. An interesting point here is that in many learning contexts, including SL, a strong test of learning is its perseverance in contexts in which the statistical imbalance changed (e.g., Britton and Anderson, 2020). Here, we did not have such a phase, with the reason mostly being that we wanted to maximize the number of trials that could be used for our EEG data analysis. As such,

we cannot dissociate an unlearning phase (i.e. lingering bias of SL in neutral blocks) from a re-learning phase (i.e. where new regularities are introduced), but it seems possible that the fact that the initial SL effect did not seem to linger has to do with it actively being overwritten by a new imbalance.

As mentioned above, here we also tested the link between two experience-dependent AC mechanisms, i.e., SL and inter-trial priming. The latter refers to the fact that a stimulus recently selected (or ignored) can be easily selected (or ignored) again even if this is not specifically required by the task (Kristjánsson and Campana, 2010; Failing and Theeuwes, 2018). In fact, a scenario under which our SL effects would have largely been driven by short-term inter-trial priming effects would have also been in line with the fast (re-)learning that we ascribed to more long-term SL, since the inter-trial contingencies obviously change immediately (more HTFL after HTFL in the respective hemifield). Nevertheless, while inter-trial priming requires consecutive repetition of a specific element to induce an attentional bias, the SL effect observed here seemed not to depend on this (e.g., Jones and Kaschak, 2012; Ferrante et al., 2018). In contrast, it seems to be based on a more general computation of regularities that do not necessarily need to occur one right after the other. In the present study, we examined whether the SL effect could orient participants' attentional resources toward the high- (vs. low) target frequency location even in trials (N) where target did not appear in the same location of the immediately previous trial (N-1). Our results confirmed our previous findings, i.e., a better performance to detect the target in the HFTL (vs. LFTL), suggesting that the benefit of high-frequency location was not strongly dependent on inter-trial priming, but participants learnt a more general and long-term attentional bias.

Even if inter-trial priming and SL are both related to selection history, it is possible that they are guided by different processes. Inter-trial priming can be linked to simple memory types (e.g., habituation and sensitization), which recruit only the neural circuits that were active during the previous perception. In contrast, SL can refer to the extraction of more complex regularities among elements/spatial locations in the environment (Batterink et al., 2019) which can involve the hippocampus and MTL. This distinction at the neuronal level seems to correspond well with behavioural findings, showing that the effect of SL is often-times considerably larger than the effect of inter-trial priming (Theeuwes and Failing, 2020).

5. Conclusions

Overall, the evidence collected here suggests salience processing and SL can independently contribute to establishing the attentional priority within the priority map. The two mechanisms might indeed rely on different neural substrates (Theeuwes and Failing, 2020), such that the activity of one mechanism does not interfere with the activity of the other. Salience processing could not totally prevent the benefit of SL and vice versa. Yet, the strength with and the time point in which one AC mechanism acts, seems to depend on the presence or absence of the other mechanism.

Furthermore, our data supports the view for which SL is a strong attentional control bias that can be as quickly established as it can be adjusted. When being exposed to new statistical regularities, people are able to rapidly adjust their attentional bias accordingly. Importantly, SL seemed to be independent of inter-trial priming effects, and generally occurred despite the fact that people were not instructed about any statistical regularities, thus they were largely unaware of their existence.

CRedit authorship contribution statement

Carola Dolci: Writing – original draft, Methodology, Formal analysis, Data curation, Conceptualization. **Einat Rashal:** Writing – review & editing, Methodology, Conceptualization. **Elisa Santandrea:** Writing – review & editing, Methodology, Funding acquisition,

Conceptualization. **Suliann Ben Hamed:** Writing – review & editing, Methodology, Funding acquisition, Conceptualization. **Leonardo Chelazzi:** Writing – review & editing, Methodology, Funding acquisition, Conceptualization. **Emiliano Macaluso:** Writing – review & editing, Methodology, Funding acquisition, Conceptualization. **C. Nico Boehler:** Writing – review & editing, Supervision, Methodology, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on EBRAINS repository. Other materials for the experiment reported here are available upon request

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