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Altering spatial priority maps via statistical learning of target selection and distractor filtering

Oscar Ferrante[a], Alessia Patacca[a], Valeria Di Caro[a],

Chiara Della Libera[a, b], Elisa Santandrea[a], Leonardo Chelazzi[a, b, §]

[a] Department of Neuroscience, Biomedicine and Movement Sciences, University of Verona - ITALY

[b] National Institute of Neuroscience – Verona Unit, Verona - ITALY

§ Corresponding author:

Prof. Leonardo Chelazzi,

Department of Neuroscience, Biomedicine and Movement Sciences

Section of Physiology and Psychology, University of Verona, Verona – ITALY

Strada Le Grazie 8, 37134, Verona – ITALY

Tel.: +39-045-8027149

Email: leonardo.chelazzi@univr.it

Abstract

The cognitive system has the capacity to learn and make use of environmental regularities – known as statistical learning (SL), including for the implicit guidance of attention. For instance, it is known that attentional selection is biased according to the spatial probability of targets; similarly, changes in distractor filtering can be triggered by the unequal spatial distribution of distractors. Open questions remain regarding the cognitive/neuronal mechanisms underlying SL of target selection and distractor filtering. Crucially, it is unclear whether the two processes rely on shared neuronal machinery, with unavoidable cross-talk, or they are fully independent, an issue that we directly addressed here. In a series of visual search experiments, participants had to discriminate a target stimulus, while ignoring a task-irrelevant salient distractor (when present). We systematically manipulated spatial probabilities of either one or the other stimulus, or both. We then measured performance to evaluate the _direct_ effects of the applied contingent probability distribution (e.g., effects on target selection of the spatial imbalance in target occurrence across locations) as well as its _indirect_ or "transfer" effects (e.g., effects of the same spatial imbalance on distractor filtering across locations). By this approach, we confirmed that SL of both target and distractor location implicitly bias attention. Most importantly, we described substantial indirect effects, with the unequal spatial probability of the target affecting filtering efficiency and, vice versa, the unequal spatial probability of the distractor affecting target selection efficiency across locations. The observed cross-talk demonstrates that SL of target selection and distractor filtering are instantiated via (at least partly) shared neuronal machinery, as further corroborated by strong correlations between direct and indirect effects at the level of individual participants. Our findings are compatible with the notion that both kinds of SL adjust the priority of specific locations within attentional priority maps of space.

Keywords

probability cueing; target selection; distractor filtering; attentional capture; priority maps

Highlights

- Statistical learning (SL) processes exert implicit attentional guidance.
- Exposure to spatial imbalances in target or distractor occurrence biases attention.
- SL of target or distractor location affects both selection and filtering mechanisms.
- Target selection and distractor filtering reflect (partly) shared neural machinery.
- SL of target selection and distractor filtering induce plasticity in priority maps.

1. Introduction

Most kinds of daily activities, from watching a movie to driving a car along a busy street, require the normal functioning of the attentional system. Visual selective attention enables individuals to commit cognitive resources to relevant elements in the visual environment while filtering irrelevant and potentially interfering sensory input, including from other sensory modalities (Jonides & Yantis, 1988; Yantis & Jonides, 1990; Theeuwes & Burger, 1998; Forster & Lavie, 2008; Marini et al., 2013). Traditionally, visual selective attention is thought to operate under the influence of two types of control signals: when attention is summoned – or captured - by a salient stimulus, such as a bright flash of light, it is said to be under bottom-up (or stimulus-driven) control (Yantis & Egeth, 1999; Theeuwes, 2010); instead, when attentional selection is guided by a deliberate act of will, and is aimed at task-relevant information, it is said to be under top-down (or goal-driven) control (Egeth & Yantis, 1997).

Over recent years, however, researchers have identified a number of factors that can exert control over visual attention, above and beyond bottom-up and top-down influences. The focus here is on a family of phenomena that have been revealed by a panoply of experimental paradigms, and that cannot be readily accounted for in terms of either stimulus salience or behavioral relevance. All these phenomena tend to share one key feature, namely, they reflect implicit processing. Sometimes they are referred to with the overarching term of "selection history" effects (Awh et al., 2012). Notable examples of this family of phenomena are the different types of inter-trial priming effects (Tipper, 1985; Maljkovic & Nakayama, 1994; 1996; Kristjánsson & Campana, 2010), whereby the repetition of target- and distractor-defining features across consecutive trials improves performance, and contextual cueing (Chun & Jiang, 1998; 2003), i.e., the improved performance in target selection that is supported by spatio-temporal regularities in the visual context picked up by the observer over the course of the experiment. Other forms of control belonging to the same general category

include the impact on visual attention of semantic associations (Moores et al., 2003; Belke et al., 2008; Telling et al. 2010; De Groot et al., 2016), i.e., the tendency for attention to select items in the display that, albeit task-irrelevant, bear a semantic associative link to the sought target, and other kinds of familiarity/novelty effects (Christie & Klein, 1995; Horstmann, 2002). Finally, research over recent years has revealed that reward (and punishment) can exert a strong and multifaceted influence on attention, for example in the form of increased effective salience acquired by stimuli and locations systematically associated with reward (Della Libera & Chelazzi, 2006; 2009; Kristjansson et al., 2010; Della Libera et al., 2011; Anderson et al., 2011a; 2011b; for reviews, see Chelazzi et al., 2013; Anderson, 2016; Bourgeois et al., 2016). To reiterate, it is typically assumed that all the above influences on attention occur implicitly, without the participant knowing that they are at play. Key to the expression of all those kinds of attentional control, as already said, is that they reflect past encounters with certain stimuli and contexts, as well as past episodes of attentional processing of the stimuli – from this, the term "selection history" effects (Awh et al., 2012; see also Todd & Manaligod, this issue).

Here we concentrate on yet another form of selection history effect, again reflecting implicit control of attention, called statistical learning (SL) of target and/or distractor location. In general, with the term SL we refer to the brain capacity to learn and make good use of environmental regularities whose existence is registered over repeated exposures to the given context and situation (for a review, see Schapiro & Turk-Browne, 2015). SL is thought to play a key role in a variety of cognitive domains, such as language acquisition (Saffran et al., 1996; Aslin & Newport, 2012; Erickson & Thiessen, 2015), efficient coding of feature combinations (Fiser & Aslin, 2001; 2002), memory (Umemoto et al., 2010; Schapiro et al., 2017) and motor skill learning (Altamura et al. 2014; Perruchet & Pacton, 2006). In the attentional domain, SL constitutes a strong determinant of stimulus priority and has been investigated in relation to various kinds of sequential regularities in stimulus presentation (Zhao et al., 2013; Yu & Zhao, 2015), or regularities in the spatial distribution of visual elements (typically the target), also known as *spatial probability cueing* (Shaw and Shaw, 1977; Miller, 1988; Hoffmann

& Kunde, 1999; Geng & Behrmann, 2002; 2005; Walthew & Gilchrist, 2006; Druker & Anderson, 2010; Jiang et al, 2013a; 2013b; 2015a; 2015b; Sha et al., 2017). For instance, Geng and Behrmann (2002, 2005) provided an elegant demonstration that attention is biased in accordance with the spatial probability of the target over the course of the experiment. In their studies, participants had to indicate the orientation of a task-relevant stimulus presented amongst irrelevant ones in a visual search array. Unbeknownst to participants, target location was not equally probable across display regions: the target appeared with high probability (80%) in one half of the screen and with low probability (20%) in the other half. Compared to a baseline condition without spatial probability manipulation, target selection was speeded up in the high probability region and slowed down in the low probability region. These studies demonstrated that attentional allocation is implicitly adjusted on the basis of display statistics over time, indicative of an attentional bias towards locations where the sought target occurred more frequently (Geng & Behrmann, 2002; 2005), perhaps reflecting changes in the priority of individual locations within priority maps of space (Zelinsky & Bisley, 2015). This type of phenomenon has been systematically investigated in recent years, especially by Jiang and colleagues (see Jiang, this issue, for an extensive review) and several of its key features have been firmly established. Among others, these include: 1) its resistance to extinction, or the persistence of the bias once the imbalance in target probability across locations has been eliminated; 2) its implicit nature, with only few participants typically becoming aware of the probability manipulation (in fact, if anything, effects tend to be stronger when explicit knowledge is not formed); 3) its independence from cognitive load, such as the engagement of working memory on a different task; 4) and finally its relatively intact expression in ageing (unlike the typical deficits in declarative memory that are often found in ageing) (Jiang, this issue). In spite of considerable progress in our understanding of this type of attentional phenomenon, several important aspects still need to be clarified, as detailed in the sections below.

One aspect of probability cueing of target location that is still unsettled is the extent to which the phenomenon is independent from inter-trial (priming) effects.

To clarify, a spatial probability manipulation of target location brings with it a natural imbalance in the probability of immediate repetitions of target location (unless this is deliberately avoided by the experimenter). For instance, if two locations are associated with target probabilities of 80% and 20%, respectively, the chance that the target stimulus is presented for two consecutive trials in the same location is much higher at the high probability location compared to the low probability location (64% vs. 4%). It should be made clear immediately that the role of inter-trial priming in SL of target location is twofold. On the one hand, inter-trial priming of target location could produce benefits in performance that greatly contribute to what might appear to be solely determined by statistical learning of target probability across locations. In other words, the two effects being naturally conflated, it is important to establish to what extent each of them individually contributes to overall performance. On the other hand, however, one might argue that immediate repetitions, in addition to any direct benefit in performance that they may produce, represent a crucial "diagnostics" for the system to learn from the probabilistic spatial distribution of targets over time. Clearly, the latter consideration relates to the underlying learning mechanism, and how it is supposed to gather statistical evidence from experience (Friston & Kiebel, 2009; Clark, 2013; Vossel et al., 2014, 2015). The two problems can be dealt with in different ways. If the only concern is to parse out the influence on performance of immediate repetitions in target location from the more general SL effect, then it will suffice that when analyzing the data any inter-trial priming effect is subtracted away, in practice by calculating performance measures after eliminating from the data set all trials where the location of the target repeats between consecutive trials (of course, eliminating immediate repetitions still allows for influences resulting from more distant trials in the past, such as N-2, N-3, etc., according to some decaying function (Maljkovic & Nakayama, 1994)). Instead, if one plans to remove any role of immediate repetitions, then trial sequences will have to be constructed beforehand in such a way as to exclude entirely immediate repetitions in target location, or to make them equally probable for all locations. Walthew and Gilchrist (2006) reported that when by design target location did not repeat within a short sequence of trials (i.e., going beyond immediate repetitions), there was no longer

an effect of the unequal probability of target location on the participants' performance. Based on these results, the authors suggested that short-term target location priming is entirely responsible for the modulations in performance that are found in spatial SL studies. However, this view was rejected in a subsequent study by Jones and Kaschak (2012). In their replication of Walthew and Gilchrist work, the spatial probability of targets was manipulated while target locations did never repeat over short trial sequences, as before. Contrary to the original claim, the participants' performance was affected by the spatial probability of the target even in the absence of inter-trial priming effects. Therefore, it is important to provide new evidence bearing on this issue, something we will do with this work.

It has been long debated whether the attentional capture generated by a salient distractor is obligatory or can be avoided, or at least greatly reduced, under certain conditions, e.g., when powerful top-down control of attention is exerted (Folk & Remington, 1998; Theeuwes, 2010; for a hybrid position, see Sawaki & Luck, 2010). Regardless of the theoretical standing with regard to this point, it is a fact that reduced capture has been shown in a number of conditions, such as when the given search task requires focusing on a specific visual feature (Bacon & Egeth, 1994), when the given context is highly distracting (Müller et al., 2009; Marini et al., 2013), or finally after substantial exposure to a certain distractor, perhaps reflecting a form of habituation (Neo & Chua, 2006; Pascucci & Turatto, 2015; Turatto & Pascucci, 2016). More relevant to our purposes, an emerging literature has recently begun to address changes in the cost engendered by a distracting stimulus under conditions where the distractor appears with uneven probability across display locations, reflecting another form of SL in the attention domain (Reder e al., 2003; Goschy et al., 2014; see also Leber et al., 2016; Wang & Theeuwes, in press). In a study conducted by Reder and colleagues (2003), participants had to report the position of a target presented in one of four locations with equal probability. In most of the trials (80%), a distractor was also presented in one of the remaining locations. Unlike the target, the distractor appeared more frequently in one position (60% of distractor present trials), with intermediate frequency in another position (30%), only rarely in yet another position

(10%), while it was never presented in the remaining position (0%). Results showed that participants produced faster responses when the distractor was displayed in the frequent-distractor location, indicative of lesser distraction, whereas their reaction times (RTs) increased as distractor probability at a given position decreased. The results reported by Reder et al. (2003) are in good agreement with studies showing relatively rapid decline of the interference generated by a salient distractor when its location is constant over a number of trials, and a resurgence of interference when the distractor is subsequently presented at a different location (Kelley & Yantis, 2009; Pascucci & Turatto, 2015; Turatto & Pascucci, 2016). One can account for these results by assuming that the priority of the different positions was adjusted to cope optimally with the probability of distraction, with attentional priority being adaptively decreased for locations with relatively frequent distraction relative to locations with rare distractors. However, an explanation in terms of altered priorities might predict that target processing should also be altered as a result of the learning process, assuming that target selection and distractor filtering both depend on the level of location-specific activity within priority maps of space (e.g., Zelinsky & Bisley, 2015). Specifically, decreased priority should lead to worse target-related performance at the given location, whereas increased priority should enhance target processing at the same location. Importantly, Reder et al. (2003) assessed whether SL of distractor location affected target processing by analyzing the participants' performance as a function of the location of the target with respect to distractor probability at the various display locations. Although the target occurred equally often at all positions, the efficiency of target processing appeared to differ across locations, with relatively faster responses for targets at the location with rare distractors. However, the effect was rather weak and was found in a first experiment but not in a subsequent one (but see Wang and Theeuwes, in press, for a consistent observation). Therefore, doubts remain as to whether manipulations of distractor probability will affect target processing across locations. In fact, to our knowledge, no systematic attempt has been made so far to assess whether manipulations of target probability affect the level of distraction engendered by a distractor shown at the

various display locations. With the experiments reported here our primary goal will be to shed light on this critical point (see below).

As before, researchers have asked whether what appears to be the consequence of SL of distractor location might instead be due to inter-trial priming. This specific question has been examined by Goschy et al. (2014). In their experiments, a tilted bar was presented amongst vertical bars and the task for the participants was to indicate whether the target bar had a gap at the top or at the bottom. In half of the trials, a red-colored bar was shown as a salient singleton distractor. The distractor was presented in one half of the screen with high probability (90%) and in the other half with low probability (10%). The cost engendered by the distractor was modulated by the spatial probability manipulation, as reflected by faster RTs in trials with the distractor in the high probability region. In a control experiment, any distractor location repetitions were prevented. Also in this case, reduced distractor cost was found for the high distractor probability region, though the effect was smaller than in the original experiment. Thus, both inter-trial priming and genuine SL effects appear to contribute to the reduction of the distractor cost in this context. As we have argued for SL of target location, here too it will be important to provide further evidence on the contribution of inter-trial priming to the observed influence on performance of a probability manipulation of distractor location.

The key question that we wish to address in the present paper concerns the mechanisms involved in SL for target and distractor location. As already discussed, in visual search, attentional allocation can be altered by the uneven spatial probability with which the target or the distractor is presented across display locations. What is the mechanism underlying changes in performance? One obvious possibility is that spatial SL – be it for the target or the distractor location, affects activity within priority maps of space that are deemed responsible for attentional allocation (Itti & Koch, 2001; Fecteau & Munoz, 2006; Serences & Yantis, 2006; Gottlieb, 2007; Bisley & Goldberg, 2010; Ptak, 2012; Zelinsky & Bisley, 2015). These maps are usually conceived as neural representations of the visual space wherein the level of activity at each location in the map determines the (relative)

attentional priority of that location in space. It is also assumed that local activity levels within the maps reflect the highly dynamic, combined influence of a variety of factors, including the strength of the visual drive at each location (bottom-up, or saliency signal), the task relevance of the input at each location, any location-specific preparatory or biasing signal (see, e.g., Luck et al., 1997; Kastner et al., 1998; Sani et al., 2017), as well as signals generally ascribed to past selection history and reward associations (e.g., Klink et al., 2014). In this perspective, when two (or more) visual stimuli compete for attention, activity in priority maps will favor the stimulus presented at the location with the highest activity level (i.e., the location with the highest priority), which thus wins the competition and consequently gains privileged access to further stages of processing (e.g., Desimone & Duncan, 1995). This account entails that brain activity for prioritized elements is enhanced at the expense of low priority elements (for a review, see Duncan, 2006). Within this framework, one can interpret the modulations of behavior generated by manipulations of target and distractor spatial probabilities as the result of a unique system that calibrates the "weights" in the priority maps for the different locations. Specifically, one might conjecture that priorities will be increased for locations that more often generated a correct selection (SL of target location) or that less often generated correct distractor filtering (SL of distractor location) and, respectively, decreased for locations that more often generated a correct distractor filtering (SL of distractor location) or that less often generated a correct selection (SL of target location). In turn, this view assumes that attentional allocation is a result of a unitary mechanism – namely, activity in priority maps of space, whereby selecting and ignoring are just the two sides of the same coin. However, over the years many studies have provided evidence against this idea by showing that distinct attentional mechanisms implement target selection and, respectively, distractor filtering (Houghton & Tipper, 1994; 1996; Luck, 1995). For example, studies employing the scalp recording of electrical brain activity, in particular the event-related potential (ERPs) methodology, have revealed separate and dissociable correlates of target selection and distractor filtering (Hickey et al., 2009; Sawaki & Luck, 2010; 2013; Couperus & Mangun, 2010). Similarly, a number of studies using fMRI have shown that different brain networks are responsible for the selection of

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targets and, respectively, the filtering of distractors (Serences et al., 2004; Ruff & Driver, 2006; Marini et al., 2016). Further support to the notion that target selection and distractor filtering mechanisms are dissociated in the human brain comes from a very recent study by Noonan et al. (2016). In this study, participants had to indicate the spatial frequency of two superimposed Gabor patches while a randomly oriented Gabor patch was used as distractor. At the beginning of each trial, a cue indicated either the location of the forthcoming target, the location of the distractor, or provided no information (neutral cue). No correlation was found between the ability to use target-relevant cues to facilitate target selection and the ability to engage distractor filtering mechanisms at correspondingly cued locations, leading the authors to conclude that target selection and distractor suppression depend on distinct mechanisms. In summary, based on the above literature, we think it is of paramount importance to establish whether target selection and distractor filtering processes should be viewed as interdependent and based on shared neural mechanisms or instead as distinct and performed by dissociable mechanisms. In particular, in the present context, it is crucial to establish whether SL of target selection and, respectively, of distractor filtering will lead to modulations of performance that are compatible with one or the other of the two notions. Hence here we took advantage of SL for target and distractor location to directly and systematically assess the level of interdependence between target selection and distractor filtering mechanisms. Specifically, the principal question that we aimed to ask was whether SL of target location will lead to indirect changes in the efficiency of distractor filtering and, similarly, whether SL of distractor location will lead to indirect changes in the efficiency of target selection, or whether each form of SL will exert selective effects on one or the other process. If the same priority maps of space guide target selection and distractor filtering, then modulation of target selection through SL of target location should transfer to the efficiency of distractor filtering (Experiment 1). By the same logic, a change in distractor filtering brought about by SL of distractor location should be expected to modulate the efficiency of target selection (Experiments 2 and 4). Finally, we developed a within-subject experimental approach in which the two forms of SL co-existed in order to more directly compare the effects

generated by the two kinds of spatial contingency, including their indirect effects (Experiment 3).

2. Experiment 1

In Experiment 1, we assessed the direct impact of statistical learning (SL) on selection mechanisms by manipulating the probability with which the target occurred at the various display locations. In line with previous literature (i.e., Geng & Behrmann, 2002; 2005; Jiang et al, 2013a; 2013b; 2015a; 2015b), we predicted better performance for targets at relatively high probability locations, and impaired performance for targets at relatively low probability locations. Central to our goals, we also planned to establish whether the primary manipulation of target probability across display locations would not only affect the efficiency of target selection (direct effect), as expected, but also the efficiency of distractor filtering (indirect, or "transfer" effect). As already argued, if target selection and distractor filtering mechanisms are functionally linked, for instance because they reflect at least partly shared neural machinery, such as the same priority maps of space, one would predict that a manipulation of target probability will affect both target selection and distractor filtering mechanisms. Specifically, one should expect reduced interference by distractors shown at a low target probability location and increased interference by distractors shown at a high target probability location. This is because, as a result of statistical learning of target probability, a reduced priority should be acquired by a location with rare targets, whereas an increased priority should be acquired by a location with frequent targets. In turn, such changes in priority should transfer to the effect of distractors, with lesser distraction in the former case and greater distraction in the latter case. Alternatively, and in line with a vast literature suggesting separate and dissociable neural mechanisms to support target selection and distractor filtering (e.g., Hickey et al., 2009; Noonan et al., 2016), one might predict no transfer from target selection to distractor filtering of the target probability manipulation.

2.1. Methods

All experiments in the present study were conducted in accordance with the Declaration of Helsinki and approved by the Institutional Ethics Committee.

2.1.1. Participants

Twenty-four healthy volunteers (7 males; mean age ± SD, 22.75 ± 3.76) took part in Experiment 1. All participants in this and the following experiments were right-handed, and with normal or corrected-to-normal visual acuity. They were naïve as to the purpose of the study and received a fixed monetary compensation for their participation (€8) at the end of the experiment. All subjects gave their informed consent before participation.

2.1.2. Materials and Stimuli

The participants sat in a dimly lit, quiet room, facing a 17-in. CRT monitor. A chin rest was used to keep the viewing distance constant at 57 cm during the whole session. The experiments were run with the Open-Sesame software (Mathôt et al., 2012).

For all experiments reported here, except where we state otherwise, we used variants of the additional singleton paradigm, as pioneered by Theeuwes and colleagues (e.g., Theeuwes, 1992). The visual search display consisted of four stimuli presented equidistantly from one another (one per visual quadrant) along an imaginary circle with a radius of 4°, centered on a central fixation point. All stimuli were composed of two green (RGB color coordinates: 134, 148, 0; luminance: 15.7 cd/m^2) or red (246, 0, 0; 15.6 cd/m^2) triangles (1° x 1° each) presented on a light grey background (186, 186, 186; 32.7 cd/m2). In one half of the trials all display items were of the same color, e.g. red, whereas in the other half of the trials three items were of one color, e.g. red, but the fourth item (the additional singleton) was of the alternative color, e.g. green. The target was designated as the only item in the display with the two triangles pointing in the same direction, namely upward or downward (a double arrow-head), while the singleton distractor, when present, was a color-singleton stimulus with both triangles pointing outwardly. The remaining

stimuli (non-targets or fillers), were always of the same color as the target and with both triangles pointing inwardly (Fig. 1A).
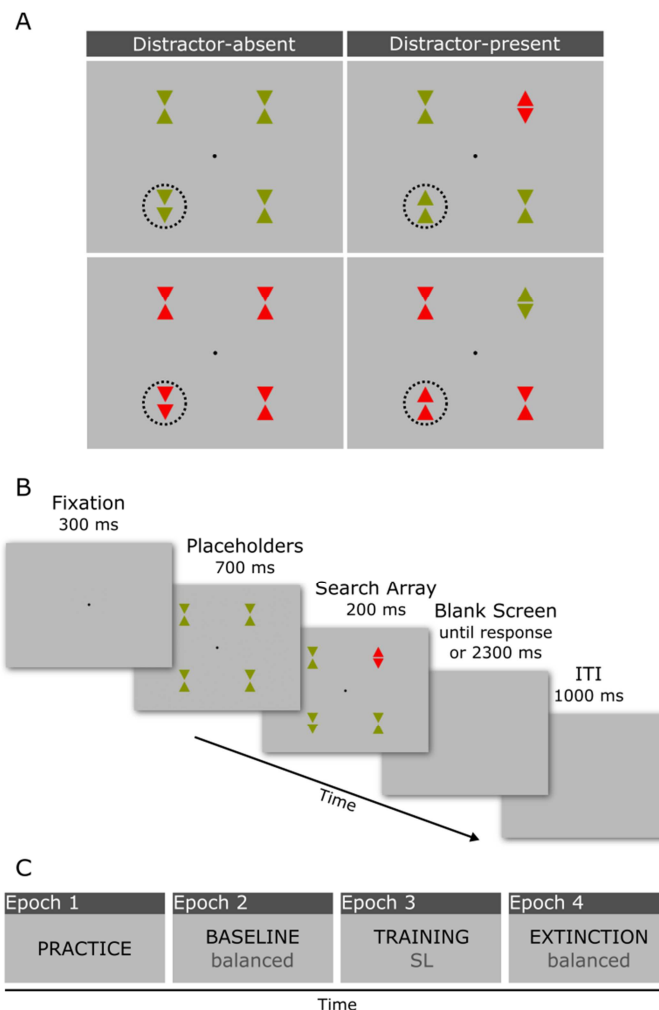

Fig. 1 – Experimental procedure for Experiments 1-3. *(A)* Illustration of all possible types of search arrays used in the task. Each array comprised four stimuli presented equidistantly from one another. The target (indicated in the figure by a dashed circle, not visible during the actual task) corresponded to the only double arrow-head item. In the Distractor-absent condition (50% of the trials; left panels), all stimuli (target and fillers) were either green or red. In the Distractor-present condition (50% of the trials; right panels), three items were of one color (e.g., red), while the fourth item (additional singleton) was of the alternative color (e.g., green). *(B)* Schematic representation of the temporal sequence of events in an example trial (see text for a detailed description). After 300 ms of fixation display, the placeholder screen was shown for 700 ms. The search array was then presented for 200 ms, after which a blank screen was displayed. Participants had a maximum of 2500 ms to indicate the orientation of the target. A new trial started after 1000 ms. *(C)* Temporal unfolding of the entire experimental session. Participants initially performed a practice block of 64 distractor-absent trials (epoch 1). Subsequently, a baseline block of 144 trials was administered, which entailed no frequency imbalance in target and distractor probability across locations (epoch 2). Afterwards, the statistical learning (SL) phase started (epoch 3), comprising a total of six blocks of 144 trials each, in

which presentation of critical items (either the target or the distractor, or both) followed a contingent probability distribution (see text and Table 1 for details). Finally, the session ended with an extinction block of 144 trials, wherein the target and distractor were displayed with balanced probability at all four locations (epoch 4).

2.1.3. Design and Procedure

Each trial began with a fixation display lasting 300 ms. This was followed by a 700-ms display containing four placeholders, identical to the forthcoming non-targets. At the end of the 700-ms period, one of the placeholders was immediately replaced by the target and, on one half of the total trials, another was replaced by the singleton distractor (see Tommasi et al., 2015). The search display remained visible for 200 ms, followed by a blank screen that stayed on until the participant's response, or a maximum duration of 2300 ms. A new trial started after a 1000 ms inter-trial interval (Fig. 1B). The participants' task was to indicate as quickly and accurately as possible whether the target element was pointing up or down. One half of the participants pressed key 1 of the numerical keypad for 'up' responses and key 2 for 'down' responses; for the other half, the opposite key assignment was in place.

	Spatial Probabilities (%)				
	Stimulus	**Location**			
		1	**2**	**3**	**4**
Exp. 1	Target	42	25	8	25
	Distractor	25	25	25	25
Exp. 2 & 4	Target	25	25	25	25
	Distractor	25	42	25	8
Exp. 3	Target	42	25	8	25
	Distractor	25	42	25	8

Table 1 - Spatial probability of target and distractor in the various experiments (example configuration).

Crucially, unbeknownst to the participants, target location followed a contingent probability distribution, with one location associated with high probability (42%; high target probability location, *HTPL*), another with low probability (8%; low target probability location, *LTPL*), and the remaining two with intermediate probability (25%; intermediate target probability locations, *ITPLs*). The location of the distractor was instead equally probable (25% per location) (Table 1). Participants were randomly assigned to one of four different groups, each with a different spatial configuration of the probabilities.

After receiving verbal instructions from the experimenter, participants completed a first practice block of 20 trials, followed by a single session for the experiment proper. The session comprised 4 different epochs (Fig. 1C). The first epoch (epoch 1) comprised 64 distractor-absent trials and served no other purpose but allowing for further practice at the task. In this epoch target probability was equal across display locations. Epoch 2 consisted of 144 trials, half distractor-present and half distractor-absent trials, and with both the target and the distractor shown equally often at all locations (the "balanced" baseline epoch). The main purpose of this epoch was to establish and characterize baseline performance against which to compare performance in the subsequent SL epoch. The epoch of SL (epoch 3) consisted of six blocks (144 trials each), with a short pause every two blocks. The target probability manipulation was applied throughout this epoch. Epoch 4 (balanced extinction epoch) was in all respects identical to epoch 2 and mainly served to test for any persisting effects from the preceding epoch, i.e., to assess whether effects due to SL of target location would persist in the extinction regimen.

In order to evaluate whether participants were aware of the spatial contingency applied during the SL epoch, an explicit/implicit survey was conducted at the end of the experiment. Participants were first asked to report whether they had noticed something peculiar about the spatial distribution of target and/or distractor stimuli and, second, to report (or guess) the locations where the target and, respectively, the distractor were presented most and least frequently.

2.1.4. Data analysis

Analyses were performed using R 3.3.2 (R Core Team, 2016). Repeated-measures analyses of variance (ANOVAs) were performed on reaction times (RTs), excluding trials with a wrong response (5% of the data) or a RT below 200 ms (less than 1% of the data). In order to more directly assess the cost associated with the distractor, further analyses were conducted on the distractor cost, namely, the difference in RT between distractor-present and distractor-absent mean RTs. In addition, we performed similar analyses on accuracy data. When appropriate, p values for statistical significance were adjusted for multiple comparisons (Holm–Bonferroni correction). Along with significance levels, for each analysis we also provide estimates of effect size (η_p^2 and Cohen's d; for a discussion, see Nakagawa & Cuthill, 2007).

2.2. Results

2.2.1. SL of target location - *SL epoch*

A repeated-measures ANOVA on mean RT with Target Location (HTPL, ITPL, and LTPL), Distractor Presence (present and absent), and Block (1-6) as the main factors revealed a highly significant main effect of Target Location, $F_{(2, 46)} = 31.11$, $p < 0.001$, $\eta_p^2 = 0.703$ (Fig. 2A). Post-hoc comparisons uncovered significant ($p < 0.01$ and $d > 0.728$ in all cases) differences across all conditions, with increasingly faster responses as a function of target probability at the given location (mean ± SE; LTPL = 595 ms ± 26; ITPL = 573 ms ± 24; HTPL = 554 ms ± 23). There was also a significant main effect of Distractor Presence, $F_{(1, 23)} = 136.80$, $p < 0.001$, $\eta_p^2 = 0.856$, reflecting faster responses in the distractor-absent (519 ms ± 19) compared to the distractor-present condition (629 ms ± 25), and Block, $F_{(5, 115)} = 4.47$, $p < 0.001$, $\eta_p^2 = 0.459$, reflecting slower responses in the initial part of the session (from 598 ms ± 27 in block 1 to 561 ms ± 22 in block 6). The lack of a significant interaction between Target Location and Block, $F_{(10, 230)} = 1.33$, $p = 0.21$, should be ascribed to the fast appearance (within the first block) and subsequent stable maintenance of the SL-dependent modulation (see below). The interaction between Target Location and

Distractor Presence was significant, $F_{(2, 46)} = 15.34$, $p < 0.001$, $\eta_p^2 = 0.533$ (Fig. 2B). As confirmed by post-hoc comparisons, SL affected responses in both distractor-absent and distractor-present conditions (HTPL *vs.* LTPL in both conditions: $p < 0.001$ and $d > 0.7$); however, the effect was intensified by the presence of the distractor (RTs in the LTPL *minus* HTPL condition, without distractor: 18 ms ± 4; LTPL *minus* HTPL condition with distractor: 64 ms ± 3), presumably because a more efficient guidance of attention onto the target, due to SL, was especially advantageous under conditions of strong distraction, as elicited by the color singleton. The analysis of accuracy data only revealed a significant main effect of Distractor Presence, $F_{(1, 23)} = 6.60$, $p = 0.02$, $\eta_p^2 = 0.223$, with higher accuracy in the distractor-absent (96.27% ± 1.74) compared to the distractor-present condition (94.40% ± 2.19).

In order to verify whether the reported effect of Target Location was genuinely caused by SL of unequal target probability across locations and was not instead a consequence of inter-trial priming, we repeated the above analysis after excluding all trials in which the location of the target was the same as in the preceding trial. All results were replicated, in particular the significant effect of Target Location, $F_{(2, 46)} = 19.22$, $p < 0.001$, $\eta_p^2 = 0.614$. Therefore, an interpretation of the modulation of performance solely in terms of inter-trial priming can be safely rejected. At the same time we could confirm that inter-trial priming benefited target selection when the location of the target repeated across consecutive trials (repeat: 553 ms ± 21; no-repeat: 575 ms ± 20; $t_{(23)} = 6.46$, $p < 0.001$, $d = 1.319$).

Finally, in order to verify whether the effects of SL are specific for the given location or are instead linked to a hemifield-based representation of space, we compared performance between the two locations with intermediate target probability (ITPLs), the one on the same side as the high probability target location and the one on the opposite side. The difference between the two locations (9 ms ± 8) was non-significant, $t = 1.36$, $p = 0.19$. Thus, the bias generated by the spatial probability manipulation appears to be location specific.
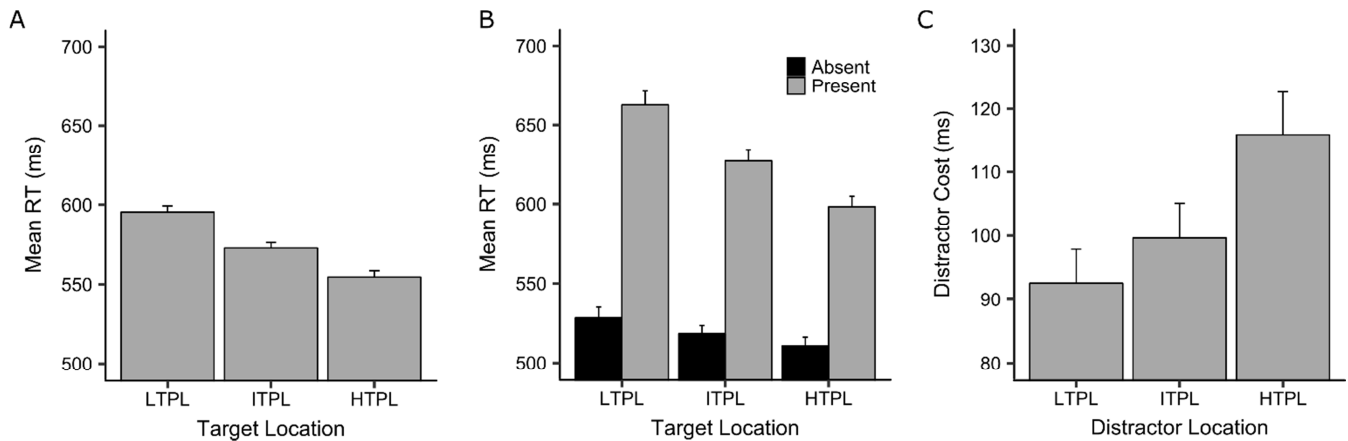
Fig. 2 – Statistical learning (SL) effects during the SL epoch in Experiment 1. *(A)* Direct effect of SL of target location. Mean RTs are reported as a function of target location (LTPL = low target probability location; ITPL = intermediate target probability location; HTPL = high target probability location). *(B)* Direct effect of SL of target location. Mean RTs are reported as a function of target location, separately for the distractor-present (gray) and distractor-absent (black) conditions. *(C)* Indirect effect of SL of target location. Average distractor costs are reported as a function of distractor location. In all panels, error bars represent standard errors for within-subject designs (Cousineau & O'Brien, 2014).

2.2.2. SL of target location - *Acquisition*

In order to assess the acquisition of the attentional bias due to SL, we compared performance in the Balanced baseline epoch (epoch 2), where no significant difference was found across locations (Target Location: $F_{(2, 46)} = 1.88$, $p = 0.16$), as expected, with performance in the first block of the SL epoch. To this aim, we first calculated the mean difference between the LTPL and HTPL conditions (direct effect of SL), separately for each block and each participant. A t-test analysis resulted in a significant difference, $t_{(23)} = 3.72$, $p = 0.001$, $d = 0.759$, reflecting a positive bias for the high target probability location in the first block of the SL epoch (23 ms ± 6) but not at baseline (-15 ms ± 9). To further analyze the acquisition process, we subdivided the first block of the SL epoch in two halves and compared the SL effect in each half against baseline performance. The comparisons resulted in a significant difference between baseline and both the first half (19 ms ± 10) and the second half (26 ms ± 10) of the first block ($p < 0.05$ and $d > 0.5$ in both cases). Moreover, we found no significant difference between the two halves of the first SL block, $t_{(23)} = 0.49$, $p = 0.63$. To sum up, the attentional

bias in target processing generated by the uneven presentation of the target across display locations appears to emerge very rapidly, with robust effects already emerging during the first half of the first block of SL (~ 72 trials).

2.2.3. SL of target location - *Extinction*

Another objective that we pursued was to establish whether the effects of SL would persist once the probability manipulation was removed (Balanced extinction epoch 4), i.e., in the extinction regimen. To this end, a one-way ANOVA was performed on data from the balanced extinction epoch with Target Location (HTPL, ITPL, and LTPL) as the main factor. The results showed a significant effect of Target Location, $F_{(2, 46)}$ = 7.01, p = 0.002, η_p^2 = 0.349, with a pattern of RTs consistent with what found during the SL epoch (HTPL, 530 ms ± 17; ITPL, 542 ms ± 18; LTPL, 555 ms ± 17).

2.2.4. SL of Target Location: Indirect effect on distractor filtering - *SL epoch*

After computing RT differences between the distractor-present and distractor-absent conditions (distractor cost), the values were submitted to a repeated-measures ANOVA with Distractor Location (HTPL, ITPL, and LTPL) and Block (1-6) as main factors. The main effect of Distractor Location was significant, $F_{(2, 46)}$ = 4.14, p = 0.02, η_p^2 = 0.232, reflecting larger distractor costs for the HTPL (116 ms ± 13), intermediate cost for the ITPL (100 ms ± 10) and lower cost for the LTPL (93 ms ± 13) (HTPL vs. ITPL: $t_{(23)}$ = 1.77, p = 0.09; HTPL vs. LTPL: $t_{(23)}$ = 2.63, p = 0.01, d = 0.537; ITPL vs. LTPL: $t_{(23)}$ = 1.06, p = 0.30) (Fig. 2C). No other effect or interaction was significant. The same analysis conducted on accuracy data did not reveal any significant effect (p > 0.11).

2.2.5. SL of Target Location: Indirect effect on distractor filtering - *Acquisition*

A one-way ANOVA with Distractor Location (HTPL, ITPL, and LTPL) as the only main factor conducted on data from the Balanced baseline epoch (epoch 2) did not result in significant differences of the distractor cost across locations, $F_{(2, 46)}$ = 1.14, p = 0.33, as should be expected. As before, we compared performance in the Balanced baseline epoch with that in the first block of the SL epoch by calculating

the mean difference in distractor cost between the HTPL and LTPL conditions as an index of the indirect effect. The analysis resulted in a significant difference, $t_{(23)}$ = 2.30, p = 0.03, d = 0.470, reflecting an indirect effect in the first block of the SL epoch (16 ms ± 11) but not at baseline (-14 ms ± 14). Moreover, an analysis on data from the first half of the first block of SL (20 ms ± 16), confirmed that the distractor cost differed significantly compared to the same cost at baseline, $t_{(23)}$ = 2.15, p = 0.04, d = 0.439, demonstrating a rapid emergence also of the indirect effect.

2.2.6. SL of Target Location: Indirect effect on distractor filtering – *Extinction*

We then performed a one-way ANOVA on the distractor cost calculated during the Balanced extinction epoch (epoch 4) with Distractor Location (HTPL, ITPL, and LTPL) as main factor in order to assess whether the effect of SL of target probability on distractor filtering would also persist in the extinction regimen. We found no evidence of modulation during this epoch, $F_{(2, 46)}$ = 1.21, p = 0.31, suggesting a relatively fast decay of the indirect effect.

2.2.7. Explicit/Implicit knowledge assessment

Seven participants (out of twenty-four) reported the impression of an uneven spatial distribution of the target. Among them, three indicated the correct location where the target was displayed most often (HTPL), one the correct location where the target appeared most rarely (LTPL), and one participant indicated both locations correctly. The remaining two participants were in fact unable to indicate any such location correctly. In order to verify whether the SL effects reflected the participants' awareness of the probability contingencies, we repeated the analysis on the direct effect (target effect) after excluding any participant who reported the impression of an uneven spatial distribution of the target and correctly identified at least one location with high or low target probability (n = 5). All results were replicated, in particular the significant main effect of Target Location, $F_{(2, 36)}$ = 19.95, p < 0.001, η_p^2 = 0.663. Thus, we can exclude that the reported effects engendered by the uneven distribution of targets across locations were due to explicit knowledge of the statistical contingencies guiding a form of deliberate strategy of attentional deployment.

2.3. Discussion

Experiment 1 proved the efficacy of our probability manipulation in inducing SL for target location, with performance varying as a function of target probability across display locations. In particular, increased attentional priority was acquired by a location with relatively higher probability of containing the target, whereas reduced priority was acquired by a location where targets appeared only rarely, with intermediate performance for locations where targets occurred with intermediate probability. This modulation emerged very quickly within the first block of trials (in fact, during the first half of the block) and persisted along the entire epoch of SL. Importantly, performance was still affected in a subsequent epoch (the balanced retest epoch 4) after the probability manipulation was removed.

We further characterized the influence of SL on the efficiency of target selection. First, we were able to show that the effect was limited to the specific location where target probability was manipulated and did not spread to the corresponding visual hemifield. However, we would need much denser stimulus arrays if we wished to establish the fine-grained spatial spread of the reported effects. Moreover, we rejected the possibility that the effects produced by SL could instead reflect an unequal number of immediate repetitions in target location across consecutive trials for the different conditions. However, it should be noted that with our approach influences on performance due to repetitions in target location at longer lags (N-2, N-3, etc., effects) cannot be excluded. In fact, future studies will have to unravel the exact relationship between "local" contingencies in display composition along short sequences of trials and the more "global" statistical structure across the whole experiment.

More relevant to our primary objective, we found that the unequal target probability across display locations not only affected performance in relation to

targets appearing at those locations, but it also affected the detrimental effect of the color singleton distractor appearing at the same locations. The level of interference generated by the distractor was unequal across locations, in spite of the fact that distractor probability, unlike target probability, was the same across display locations. Specifically, the distractor generated relatively greater costs when presented at the location with higher target probability compared to the low target probability location. This can be interpreted by assuming that a high target probability location gained increased priority as a result of SL, therefore rendering the distractor more interfering at that location. Of course the reversed argument applies to the low target probability location, wherein the distractor elicited relatively smaller costs. We will return to this important feature of the results in the General Discussion.

Finally, the reported effects cannot be ascribed to the deliberate and explicit adoption by the participants of a strategy of attentional deployment that takes into account the unequal probability of target occurrence at the various display locations. Only a few participants appeared to have some hint as to the target probability distribution across locations. Crucially, we found strong SL effects in those participants who were completely unaware of the spatial contingencies.

In Experiment 1 we have demonstrated that SL of target location probability can influence performance in multiple ways, presumably through changes in the attentional priority of display locations: on the one hand, it modulated responses in relation to the target, with monotonic increase in RT at locations characterized by progressively decreased target probability; on the other, it affected the impact of the color singleton distractor, with monotonic increase in attentional capture at locations with progressively more frequent targets. In Experiment 2 we set out to apply a manipulation of distractor probability across display locations in order to assess whether by doing so we could again demonstrate robust effects of SL and, more specifically, we could demonstrate a similar generalization of the effects, from distractor filtering to target selection.

3. Experiment 2

In Experiment 1, we manipulated the spatial probability of the target and found evidence to indicate that SL affected both target selection and distractor filtering mechanisms. These results suggest cross-talk between the two kinds of mechanism, likely reflecting at least partly shared neural machinery, for example the same priority map(s) of space. In Experiment 2 we tested whether a reciprocal effect could be found by applying an uneven probability of distractors across locations. As before, if target selection and distractor filtering mechanisms depend on at least partly shared neural substrates, then one would predict that a manipulation of distractor probability across locations should influence not only distractor filtering but also target selection processes. More specifically, if that turned out to be the case, then target selection should be facilitated when the target appears at a location associated with lower distractor probability relative to locations with greater probability of distraction. Alternatively, if the type of cross-talk observed in Experiment 1 were not replicated in the present experiment, then one would be led to conclude that SL for target and distractor location differ in some important property.

3.1. Methods

3.1.1. Participants
Twenty-four volunteers (12 males; mean age ± SD, 23.29 ± 2.74) took part in Experiment 2.

3.1.2. Materials and Stimuli
These were identical to those used for Experiment 1.

3.1.3. Design and Procedure
Design and procedure were identical to those for Experiment 1, with the following exception. Target spatial probability was even across display locations, whereas

the distractor was presented more frequently (42%) at the high distractor probability location (HDPL), more rarely (8%) at the low distractor probability location (LDPL), and with intermediate probability (25%) at the intermediate distractor probability locations (IDPLs; Table 1). The level of the three probabilities was therefore the same as in the previous experiment, except that here they concerned distractor and not target probability.

3.1.4. Data analysis

This followed the same approach as used before. One participant had to be excluded from the analyses because of very low accuracy (52 %).

3.2. Results

3.2.1. SL of Distractor location – *SL epoch*

A repeated-measures ANOVA on the distractor cost (RT difference between distractor-present and distractor absent trials) with Distractor Location (HDPL, IDPL, and LDPL) and Block (1-6) as main factors resulted in a significant main effect of Distractor Location, $F_{(2, 44)}$ = 8.56, $p < 0.001$, η_p^2 = 0.398 (Fig. 3A). Distractors engendered the largest interference when presented at the LDPL (145 ms ± 18), as confirmed by post-hoc analyses showing significant differences between the LDPL and both the IDPL (113 ms ± 12) and HDPL conditions (103 ms ± 13; $p < 0.01$ and $d > 0.6$ in both cases). Instead, the difference between the IDPL and HDPL conditions was not significant, $p > 0.2$. The effect of Block was also significant, $F_{(5, 110)}$ = 3.08, $p = 0.01$, η_p^2 = 0.521, reflecting a general reduction in the distractor cost as the experiment advanced (from 130 ms ± 16 in block 1 to 104 ms ± 14 in block 6). Finally, the interaction between Distractor Location and Block was not significant, $F_{(10, 220)}$ = 0.33, $p = 0.97$. As for the first experiment, this was due to fast emergence of the effects of the probability manipulation during the first block of trials (see below). The same analysis conducted on accuracy data did not reveal any significant effect ($p > 0.41$).

We obtained the same reliable effect of Distractor Location ($F_{(2, 44)}$ = 7.44, p = 0.002, η_p^2 = 0.375) after excluding trials in which the distractor was presented in the same location as in the immediately preceding trial (repeated suppression effect), which makes an interpretation of the modulation solely in terms of inter-trial effects untenable. However, RT was significantly reduced when the distractor was presented at the same location on two consecutive trials (repeat: 623 ms ± 25; no-repeat: 650 ms ± 24; $t_{(22)}$ = 2.45, p = 0.02, d = 0.510), confirming that this type of inter-trial effect was able to influence performance.
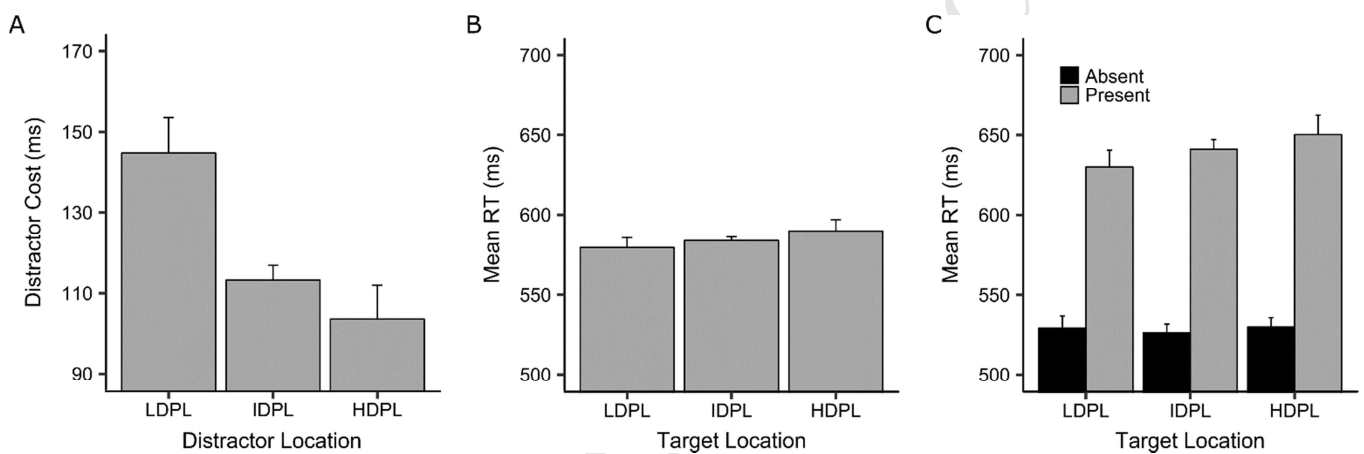

Fig. 3 – Statistical learning (SL) effects during the SL epoch in Experiment 2. *(A)* Direct effect of SL of distractor location. Average distractor costs are reported as a function of distractor location (LDPL = low distractor probability location; IDPL = intermediate distractor probability location; HDPL = high distractor probability location). *(B)* Indirect effect of SL of distractor location. Mean RTs are reported as a function of target location. *(C)* Indirect effect of SL of distractor location. Mean RTs are reported as a function of target location, separately for the distractor-present (gray) and distractor-absent (black) conditions. All conventions as in Fig. 2.

3.2.2. SL of Distractor location - *Acquisition*

RT data collected in the balanced baseline epoch showed a statistically indistinguishable distractor cost across locations, as confirmed by a one-way ANOVA with Distractor Location (HDPL, IDPL, and LDPL) as main factor ($F_{(2, 44)}$ = 1.28, p = 0.29). Next, we compared the direct effect of SL (difference in distractor cost between LDPL and HDPL) in the first block of the SL epoch (40 ms ± 23) with the corresponding baseline value (-3 ms ± 16). Such comparison only resulted in a

non-significant trend, $t_{(22)}$ = 1.62, p = 0.12. Dividing the first block of the SL epoch in two halves, the direct effect was not significantly different from the baseline value in either the first (33 ms ± 23; $t_{(22)}$ = 1.26, p = 0.22) or the second half of the block (44 ms ± 34; $t_{(22)}$ = 1.31, p = 0.20). To further explore the acquisition of the SL of distractor location, we then compared the direct effect in the second block of the SL epoch (43 ms ± 21) with the corresponding baseline value and found a significant difference, $t_{(22)}$ = 2.14, p = 0.04, d = 0.446. These analyses provide some evidence to suggest that SL of distractor location might be relatively slow to emerge, at least compared to SL of target location, but we believe the evidence is not strong enough to make a strong claim in this direction.

3.2.3. SL of Distractor location – *Extinction*

At retest, the distractor cost was somewhat different across locations (HDPL = 126 ms ± 13; IDPL: 116 ms ± 14; LDPL = 147 ms ± 19), and the difference between the HDPL and LDPL conditions was in the expected direction. However, the statistical analysis failed to reveal a significant effect of Distractor Location, $F_{(2, 44)}$ = 1.93, p = 0.16, perhaps suggesting a relatively fast decay of the effects engendered by SL of distractor location once even probability of distractor occurrence at the various locations was re-established.

3.2.4. SL of Distractor Location: Indirect effect on target selection - *SL epoch*

Qualitative inspection of the data revealed that the higher the distractor probability at a given location, the worse was target selection at the same location (LDPL = 579 ms ± 20; IDPL = 584 ms ± 20; HDPL = 590 ms ± 22; Fig. 3B-C). However, a repeated-measures ANOVA on mean RT with Target Location (HDPL, IDPL, and LDPL), Distractor Presence (absent and present), and Block (1-6) as main factors indicated that the main effect of Target Location was not significant, $F_{(2, 44)}$ = 0.90, p = 0.41. The main effect of Distractor Presence was instead highly significant, $F_{(1, 22)}$ = 119.52, p < 0.001, η_p^2 = 0.845, as was its interaction with Block, $F_{(5, 110)}$ = 3.32, p = 0.008, η_p^2 = 0.588. The latter effects reflected the expected cost generated by the distractor (absent: 528 ms ± 21; present: 640 ms ± 24) and its reduction along the experiment (present minus absent: from 119 ms ± 10 in block 1

to 99 ms ± 10 in block 6). Other effects or interactions were not significant. Analysis of accuracy data only revealed a significant main effect of Distractor Presence (absent: 98% ± 0.7; present: 96.3% ± 1), $F_{(1, 22)} = 18.81$, $p < 0.001$, $\eta_p^2 = 0.461$.

3.2.5. Explicit/Implicit knowledge assessment

None of our participants were able to correctly report the spatial contingencies of distractor probability across display locations. Therefore, we can exclude that participants may have adopted a deliberate strategy in order to optimize performance on the basis of explicit knowledge of the applied spatial contingencies.

3.3. Discussion

With Experiment 2 we could demonstrate that a manipulation of the spatial probability of the distractor is able to modulate distractor filtering mechanisms, which is in agreement with prior reports of analogous influences (Reder e al., 2003; Goschy et al., 2014; Leber et al., 2016; Wang & Theeuwes, in press): the higher the distractor probability at the given location, the smaller the distractor cost at the same location. As in the previous experiment, the effect of the distractor probability manipulation cannot be accounted for solely in terms of inter-trial priming effects. Importantly, in line with what found in Experiment 1, the modulation of the distractor cost due to SL emerged rather rapidly during the SL epoch, although perhaps not as rapidly as was found in Experiment 1, and did not appear to reflect the adoption of a deliberate strategy guided by explicit knowledge of the distractor probability distribution across locations.

Unlike what we found in Experiment 1, here we failed to detect a reliable persistence of the effect of SL of distractor location during the extinction phase. However there was a numerical trend in the expected direction, which suggests that the effect might persist in the extinction regimen, though in an attenuated form.

During the SL epoch, not only the distractor cost became unequal across locations, but also the efficiency of target selection became modulated by distractor probability, with faster responses for targets at low distractor probability locations compared to high and intermediate distractor probability locations, especially in the distractor-present condition (Fig. 3C), albeit this effect was not significant.

In summary, the present experiment demonstrated that an uneven probability of distractor occurrence across locations affects the efficiency of distractor filtering. However, in this experiment we found weaker evidence of cross-talk between target selection and distractor filtering mechanisms, with weak, if any, indirect effects of the distractor probability manipulation on target selection processes. This might indicate an asymmetry between the two forms of statistical learning, with SL of distractor location producing less widespread effects compared to SL of target location (but see Wang & Theeuwes, in press). Importantly, however, the asymmetry is unlikely due to much stronger direct effects of the target vs. distractor probability manipulation (direct, or primary effects in Experiment 1 and 2), as both effects were very robust and of the same order of magnitude (~ 40 ms). In the following experiment we wished to replicate the observations from Experiment 1 and 2 and also assess whether it is possible to induce SL of both target and distractor location within the same session.

4. Experiment 3

Previous experiments have shown that observers can learn and use the spatial distribution of targets and distractors in order to prioritize and, respectively, de-prioritize locations where a target or a distractor is more likely to occur. More relevant for our specific purposes, we also found some evidence of cross-talk between the direct effect – be it SL of target selection or SL of distractor filtering, and the indirect, transfer effect, namely distractor filtering and target selection, respectively. Some evidence of cross-talk emerged in both experiments, although it appeared to be stronger in one direction than the other, namely from target selection to distractor filtering than vice versa. Specifically, in Experiment 1, we observed that higher target probability at a given location generated more efficient target selection (direct effect) but also greater distractor interference (indirect effect), whereas in Experiment 2 we found that higher distractor probability led to more efficient distractor filtering (direct effect) but also less efficient target selection (indirect effect). However, while the former effect was statistically reliable, the latter was only a trend in the data. Of course, it is very difficult to establish to what extent such asymmetry in transfer, or cross-talk, may simply be due to noise rather than to a true functional asymmetry. Experiment 3 was designed to arbitrate between the two possibilities by using a within-subject approach wherein both kinds of SL were jointly implemented and measured. In particular, in Experiment 3, we separately and independently manipulated the spatial probability of target and distractor stimuli within the display, so as to compare the direct and indirect effects of the two kinds of SL within the same learning episode.

4.1. Methods

4.1.1. Participants

Twenty-four volunteers (7 males; mean ± SD age, 23.17 ± 2.87) took part in Experiment 3.

4.1.2. Materials and Stimuli

These were identical to those used in Experiment 1 and 2.

4.1.3. Design and Procedure

Design and procedure remained identical to previous experiments, except for the SL manipulation. The target was made more probable at one location (42%; HTPL) and less probable at another location (8%; LTPL), with the remaining two locations containing the target with intermediate probability (25%; ITPL). Also the distractor spatial probability was manipulated, as it was more probable at one location (42%; HDPL) and less at another location (8%; LDPL), with the remaining two locations containing the distractor with intermediate probability (25%; IDPL). Importantly, target and distractor spatial probability manipulations were applied independently: the target was presented with intermediate (chance) probability at the locations where distractor probability was high or low; similarly, the distractor was presented with intermediate (chance) probability at the locations where target probability was high or low (Table 1).

4.1.4. Data analysis

This was performed according the same approach as used for Experiments 1 and 2.

4.2. Results

4.2.1. SL of Target location - *SL epoch: direct and indirect effects*

An ANOVA on the target probability manipulation, with Target Location (HTPL and LTPL), Distractor Presence (present and absent), and Block (1-6) was performed. The direct effect of target spatial probability (main effect of Target Location), reflected in the difference between HTPL (633 ms ± 37) and LTPL (676 ms ± 38), was highly significant, $F_{(1, 23)} = 44.37$, $p < 0.001$, $\eta_p^2 = 0.659$ (Fig. 4A). Thus, the statistical distribution of the target can be learned and used to support target selection

processes also in a more complex context wherein both target and distractor probabilities are uneven across locations. As before (Exp. 1), control analyses replicated the effect ($F_{(1, 23)}$ = 44.37, p < 0.001, η_p^2 = 0.659) after excluding trials where the target appeared at the same location as in the immediately preceding trial (inter-trial repetition effect). A significant main effect of Distractor Presence was also found, $F_{(1, 23)}$ = 84.57, p < 0.001, η_p^2 = 0.786, with faster responses in the distractor-absent (595 ms ± 31) than in the distractor-present condition (715 ms ± 40), as expected, as well as a significant interaction between Target Location and Distractor Presence, $F_{(1, 23)}$ = 13.49, p = 0.001, η_p^2 = 0.370. Once again, the presence of the distractor increased the magnitude of the SL effect (Fig. 4B). The RT difference between the LTPL and HTPL conditions increased from 23 ms (± 5) to 63 ms (± 11) between the distractor-absent and distractor-present conditions. T-test analyses of these differences uncovered a significant effect of target spatial probability in both conditions (p < 0.001 and d > 0.9 in both cases); however the effect was reliably stronger in the presence vs. absence of the distractor ($t_{(23)}$ = 3.67, p = 0.001, d = 0.750). All other effects were not significant (p > 0.33). The analysis of accuracy data revealed a significant main effect of Target Location, $F_{(1, 23)}$ = 8.26, p = 0.009, η_p^2 = 0.264, reflecting better performance in the HTPL (97.4% ± 0.8) vs. LTPL (96.2% ± 1.8) condition.

Importantly, as shown by an ANOVA with Distractor Location (HTPL, and LTPL) and Block (1-6) as main factors, also the distractor cost differed between the HTPL and the LTPL condition (indirect effect; Fig. 4C), $F_{(1, 23)}$ = 4.42, p = 0.047, η_p^2 = 0.161, with greater interference when the distractor appeared at the HTPL (126 ms ± 15) than at the LTPL (105 ms ± 15). Accuracy analyses resulted in a non-significant trend toward better performance in the HTPL (1% ± 1.2) vs. LTPL (2.4% ± 1) condition, $F_{(1, 23)}$ = 3.26, p = 0.08, in line with what found in RT data. These results demonstrate that SL of target location probability not only affected the efficiency of target selection but also the efficiency of distractor filtering, with relatively larger costs for distractors appearing at a high target probability location, in turn confirming the results of Experiment 1.
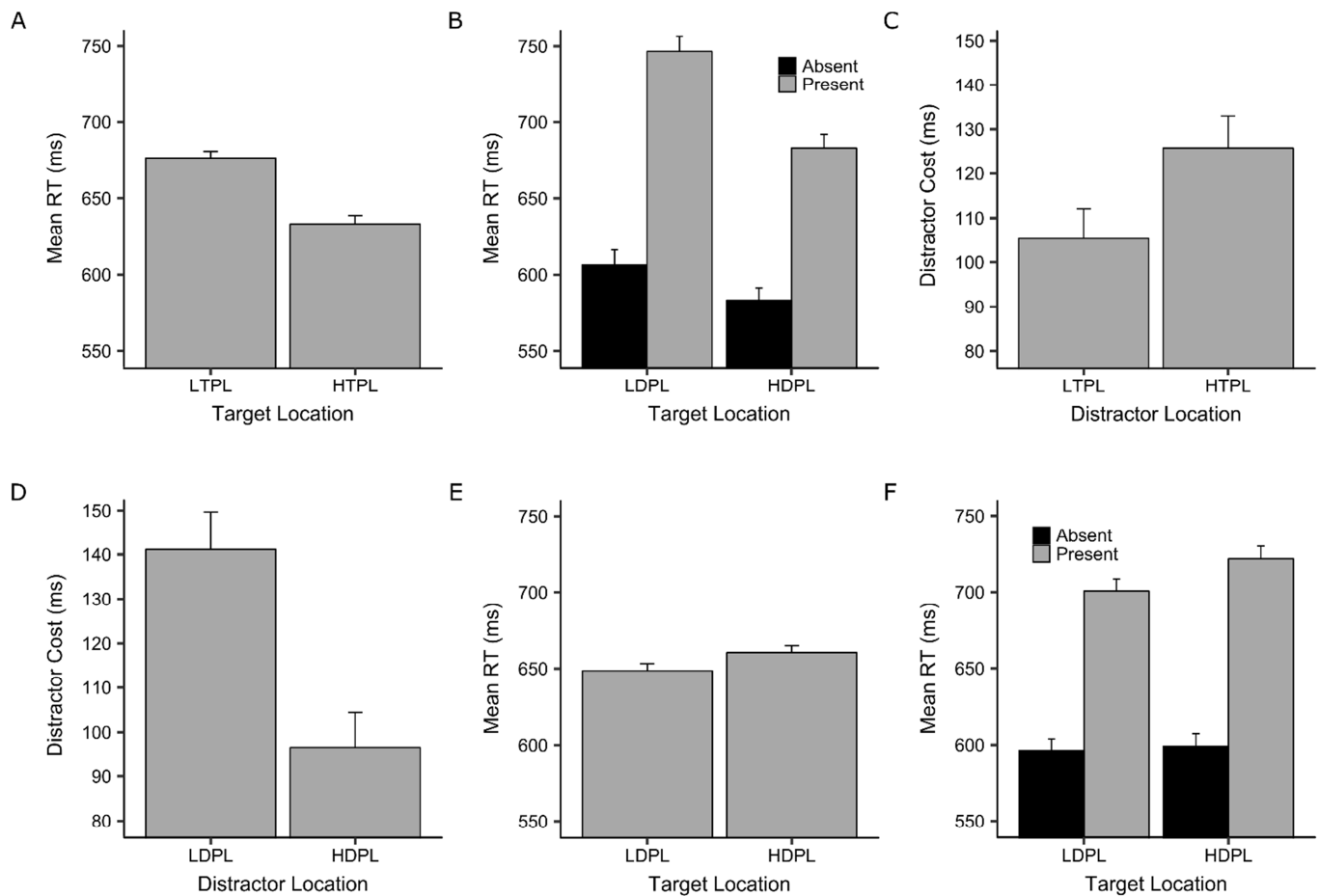
Fig. 4 – Statistical learning (SL) effects during the SL epoch in Experiment 3. *(A)* Direct effect of SL of target location. Mean RTs are reported as a function of target location (LTPL = low target probability location; HTPL = high target probability location). *(B)* Direct effect of SL of target location. Mean RTs are reported as a function of target location, separately for the distractor-present (gray) and distractor-absent (black) conditions. *(C)* Indirect effect of SL of target location. Average distractor costs are reported as a function of distractor location. *(D)* Direct effect of SL of distractor location. Average distractor costs are reported as a function of distractor location (LDPL = low distractor probability location; HDPL = high distractor probability location). *(E)* Indirect effect of SL of distractor location. Mean RTs are reported as a function of target location. *(F)* Indirect effect of SL of distractor location. Mean RTs are reported as a function of target location, separately for the distractor-present (gray) and distractor-absent (black) conditions. All conventions as in Fig. 2.

4.2.2. SL of Target location - *Acquisition: direct and indirect effects*

We did not find any reliable RT difference between the HTPL (724 ms ± 35) and LTPL (721 ms ± 37) conditions in the balanced baseline epoch, $t_{(23)}$ = 0.2, p = 0.84, as should be expected. Instead, a reliable difference between the HTPL and LTPL conditions (direct effect) was present in the first block of the SL epoch (36 ms ± 11)

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compared to the baseline (-2 ms ± 12), $t_{(23)}$ = 2.51, p = 0.02, d = 0.512. This result was confirmed by the accuracy data (baseline: -1.4% ± 0.9; first block of SL: 1.8% ± 1), $t_{(23)}$ = 2.29, p = 0.03, d = 0.468. We then compared performance in the first half of the first block of SL (32 ms ± 15) with performance at baseline, and they did not differ significantly, $t_{(23)}$ = 1.7, p = 0.10. However, the difference was significant in the analysis of accuracy data (baseline: -1.4% ± 0.9; first half of the first block of SL: 1.9% ± 1.3), $t_{(23)}$ = 2.32, p = 0.03, d = 0.474. One again, SL of target location appears to quickly exert its influence on target selection.

During baseline, the distractor cost in RT (indirect effect) did not differ between the HTPL and LTPL conditions (HTPL: 153 ms ± 20; LTPL: 145 ms ± 19; $t_{(23)}$ = 0.50, p = 0.62). However, relative to baseline, we failed to reliably detect the onset of the indirect effect in any of the individual blocks of the SL epoch (p > 0.23 in all cases) though, as already reported, the effect was significant overall.

4.2.3. SL of Target location – *Extinction: direct and indirect effects*
In the extinction epoch, an analysis of RTs revealed a nearly significant trend in the expected direction, with faster responses in the HTPL (617 ms) relative to the LTPL (635 ms) condition, $t_{(23)}$ = 2.02, p = 0.055, indicating that SL of target location still had an effect on performance in the extinction regimen.

There was no significant difference between the HTPL and LTPL conditions in terms of the distractor cost during the extinction epoch ($t_{(23)}$ = 0.74, p = 0.47). This suggests a fast decay of the indirect effects of SL of target location once even probability of target occurrence at the various locations was re-established.

4.2.4. SL of Distractor location - *SL epoch: direct and indirect effects*
An ANOVA with Distractor Location (HDPL and LDPL) and Block (1-6) as main factors revealed a significant effect of Distractor Location, $F_{(1, 23)}$ = 15.70, p < 0.001, η_p^2 = 0.406. The distractor cost was greater in the LDPL (141 ms ± 23) than in the HDPL condition (97 ms ± 14), confirming that an uneven probability of the distractor across locations is able to modulate the efficiency of distractor filtering (Fig. 4D).

Since we replicated these results after removing from the data set all trials where the distractor appeared at the same location as in the immediately preceding trial, (HDPL vs. LDPL: $F_{(1, 23)}$ = 13.26, p = 0.001, η_p^2 = 0.366), an interpretation of the effects of the distractor probability manipulation on the distractor cost solely in terms of inter-trial priming (repeated suppression) can be safely rejected. Incidentally, a repeated suppression effect was found, $t_{(23)}$ = 10.68; p < 0.001, d = 2.180, with faster RTs when the location of the distractor repeated (606 ms ± 29) compared to when it did not (664 ms ± 33). Moreover, there was a marginally significant two-way interaction between Distractor Location and Block, $F_{(5, 115)}$ = 2.34, p = 0.046, η_p^2 = 0.326. The analysis of accuracy revealed a significant main effect of Distractor Location, $F_{(3, 69)}$ = 5.53, p = 0.03, η_p^2 = 0.194, reflecting higher distractor cost in the LDPL (2.1% ± 1.8) than in the HDPL (-0.1% ± 0.7) condition.

We next explored the influence of the distractor probability manipulation on the efficiency of target selection across locations (indirect effect). Here we found a small difference in the expected direction between the HDPL (660 ms ± 35) and LDPL (649 ms ± 35) conditions, replicating the effect found in Experiment 2 (Fig. 4E). However, an ANOVA with Target Location (HDPL and LDPL), Distractor Presence (present and absent), and Block (1-6) as the main factors showed that this difference did not reach statistical significance, $F_{(1, 23)}$ = 3.34, p = 0.08. Furthermore, in addition to a significant distractor-presence effect (Distractor Presence: $F_{(1, 23)}$ = 113.64, p < 0.001, η_p^2 = 0.832), a nearly significant trend indicated that the modulation of target selection due to the distractor probability manipulation (LDPL *minus* HDPL) augmented from 3 ms (± 6) to 21 ms (± 10) between the distractor-absent and distractor-present conditions, $F_{(1, 23)}$ = 3.83, p = 0.06 (Fig. 4F). Critically, planned comparisons showed that the uneven distractor probability significantly affected target selection in the presence of the distractor, $t_{(23)}$ = 2.15, p = 0.04, d = 0.439, but not when the distractor was absent, $t_{(23)}$ = 0.49, p = 0.63. The analysis of accuracy revealed a significant main effect of the distractor, $F_{(1, 23)}$ = 6.93, p = 0.01, η_p^2 = 0.232, whereas all other effects did not reach significance (p > 0.15).

4.2.5. SL of Distractor location - *Acquisition: direct and indirect effects*

During the Balanced baseline epoch, the difference in distractor cost between the HDPL (134 ms ± 21) and LDPL (123 ms ± 17) conditions was not significant, $t_{(23)}$ = 0.60, p = 0.55, as expected. Furthermore, we found only a marginally significant difference between the direct effect (difference in the distractor cost between the HDPL and LDPL conditions) measured in the first block (37 ms ± 19) and the baseline value (-11 ms ± 18), t(23) = 1.90, p = 0.07. We then subdivided the first block of the SL epoch in two halves; whereas baseline performance did not differ from performance in the first half of the block, t = 0.69, p = 0.50, a significant difference emerged against the second half, t = 2.40, p = 0.02, d = 0.490. These results attest to a rather fast emergence of the effects produced by the applied manipulation.

The same analyses were performed with regard to the indirect effect on target selection, focusing on data from trials with the salient distractor, since we have previously found that the indirect effect was stronger in this condition. At baseline, there was no reliable difference in RT between the HDPL (801 ms ± 40) and LDPL (807 ms ± 43) conditions, $t_{(23)}$ = 0.47, p = 0.64, as expected. The indirect effect measured during the first block of the SL epoch (6 ms ± 16) was not significantly different from baseline (-6 ms ± 13), $t_{(23)}$ = 0.63, p = 0.53. Similarly, the indirect effect measured in the second block of the SL epoch (9 ms ± 17), was again indistinguishable from baseline, $t_{(23)}$ = 0.69, p = 0.5. Thus, it is rather difficult to characterize the time-course of acquisition of the indirect effect, which is not surprising given that the effect is rather weak, if at all present (see below).

4.2.6. SL of Distractor location – *Extinction: direct and indirect effects*

As to the direct effect of our manipulation of distractor probability, we found no significant difference in distractor RT cost between the HDPL and LDPL conditions in the extinction epoch ($t_{(23)}$ = 0.19, p = 0.85). Likewise, considering only trials with a distractor, we found no significant RT difference in the indirect effect generated by the manipulation of distractor probability in the extinction epoch ($t_{(23)}$ = 0.20, p = 0.85).

4.2.7. Explicit/Implicit knowledge assessment

Six participants (out of twenty-four) reported the impression of an uneven spatial distribution of the target. Among them, two correctly indicated the HTPL and one the LTPL. None of the participants indicated both locations correctly. An analysis of the data after excluding any participants (n = 3) that reported the impression of an irregular spatial distribution of the target and indicated at least one correct location confirmed the significant difference between the HTPL and LTPL conditions in target selection (direct effect), $t_{(18)}$ = 8.80, p < 0.001, d = 2.019, and distractor filtering (indirect effect), $t_{(18)}$ = 2.68, p = 0.02, d = 0.615.

With respect to the manipulation of distractor probability, three participants reported the impression of an uneven spatial distribution of the distractor across locations. Two of them identified correctly one location (LDPL), whereas another participant identified both locations (HDLP and LDPL) correctly. When those participants (n = 3) were excluded from the analysis, all results were replicated (direct effect on distractor filtering: $t_{(18)}$ = 3.00, p = 0.007, d = 0.689; indirect effect on target selection: $t_{(18)}$ = 1.62, p = 0.12).

Taken together, these observations confirm that the influence of SL for both the target and the distractor spatial distribution cannot be accounted for in terms of deliberate strategy of attentional deployment adopted by the participants on the basis of an explicit knowledge of the probability contingencies.

4.3. Discussion

The objective we pursued with Experiment 3 was twofold: on the one hand, we set out to replicate the results from the previous two experiments, namely, the influence on attentional deployment of SL of target and distractor probability (Experiment 1 and 2, respectively), including the direct and indirect effects of the applied manipulation; on the other hand, we wished to assess whether we could elicit SL of both target and distractor probability within the same session. Indeed,

the results from Experiment 3 provided positive evidence with regard to both questions. The results clearly showed that the efficiency of target selection can be adjusted depending on target probability at the various display locations, confirming what we had found in Experiment 1. Faster target selection was obtained for the high target probability location compared to the low probability location. We also replicated the indirect effects of the uneven distribution of targets across display locations on distractor filtering processes, with more efficient filtering (smaller distractor cost) at the low target probability location relative to the high target probability location. Moreover, the data demonstrated that the uneven spatial distribution of the distractor across locations alters the efficiency of distractor filtering (direct effect of SL of distractor probability), as we obtained in Experiment 2. Distractor filtering was relatively more efficient at the location where distractors occurred more often compared to the location where they occurred more rarely. Also, like in Experiment 2, we replicated the indirect effects of the distractor probability manipulation on the efficiency of target selection, with faster target selection at the location with rare distractors relative to the location with frequent distractors; however, this effect only approached statistical significance (although in this experiment the effect was significant for targets shown together with a distractor). Strikingly, the results obtained in the present experiment matched almost exactly the results from the previous two experiments, indicating the very high degree of reliability of the effects reported in the three experiments combined (Table 2). Moreover, Experiment 3 clearly showed that SL for target and distractor probability can co-occur within the same session, when the probability of targets and distractors are manipulated independently from one another. Finally, this experiment provided further evidence in favor of the implicit nature of the effects on attentional deployment elicited by SL of target and distractor probability distribution.

Statistical Learning Effect (ms)

	Direct Effect	Indirect Effect
Exp. 1	Target 41 ± 6 *	Distractor 23 ± 9 *
Exp. 2	Distractor 41 ± 14 *	Target 11 ± 10
Exp. 3a	Target 43 ± 6 *	Distractor 20 ± 10 *
Exp. 3b	Distractor 45 ± 11 *	Target 12 ± 7
Exp. 4	Distractor 36 ± 9 *	Target 10 ± 6

Table 2 - Summary of the results. For all experiments the statistical learning effect has been computed as the absolute difference between the high- and low- probability conditions. The asterisk (*) indicates a statistically significant effect (p < 0.05).

In general, the results reported so far are compatible with the notion that SL of both target and distractor location adjust the priority of locations within attentional priority maps of space. Specifically, a location with frequent targets or rare distractors will gain an increased priority as a result of SL; vice versa, a location with rare targets or frequent distractors will acquire reduced priority as a result of SL. In turn, the increased priority acquired by a given location during SL will enhance target processing at that location but also hinder distractor filtering. In contrast, the reduced priority acquired by a given location during SL will decrease the efficiency of target processing but aid distractor filtering.

A principal objective of the present study was to establish the extent to which SL of target and distractor probability across locations leads not only to direct effects of the applied manipulation but also indirect effects, for instance changes in the efficiency of distractor filtering due to an uneven distribution of targets across locations. The evidence gathered so far seems to indicate at least some degree of asymmetry in the indirect effects elicited by SL of target vs. distractor probability, with substantial indirect effects elicited by the manipulation of target probability but only marginal indirect effects elicited by the manipulation of distractor

probability (non-significant or marginally significant in Experiment 2 and 3, respectively). Thus it becomes crucial to establish whether the latter indirect effect actually exists or it simply reflects noise in the data. This is important because in the first case the asymmetry in the indirect effect elicited by the SL of target vs. distractor manipulation is only quantitative in nature and should therefore deserve less emphasis, whereas in the second case such asymmetry would be strong and functionally meaningful. As detailed in the next section, we set out to further explore the problem with Experiment 4, in order to exclude that the observed asymmetry in indirect effects might be merely due to some trivial factor, such as the relatively limited experience concerning distractor (vs. target) probability during the learning process.

5. Experiment 4

Experiment 3 fully confirmed what found in the previous experiments, with SL of target location producing robust indirect effects on distractor filtering and SL of distractor location producing only limited, if any, effects on target selection, even though the direct effects were very strong in both experiments. Specifically, as reported in Table 2, the direct effects (the difference in RT between high and low probability locations) elicited by SL of target and distractor location probability were of roughly the same magnitude (~40 ms, in absolute value) across experiments. Instead, the indirect effects were about twice as large in the case of SL of target location (~20 ms, in absolute value) than in the case of SL of distractor location (~10 ms, in absolute value). Results of Experiment 3 ruled out the possibility that the difference in the size of the indirect effects between the two kinds of SL, as observed in Experiment 1 and 2, could be due to inter-individual variability, because we replicated the same asymmetry in Experiment 3, wherein the two forms of SL were tested within the same population of subjects. Therefore, data from all three experiments combined appear to indicate that there is an asymmetry between the indirect effects generated by the two kinds of SL. However, it is very important to understand the nature of the asymmetry. Is it an all-or-none asymmetry, with SL of target location engendering robust indirect effects and SL of distractor location generating no such effects (in which case the trends in Experiments 2 and 3 would only reflect accidental variations in performance)? Or is it just a quantitative asymmetry, with both kinds of SL producing indirect effects, albeit of a different magnitude and statistical reliability? Before we try to tackle the problem with some other approach and draw any meaningful conclusion on this point, it is important to establish that the asymmetry is not due to some trivial factor. In this regard, as anticipated in the previous section, a plausible explanation for the asymmetry could be related to the unequal number of learning episodes that are available during the SL epoch in relation to the spatial distribution of targets vs. distractors. In all experiments, the distractor was presented on only one half of the total trials, whereas the target was shown on all trials.

Therefore, one could conjecture that the impact of learning will differ depending on the available number of learning episodes. In other words, it could be argued that the effects produced by SL of target probability were more robust because of more extended experience with the target distribution across display locations compared with a more limited experience concerning the spatial distribution of distractors. This account of the asymmetrical pattern of results does not seem very likely, in that in all three experiments the influence of the given manipulation (direct effects) emerged very rapidly during the SL epoch. Nonetheless, one could still argue that in spite of fast learning of the statistical contingencies, as revealed by the fast emergence of the direct effects, the indirect effects might instead benefit from more extended experience (a larger absolute number of learning episodes) such as it occurred for SL of target location compared to SL of distractor location. However unlikely it may be, we decided to directly test this possibility in Experiment 4.

To this aim, we set out to compare the results obtained in Experiment 2 with the results obtained in a further experiment, Experiment 4, in which the SL manipulation was identical to that used in the previous experiment, but the SL epoch was much longer and comprised an almost twice as large number of learning episodes. If the robustness of the indirect effect elicited by SL of distractor location depends on the number of learning episodes, then by almost doubling this number we should generate larger and reliable indirect effects, similar to those found in Experiment 1 and 3 in the case of SL of target location. It should be noted immediately that Experiment 4 differed from the previous ones in a number of details (see below); however, we believe that such differences do not preclude a fair comparison with the results obtained in previous experiments. This experiment was actually performed prior to the experiments already described, as a first attempt to study SL of distractor location, which explains the differences in methodology.

5.1. Methods

5.1.1. Participants

Twenty volunteers (8 males; mean ± SD age, 23.80 ± 2.98) took part in Experiment 4.

5.1.2. Materials and Stimuli

Materials and stimuli were similar to those used in Experiment 1, with the following exceptions. Differently from the previous experiments, here the target was always black and was arranged horizontally (a double arrow-head pointing either to the left or right). Also, the display contained either one stimulus, the target, or two stimuli in total, the target and a single distractor. The distractor was similar to the target, but with the two black triangles pointing in opposite directions (both inwardly or outwardly). Four white (67.8 cd/m^2) square outlines (with sides 2.25° in length) were used as placeholders (Fig. 5).
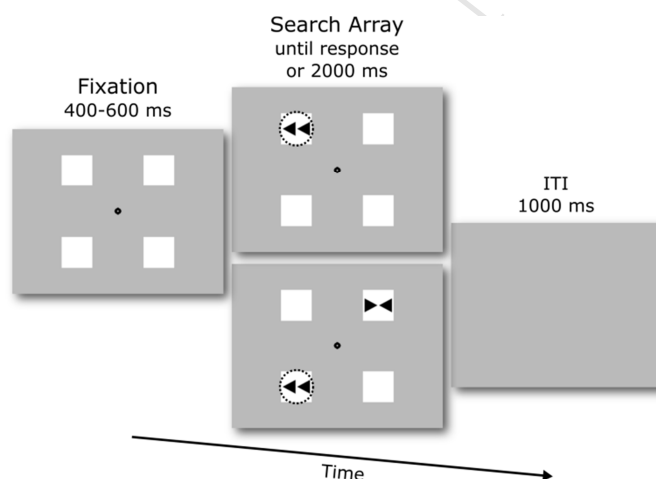

Fig. 5 – Illustration of the visual search task used in Experiment 4. After a fixation display lasting between 400-600 ms, the search array was presented. While only the target (indicated in the figure by a dashed circle, not visible during the actual task) appeared at one of the four possible locations in half of the total trials, an additional distractor was displayed in the remaining 50% of the trials (see text). Participants had a maximum of 2000 ms to indicate the orientation of the target. A new trial started after 1000 ms.

5.1.3. Design and Procedure

Unlike in the previous experiments, here four placeholders were presented concurrently with the fixation point in the fixation display. After a variable interval

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of 400-600 ms, a target was displayed at the center of one of the placeholders, and participants had to indicate as quickly and as accurately as possible whether the target pointed to the left or to the right by button press (key 1 for 'left' responses, key 2 for 'right' responses). On half of the trials a distractor was shown inside one of the remaining placeholders. The stimuli remained on the screen until the participant's response or for a maximum duration of 2000 ms. A new trial started after a 1000 ms intertrial interval (Fig. 5).

The spatial probability manipulation was as in Experiment 2 (Table 1). Target location probability was the same across locations, whereas the distractor was more likely presented at one location (42%; HDPL) and less likely presented at another location (8%; LDPL), with intermediate probability at the remaining two locations (25%; IDPLs). The experiment consisted of a single epoch of SL, comprising ten blocks of 144 trials each. No additional epochs were run before or after the SL epoch. We did not explore the level of explicit or implicit knowledge of the probability manipulation on the part of the participants.

5.1.4. Data analysis

Analysis of the data was performed according to the same approaches as used before.

5.2. Results

5.2.1. SL of Distractor location: direct effects

A repeated-measures ANOVA on the distractor cost with Distractor Location (HDPL, IDPL and LDPL) and Block (1-10) as main factors revealed a significant main effect of Distractor Location, $F_{(2, 38)} = 13.76$, $p < 0.001$, $\eta_p^2 = 0.467$, with the cost decreasing as the spatial probability of the distractor increased (LDPL = 102 ms ± 8; IDPL = 73 ms ± 5; HDPL = 65 ms ± 6). Post-hoc t-tests showed a significant difference between the cost in the LDPL and both the IDPL and HDPL conditions ($p < 0.002$, d > 0.8 in both cases). Instead, costs for the IDPL and HDPL conditions were not

significantly different from one another, $t_{(19)}$ = 1.75, p = 0.10, although the trend was in the expected direction (Fig. 6A). The main effect of Block was also significant, $F_{(9, 171)}$ = 2.20, p = 0.024, η_p^2 = 0.598, reflecting an initial reduction (block 1: 100 ms ± 13; block 4: 68 ms ± 10) and a final resurgence (block 10: 86 ms ± 11) of the distractor cost, whereas the interaction between Distractor Location and Block was not significant, $F_{(18, 342)}$ = 1.27, p = 0.2. The same analysis on accuracy data revealed only a significant main effect of Block, $F_{(9, 171)}$ = 2.15, p = 0.03, η_p^2 = 0.741, reproducing the pattern observed in RT data.

We replicated the analysis on RT after excluding from the data set all trials in which the distractor appeared at the same location as in the immediately preceding trial. The results confirmed the significant main effect of Distractor Location, $F_{(2, 38)}$ = 10.30, p < 0.001, η_p^2 = 0.393, demonstrating that once again the effect of SL is not solely due to inter-trial phenomena.
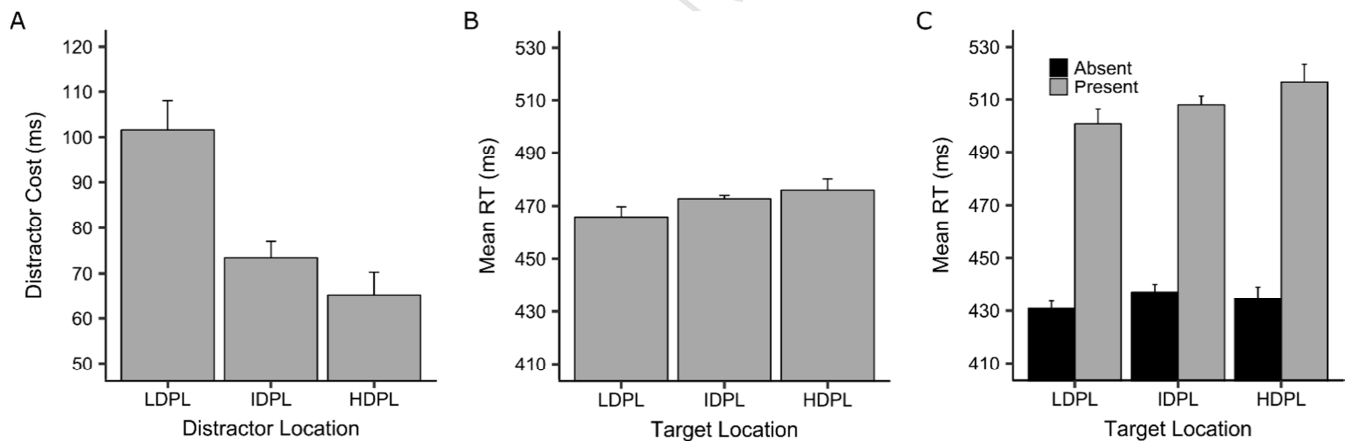

Fig. 6 – Statistical learning (SL) effects during the SL epoch in Experiment 4. *(A)* Direct effect of SL of distractor location. Average distractor costs are reported as a function of distractor location (LDPL = low distractor probability location; IDPL = intermediate distractor probability location; HDPL = high distractor probability location). *(B)* Indirect effect of SL of distractor location. Mean RTs are reported as a function of target location. *(C)* Indirect effect of SL of distractor location. Mean RTs are reported as a function of target location, separately for the distractor-present (gray) and distractor-absent (black) conditions.

5.2.2. SL of Distractor location – *Exp. 2 vs. Exp. 4: direct effects*

We compared the direct effects generated by SL of distractor location in this experiment with those obtained in Experiment 2. The direct effect – namely, the absolute difference in the distractor cost between high and low distractor probability locations – was 41 ms (± 14) in Experiment 2 and 36 ms (± 9) in Experiment 4. A one-tailed t-test for independent samples indicated that the difference between the two effects was not significant, $t_{(36.8)} = 0.31$, $p = 0.38$. Thus, prolonging the duration of the SL epoch did not increase the direct effect associated with distractor suppression.

5.2.3. SL of Distractor location: indirect effects

We performed a repeated-measures ANOVA on mean RTs with Target Location (HDPL, IDPL and LDPL), Distractor Presence (present and absent), and Block (1-10) as main factors. Data showed slightly faster RTs as the distractor probability associated with a given location decreased (HDPL: 476 ms; IDPL: 473 ms; LDPL: 466 ms; Fig. 6B-C), but the main effect of Target Location did not reach significance, $F_{(2, 38)} = 2.32$, $p = 0.11$. The main effect of Distractor Presence was significant, $F_{(1, 19)} = 279.34$, $p < 0.001$, $\eta_p^2 = 0.936$, as was its interaction with Block, $F_{(18, 342)} = 2.77$, $p = 0.005$, $\eta_p^2 = 0.639$, replicating previous results: an overall distractor cost (absent: 434 ms ± 13; present: 509 ms ± 15) and its reduction as the experiment advanced (distractor present minus absent, block 1: 95 ms ± 7; block 10: 75 ms ± 6; $t_{(19)} = 2.63$, $p = 0.02$, $d = 0.588$). All other effects were not significant ($p > 0.14$), with a non-significant trend in the three-way interaction, $F_{(9, 171)} = 1.52$, $p = 0.08$. In the analysis of accuracy data, a significant main effect was found for Distractor Presence (distractor cost), $F_{(1, 19)} = 20.39$, $p < 0.001$, $\eta_p^2 = 0.518$, and Block (practice effect), $F_{(9, 171)} = 3.45$, $p < 0.001$, $\eta_p^2 = 0.530$, and also a significant interaction between the two factors, reflecting decreasing distractor cost as the experiment progressed, $F_{(9, 171)} = 2.88$, $p = 0.003$, $\eta_p^2 = 0.885$. The main effect of Target Location did not reach significance, $F_{(2, 38)} = 0.28$, $p = 0.76$.

5.2.4. SL of Distractor location - *Exp. 2 vs. Exp. 4: indirect effects*

If the reason behind the asymmetrical indirect (transfer) effects found in the previous experiments (Experiment 1 vs. 2, but also within Experiment 3), and especially the weak and only marginally significant indirect effects engendered by SL of distractor location, is that there were fewer learning episodes for the distractor's spatial distribution relative to the target's spatial distribution, one would predict that by prolonging the SL epoch the magnitude of this indirect effect should increase. We tested this possibility by comparing the size of the indirect effect of SL of distractor location on target selection found in this experiment with that obtained in Experiment 2. Although non-significant in both cases, the indirect effect was on average of 11 ms (± 10) in Experiment 2 and 10 ms (± 6) in Experiment 4, i.e., it was almost exactly the same in two experiments. A one-tailed t-test for independent samples confirmed that this difference was not significant, $t_{(35.4)}$ = 0.05, p = 0.48. Therefore, it appears that the two indirect effects were of comparable size.

5.3. Discussion

In Experiment 4 we tested the possibility that the asymmetric transfer effects between the two forms of SL – that for the target and that for the distractor, might be due to the different number of learning episodes in the two cases, with a greater number of episodes to learn about the probability distribution of the target than of the distractor. In fact, in all experiments reported here, including Experiment 4, while the target was presented on all trials, the distractor was displayed on only half of the trials. We reasoned that if this were the reason of the asymmetry in the indirect effects, then we should find more robust indirect effects of SL of distractor location on the efficiency of target selection by increasing the number of relevant learning episodes. For this reason, although in this experiment the number of learning episodes was twice as large for target SL than for distractor SL, the total number of learning episodes for the distractor SL was much greater than before. However, the results negated this explanation. We found the exact same indirect effect in this experiment as we had found in Experiment 2 (and 3).

Therefore, increasing the total number of trials where the probability distribution of distractors could be experienced had no influence on the observed SL effects. The data thus support the conclusion that there is cross-talk between target selection and distractor filtering mechanisms, as studied here by means of SL, but that the cross-talk is asymmetrical. In the following section, we will provide evidence to better understand the nature of the asymmetry.

6. Comparison between direct and indirect effects across experiments

The experiments reported so far demonstrated that when a statistical contingency is applied to the spatial distribution of a relevant or otherwise salient stimulus, be it the target or the singleton distractor, this regularity generates spatial SL, which in turn modulates the allocation of attention. We have interpreted these effects by making reference to the notion of priority maps of space. Importantly, we found that the elicited modification in the priority of spatial locations as a result of SL not only affected processing of the stimulus whose spatial probability was manipulated (e.g., target selection when target probability was varied across display locations), but it also affected processing of the alternative stimulus (e.g., distractor filtering in the given case). We have interpreted this transfer or indirect effect as an index of cross-talk between target selection and distractor suppression mechanisms, likely resulting from one or more shared priority maps of space. We also noted that the cross-talk may be asymmetrical, with stronger spread of the effect from SL of target location to distractor filtering than from SL of distractor location to target selection. However, based on the combined evidence from all the experiments, notably Experiment 2, 3 and 4, we were hesitant to interpret this asymmetry since it was actually unclear whether the indirect effect from SL of distractor location to target selection was real or just noise in the data. In what follows we take a different approach to try and resolve this issue, as detailed below.

To gather direct evidence that any indirect effect (on target selection or distractor filtering) is the result of the primary SL of spatial contingencies, we developed an approach hinging on inter-individual variability and compared across individual participants the magnitude of the indirect effect with that of the direct effect. If any measured transfer effect is the consequence of the applied SL manipulation, then we might expect its magnitude in the individual participant to be correlated with the direct effect elicited by the applied statistical manipulation. In other words, a participant who displays a relatively large direct effect should also display a relatively large indirect effect, and vice versa. More specifically, by using this

approach, we were hoping to clarify once and for all whether what appears to be a weak transfer – if any - from SL of distractor location to target selection, as we found in Experiments 2, 3 and 4, is actually a reliable transfer or is just noise.

6.1. Results

<u>6.1.1. SL of Target Location</u>

Experiment 1 and 3 showed very clearly that manipulating the probability with which a target is presented across locations affects both target selection (direct effect) and distractor filtering (indirect effect) processes. To assess whether these two effects were correlated in the individual participants, we first calculated the SL effect – the absolute difference in RT between high and low probability locations – for both the direct and indirect effects. Overall, participants displayed a direct effect of 41 ms ± 6 in Experiment 1 and 43 ms ± 6 in Experiment 3, and an indirect effect of 23 ms ± 9 in Experiment 1 and 20 ms ± 10 in Experiment 3 (Table 2). SL effects of individual participants were then submitted to a correlation analysis. Results showed a significant correlation between the two effects (Experiment 1: $r = 0.60$, $p = 0.002$; Experiment 3: $r = 0.71$, $p = 0.0001$), with greater direct effects associated with greater indirect effects (Fig. 7A-B).

<u>6.1.2. SL of Distractor Location</u>

Experiment 2, 3, and 4 showed that the size of the indirect effect on target selection elicited by SL of distractor location is about one fourth in magnitude of the direct effect of the distractor probability manipulation (Table 2). However, although this indirect effect was remarkably stable across experiments, doubts remain concerning the reliability of the effect, especially given that only in some cases was it supported by statistical evidence. To shed light on this point, we again performed a correlation analysis between the direct and the indirect effects elicited by SL of distractor location in Experiments 2, 3 and 4. Clearly, if the indirect effect was due to noise, then no significant correlation should be found here. Hence, the direct and indirect effects observed in Experiment 2 (41 ms ± 14 vs. 11

ms ± 10), Experiment 3 (45 ms ± 11 vs. 12 ms ± 7), and Experiment 4 (36 ms ± 9 vs. 10 ms ± 6) were submitted to a correlation analysis, separately for each experiment. We found highly significant correlations between the two effects in all experiments (Experiment 2: r = 0.87, p < 0.001; Experiment 3: r = 0.53, p = 0.007; Experiment 4: r = 0.71, p < 0.001), with larger direct effects systematically associated with larger indirect effects (Fig. 7C-E).
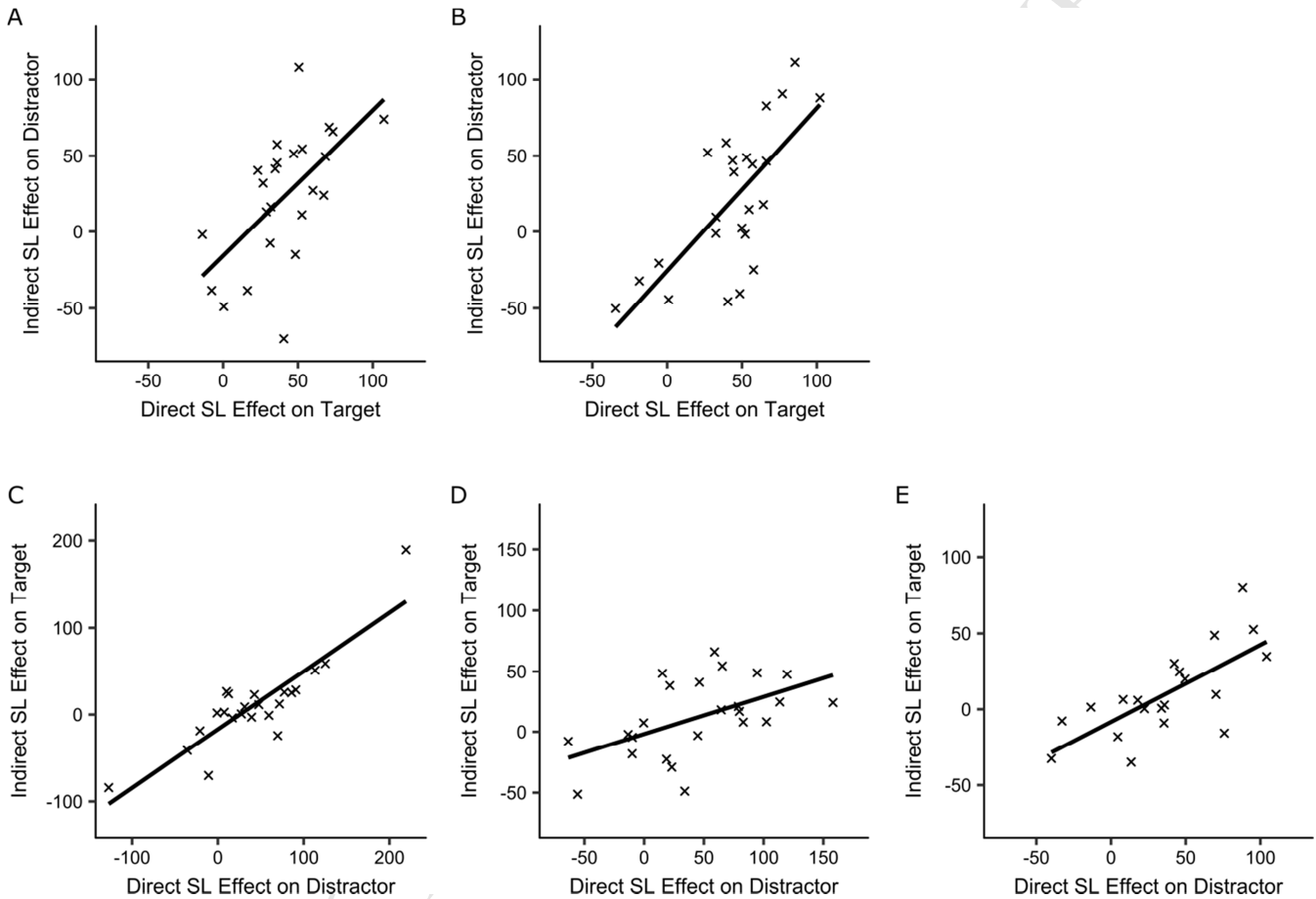

Fig. 7 – Comparison between direct and indirect effects of SL across experiments. *(A)* Correlation between direct effects (reported on the x-axis) and indirect effects (reported on the y-axis) of SL of target location measured in Experiment 1 (slope = 0.95; intercept = -15.74). In this and all other panels, data points (x) on the graph correspond to the effects calculated for each individual participant, as the RT difference in search performance for a high vs. low probability location. *(B)* Correlation between direct (x-axis) and indirect (y-axis) effects of SL of target location measured in Experiment 3 (slope = 1.07; intercept = -25.60). *(C)* Correlation between direct (x-axis) and indirect (y-axis) effects of SL of distractor location measured in Experiment 2 (slope = 0.67; intercept = -17.22). *(D)* Correlation between direct (x-axis) and indirect (y-axis) effects of SL of distractor location measured in Experiment 3 (slope = 0.31; intercept = -1.89). *(E)* Correlation between direct

(x-axis) and indirect (y-axis) effects of SL of distractor location measured in Experiment 4 (slope = 0.51; intercept = -8.43).

6.2. Discussion

Rather unexpectedly, we found that the direct and indirect effects were strongly correlated with one another in all experiments. Participants displaying a larger direct effect also tended to display a larger indirect effect, and vice versa. This finding strongly supports the notion that target selection and distractor filtering mechanisms share at least part of the same underlying neural machinery, at least when selection and filtering are governed by the implicit learning of statistical regularities concerning probability of target and distractor occurrence across display locations.

More specifically, the above findings provide further evidence in favor of a transfer effect also in the case of SL of distractor location. In all experiments with an imbalanced spatial distribution of the distractor (Exp. 2, 3 and 4), the efficiency of target selection was modulated in the hypothesized direction, with relatively worse selection at the location associated with high distractor probability. Since this effect was not fully supported by standard statistical analyses, we were hesitant to conclude that such transfer does indeed exist. However, the evidence obtained with the correlation analyses enables us to draw a firm conclusion: changes in attentional priority elicited by an uneven spatial distribution of the distractor do not only affect distractor filtering but also target selection. We found that in all experiments the size of the transfer effect on target selection was highly correlated with the size of the direct effect on distractor filtering. Therefore, we must conclude that the transfer effect found on target selection was actually produced by the probabilistic manipulation of distractor location. On this basis, we can conclude that the asymmetry we have found in the transfer effect elicited by the two forms of SL is quantitative and not qualitative in nature. The transfer elicited by SL of target location appears to be stronger than the transfer elicited by SL of distractor

location, but both effects do exist. Potential accounts of the asymmetry will be considered below.

7. General Discussion

Previous research has demonstrated that in visual search the spatial probability of target stimuli over the course of the experiment biases the allocation of attention toward the array regions that more frequently produced successful performance, namely those locations wherein the target was displayed with higher probability (Shaw and Shaw, 1977; Miller, 1988; Hoffmann & Kunde, 1999; Geng & Behrmann, 2002; 2005; Walthew & Gilchrist, 2006; Druker & Anderson, 2010; Jiang et al, 2013a; 2013b; 2015a; 2015b; Sha et al., 2017). Likewise, research has shown that attention filtering is more efficiently applied to locations wherein the distractor occurs more often or, put differently, distraction becomes progressively weaker at the same locations (Reder e al., 2003; Goschy et al., 2014; Leber et al., 2016; Wang & Theeuwes, in press). Here we explored the main characteristics of these two forms of spatial SL and the underlying mechanisms. Our principal aim was to establish whether SL of target selection and distractor filtering depend on shared or dissociable machinery and computations. Evidence in the literature bearing on this issue is very limited (Reder et al., 2003; Wang & Theeuwes, in press). One could argue that the two kinds of SL ought to occur independently from one another for the simple reason that, depending on the given situation, the system acquires statistical knowledge about the probability distribution of target or distractor stimuli, which of course are set to be defined by distinct features and/or feature dimensions in the given context. This knowledge is then used to guide target selection in one case and distractor filtering in the other. In addition, as already mentioned, an abundant literature over the years has supported the idea that target selection and distractor filtering mechanisms rely on dissociable mechanisms that affect visual processing in distinct ways (Hickey et al., 2009; Couperus & Mangun, 2010; Sawaki & Luck, 2010; 2013; Noonan et al., 2016). Conversely, one could argue that the effects engendered by both forms of SL might well reflect changes in the likelihood that attention be deployed toward a given location, i.e., changes in the attentional priority of locations, whereby changes in priority will then affect both target selection and distractor filtering. To

be more specific, an increase in priority at a given location will benefit target selection at that location but at the same time will enhance distraction at the same location. Of course, as a final possibility, a hybrid scenario could also be considered, whereby target selection and distractor filtering processes reflect partly shared and partly independent neural mechanisms. For example, one might conceive that distinct signals instantiate target selection and distractor filtering control, but then these signals converge onto the same priority maps of space to guide attention in a coordinated manner towards the relevant target and away from any irrelevant but otherwise salient distractor.

To shed light on these issues, in a series of experiments, we manipulated the spatial probabilities of either the target (Exp. 1), the distractor (Exp. 2 and 4), or both (Exp. 3). The results showed a strong impact of spatial SL on attentional allocation, with both target and distractor processing affected by the spatial probability manipulation. Specifically, when target probability was manipulated across locations, selection was more efficient for targets presented at the high target probability location and less efficient for targets at the low target probability location (direct effect in Exp. 1). Likewise, when we manipulated distractor probability across locations, greater interference was produced by distractors displayed at the low distractor probability location relative to the high distractor probability location (direct effect in Exp. 2). Most importantly, we found a clear interdependence (cross-talk) between selection and filtering mechanisms. In particular, in the first two experiments, SL not only affected processing of the stimulus that was subject to the probability manipulation, namely the target and the distractor in Experiments 1 and 2, respectively, but it also affected processing of the alternative, non-manipulated stimulus. The unequal spatial distribution of the target affected distractor interference, with greater distractor cost at a location with higher target probability (indirect effect in Exp. 1) and, vice versa, the effect of the SL of distractor location transferred to target selection, with faster target discrimination at the location with rare distractors (indirect effect in Exp. 2). Moreover, with Experiment 3 we could show that these two forms of SL can co-

occur within the same learning experience, and also provide strong confirmation to the results obtained with the previous two experiments.

7.1 SL-induced plasticity of spatial priority maps

As already noted, participants were faster to discriminate the target when presented at the frequent target location compared to when it appeared at the rare location. Although SL of target location (or probability cueing) has now been replicated several times (e.g., Geng & Behrmann, 2002; 2005; Jiang et al, 2013a; 2013b; 2015a; 2015b; Sha et al., 2017), little is known about the underlying mechanisms. On the one hand, the attention bias generated by spatial SL might seem to be very similar to other forms of attentional cueing: it facilitates processing of targets shown at locations where they are more likely to occur (Posner, 1980; Macaluso & Doricchi, 2013; Vossel et al., 2014). On the other hand, the effects generated by SL are clearly distinct from those generated by explicit endogenous and exogenous cues (Geng & Behrmann, 2005; Jiang et al., 2013a; Jiang, this issue), and cannot be classified as either top-down or bottom-up in nature (Awh et al., 2012; Jiang, this issue). More relevant to our purposes, we found that explicit knowledge by the participants of the applied probability manipulation played no role in the observed effects. Given that SL of target (and distractor) processing cannot be accounted for in terms of traditional top-down or bottom-up control, it is especially important to understand the mechanisms underlying this type of attentional guidance. We have conjectured that spatial SL operates by adjusting the weights in the priority maps which dynamically control deployment of visual spatial attention and gaze (Itti & Koch, 2001; Fecteau & Munoz, 2006; Serences & Yantis, 2006; Gottlieb, 2007; Bisley & Goldberg, 2010; Ptak, 2012; Zelinsky & Bisley, 2015). In brief, within a winner-take-all scenario, spatial priority maps encode the priority of individual visual field locations by combining a variety of signals, including bottom-up visual drive (salience), top-down relevance for the task at hand of the item at the given location, any location-specific preparatory or biasing signal (see, e.g., Luck et al., 1997; Kastner et al., 1998; Sani et al., 2017), past selection history, reward associations and other sources of motivational-emotional

salience (Klink et al., 2014; Awh et al., 2012; Bourgeois et al., 2016). As a result of such combined influence, the level of activity at each location in the map will determined the priority of the location for overt and covert selection. The location with the highest level of activity at a given point in time will be (overtly and/or covertly) selected, whereas all other locations in the visual field will be effectively ignored. In this perspective, each time that successful target selection occurs, the priority of the corresponding location is augmented, perhaps in the form of enhanced responses to bottom-up visual drive (gain increase). Likewise, each time that a location does not contain relevant information or, even more, contains distracting information, its priority in the maps is reduced, again perhaps in the form of weakened responses to bottom-up visual drive (gain decrease). Thus, after enough evidence has been gathered, updated weights are encoded in the maps, in turn favoring high priority locations over low priority ones (Fig. 8).
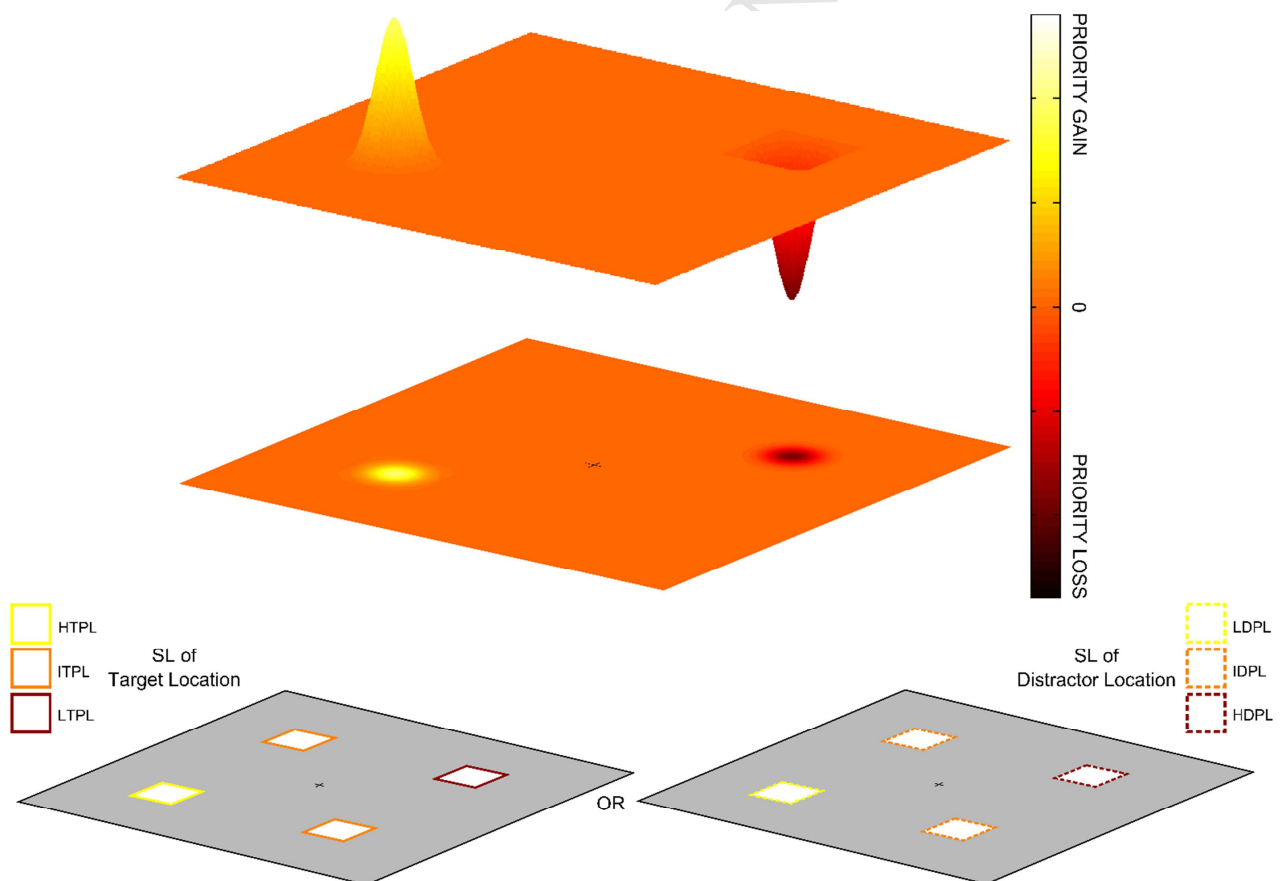

Fig. 8 – SL-induced plasticity of the spatial priority map(s). The figure illustrates changes in priority occurring for specific spatial locations as a result of statistical learning, both in a 2D plane (middle) and in a 3D representation (top). As exemplified, analogous gains and losses in the priority of a specific location might result from exposure to imbalanced

probability either of target (bottom, left) or distractor (bottom, right) probability at that location. Specifically, a gain in priority is measured for a location where targets occur frequently (HTPL; bottom, left) or where distractors occur rarely (LDPL; bottom, right); conversely, a reduction in priority is measured for a location where targets occur rarely (LTPL; bottom, left) or where distractors occur frequently (HDPL; bottom, right).

Further support to the idea that our manipulation altered priority maps of space arises from the level of spatial specificity of the effects we obtained. Most previous studies exploring SL of target location compared performance within high target probability regions of the display against display regions with less frequent targets (e.g., Geng & Behrmann, 2002; 2005; Jiang et al, 2013a; 2013b; 2015a; 2015b; Sha et al., 2017). Here instead we associated each of four distinct locations with each of three different target probabilities (high, intermediate or low). This design enabled us to apply a more localized manipulation of spatial probability across display locations and to discriminate between two possible scenarios. On the one hand, the probability manipulation employed here could affect all the locations within the given visual hemifield, in line with the general notion of preferential orienting of attention towards one or the other half of space, for instance as a result of inter-hemispheric competition mechanisms (lateral bias; Tassinari et al., 1987; Duecker et al., 2017). On the other hand, a considerable level of spatial specificity could be found, with task performance varying as a function of the given target probability at the individual location. The pattern of results we obtained in Experiment 1 is in line with the latter scenario, as the effect was location-specific and did not spread to the intermediate probability location within the same visual hemifield. Thus, spatial SL seems to operate in a location-specific fashion, and this is fully in line with the notion that it affects activity within priority maps of space. However, denser stimulus arrays will be needed to obtain a more detailed characterization of the spatial profile of the effects reported here.

One implication derived from the idea that SL of target (and distractor) location, as studied here, reflects location-specific changes in excitability in one or more spatial priority maps is that the effects acquired in one behavioral context should transfer to a different context, as long as attentional deployment depends on activity within the same priority maps in both contexts. To establish whether this is

the case requires the use of different behavioral paradigms between the learning phase and a subsequent testing phase. We did not test this possibility in the present work. However, evidence bearing on this point was provided by a recent study conducted by Jiang and colleagues (2015a). In their experiments, during a learning phase, participants performed a visual search task in which target spatial probability was uneven across display regions. In a subsequent testing session, with no spatial contingency, participants performed a high-level decision-making task (foraging task). Under those circumstances, the probability cueing effect did not transfer from learning to testing. However, when the testing phase involved variants of visual search, i.e., different stimuli were used between learning and testing, the spatial bias generated by SL generalized to the new context and stimuli. Therefore, at least to some extent, the effects of spatial SL appear to generalize, as one should expect based on the notion of altered priority maps. In the future it will extremely important to shed light on the boundary conditions determining whether generalization does or does not occur.

Neurophysiological investigations have indicated nodes of the oculomotor control network as the neural incarnation of spatial priority maps (Fecteau & Munoz, 2006; Zelinsky & Bisley, 2015). This network consists of several cortical areas, including the frontal eye field (FEF; Thompson et al., 1996; Moore & Zirnsak, 2017) and the lateral intraparietal area (LIP; Thomas & Paré, 2007; Bisley & Goldberg, 2010; Wardak et al., 2011), as well as subcortical structures such as the superior colliculus (McPeek & Keller, 2002; Krauzlis et al., 2013). A further brain structure that is likely to contribute to the encoding of the priority of spatial locations at the service of oculomotor and attentional control is the *caudate nucleus* in the basal ganglia (Hikosaka et al., 2000). All structures above are involved in the control of covert as well as overt attention (Kustov & Robinson, 1996; Wardak et al., 2006; Moore & Zirnsak, 2017) and their neurons instantiate a topological representation of the visual field (Zelinsky & Bisley, 2015). For instance, focal activity in LIP has been shown to encode the attentional priority at the corresponding visual field location in addition to the intention to execute an eye movement toward the same location (Bisley & Goldberg, 2003). Thus, we argue that spatial SL changes the level of excitability

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(gain change) in one or more of those structures involved in the control of spatial attention (and gaze) through some form of neural plasticity. In fact, given the current emphasis on the projection systems going through the basal ganglia as the basis for forms of motor and non-motor learning (Jin & Costa, 2015; Kim & Hikosaka, 2015; Hart et al., 2014), including habit learning (Graybiel, 2008), we think it likely that SL of target (and distractor) location might primarily reflect changes in neuronal excitability at one or more levels within specific cortico-basal ganglia loops, perhaps especially within the *caudate nucleus*. Interestingly, work from Hikosaka's group has elegantly shown that neural activity in the tail of the *caudate nucleus* encodes both the identity and location of objects for the sake of controlling saccades (Yamamoto et al., 2012). More relevant to our purposes, activity within the same region is affected by manipulations that change the probability that a saccade is made towards a given object or location (Hikosaka et al., 2014), including through the controlled delivery of reward (Kim & Hikosaka, 2015). Based on the close link between the neural mechanisms responsible for saccades and covert spatial attention (Rizzolatti et al., 1987; Moore & Zirnsak, 2017), it seems highly plausible that the *caudate nucleus*, and especially its tail, might be a key structure to mediate the sort of learning-dependent changes in performance reported here, likely in concert with other cortical and subcortical nodes of the oculomotor network. In this vein, the type of implicit guidance of attention explored here can be thought of as a manifestation of habitual control of attention, both in terms of habitual selection of targets occurring at target-rich locations and in terms of habitual filtering of distractors occurring at distractor-rich locations. Location-specific gain changes in one or more priority maps of space will effectively incarnate habit formation in the attention domain.

7.1. Critical features of the SL process

If one or more of the brain regions considered above might be crucial to mediate changes in priority due to SL, a separate question is whether other structures might be specifically responsible for instructing the learning process on the basis of the available statistical information. A key region involved in this process of updating

an internal, predictive model of the external world might be the temporo-parietal junction (TPJ), perhaps mainly in the right hemisphere. Within the realm of attentional processes, TPJ has been sometimes involved in attentional re-orienting (Corbetta and Shulman, 2002), particularly at times of low predictability (Nastase et al., 2014), though this role of TPJ has been questioned (Geng & Vossel, 2013; Nobre & Mesulam, 2014). However, there is also indication that TPJ plays an important role in updating contextual information and setting expectations for attentional control (Geng & Vossel, 2013), not to mention several other contributions made by this structure to cognitive processing of various kinds (Carter & Huettel, 2013; Igelström & Graziano, 2017). Therefore, one possibility is that, within the context of our experiments, TPJ might have mediated the learning of target and distractor contingencies along the experimental session to guide attention accordingly, likely through interactions with brain regions directly responsible for attentional guidance (see above).

Previous studies have indicated that SL of target location occurs relatively rapidly (e.g., Jiang et al., 2013b), with the spatial bias in performance appearing after a few tens of trials. Our results provided further support to this notion. In all the experiments reported here, the spatial bias could be detected after few tens of trials and the pattern persisted more or less unaltered along the entire epoch of SL. Furthermore, the effect persisted during the retest epoch – i.e., in the extinction regimen, after the spatial contingency was eliminated. Therefore, once SL has taken place, it appears that the resulting bias is highly resistant to new statistical information and considerable time is needed to readjust the system to new statistical information (Jiang et al., 2013b). In the future, more effort should be invested in trying to uncover the precise temporal dynamics with which SL of target (and distractor) location takes place, especially to better understand the precise kind of evidence that is needed to update the internal model and adjust the spatial priority maps accordingly.

In the Introduction we have argued for the importance of distinguishing between true effects of SL and the consequences on performance of inter-trial

contingencies. Therefore, we ensured that effects attributed to SL were not contaminated by inter-trial priming. As already noted, the unequal probability of target occurrence across display locations generates an unequal number of immediate repetitions in target location across consecutive trials for the different locations (unless this is avoided by design). Given that inter-trial priming effects are likely to produce changes in performance, it is important to separate this source of bias from the pure effects generated by SL. There is some inconsistency in the literature concerning this point. While in some cases the effects of SL were abolished by constraining target location across consecutive trials, i.e., by eliminating by design immediate repetitions of target location (i.e., Walthew & Gilchrist, 2006), this finding was not replicated in a later study (i.e., Jones & Kaschak, 2012). Here, instead of eliminating immediate repetitions of target location by design, we approached the problem by excluding immediate repetitions from control analyses. By so doing, we could demonstrate that the SL effect is maintained when immediate repetitions are excluded, supporting the view that the effects produced by our target probability manipulation are the genuine consequence of a statistical learning mechanism occurring over the course of the session, reflecting a long-term memory phenomenon independent from inter-trial influences. At the same time, the data demonstrated that inter-trial effects also existed and contributed to the overall performance when immediate repetitions in target location are not eliminated.

It is important to note that, of course, eliminating immediate repetitions still allows for influences resulting from more distant trials in the past, such as N-2, N-3 and so forth, potentially exerting an influence on the current trial according to some decaying function (Maljkovic and Nakayama, 1994; 1996; Hillstrom, 2000). In fact, using paradigms of the kind adopted here, it is simply impossible to equalize selection (or suppression) history across locations, as in the end such history is what contains the applied statistical manipulation. Therefore, while *prima facie* the exercise of purifying SL effects from any influence of inter-trial contingencies appears perfectly correct, the problem is actually more complex than one might first think. The notion of SL aims to account for changes in performance that reflect

the global spatio-temporal statistical structure of events occurring during the course of the experiment, whereas inter-trial effects account for changes in performance that are entirely explained by the "local" contingencies. However, it is also clear that the global and local levels cannot be entirely decoupled, as the former necessarily results from the serial assembly of multiple local episodes (Martini, 2010; Thiessen, 2017). Therefore, a key issue to be clarified in order to fully understand the type of learning phenomenon reported here pertains to the computational level of analysis. More specifically, it will be of major importance to uncover the type of algorithms (heuristics) used by the relevant brain systems to detect the statistical regularities that are relevant in a given behavioral context. Indeed, computational modeling studies have tried to explain in which way the brain infers the statistical structures embedded in the environment to adapt behavior accordingly (Anderson & Carpenter, 2006; Brodersen et al., 2008; Vossel et al., 2014). For instance, a recent study directly compared different models to explain changes in attentional allocation within a location-cueing task where the level of cue validity changed unpredictably over time (Vossel et al., 2014). Even though the participants received no explicit information about the validity transitions, their performance was clearly influenced by the probabilistic context (i.e., the level of cue validity within a series of trials). The results were most plausibly explained by a hierarchical Bayesian model in which attention optimizes the confidence in (or precision of) the inference on sensory input. A similar approach could presumably be used to describe the processes and neural mechanisms involved in the adjustment of spatial priority maps of the kind reported here and we plan to make systematic attempts in this direction.

7.3. Shared neural machinery for target selection and distractor suppression: evidence from direct and indirect SL effects

If the attentional priority of a certain location is altered by the probability with which the target occurs there, then the change should affect processing of any stimulus presented at the same location. Thus, also the attentional capture generated by a salient distractor ought to be modulated according to the

acquired priority of the given location. However, if the mechanisms responsible for target selection and distractor filtering are distinct (e.g., Hickey et al., 2009; Couperus & Mangun, 2010; Noonan et al., 2016), it is reasonable to expect that SL of target location might not exert any influence on distractor processing. Here we directly tested whether SL of target location affects the efficiency of distractor filtering processes. We found that the cost generated by a distractor varied with the spatial probability of the target at each location. The distractor elicited larger costs when shown at the high target probability location relative to the low target probability location, even though the distractor was presented with equal probability across locations. Therefore, the participants' performance was fully consistent with the idea that target selection and distractor filtering depend on at least partly shared neural machinery, likely including the same priority maps of space. An increase in priority brought about by frequent targets at a given location will produce the unavoidable side-effect of increased capture at the same location; likewise, a decrease in priority brought about by rare targets at another location will lead to reduced capture at the same location. Incidentally, as in the case of the direct effects of the target probability manipulation, also the indirect effects on distractor filtering could not be accounted for in terms of inter-trial priming.

In addition to assessing the main features of SL for the target location, we were also especially interested in exploring manifestations of SL induced by manipulating the spatial probability of the salient distractor, as found in previous studies (Reder et al., 2003; Goschy et al., 2014; Leber et al., 2016; Wang and Theeuwes, in press). In Experiment 2, the spatial probability of the distractor was uneven across locations, whereas an even distribution of targets was applied. We found clear evidence of SL, with smaller distractor cost at a high distractor probability location relative to a low distractor probability location, in line with prior studies (Reder e al., 2003; Goschy et al., 2014; Leber et al., 2016; Wang and Theeuwes, in press). Just like for SL of target location, effects of the distractor probability manipulation could not be accounted for solely in terms of inter-trial priming. In numerical terms this direct effect was very similar in magnitude to that

found for SL of target location (see Table 2). Confirming evidence was then obtained in a new experiment, Experiment 3, wherein we independently manipulated the probability of both targets and distractors within the same session.

As already noted, in Experiment 1 (and 3) we observed a propagation of the effects induced by SL of target location to the process of distractor filtering (indirect effect). These results suggest a cross-talk between the two attentional mechanisms. In order to provide further evidence in favor of this notion, we tested whether SL of distractor location similarly generated an indirect effect on target selection. In all experiments in which SL of distractor location was elicited (Experiments 2, 3 and 4), we found some evidence of such indirect effect. Target selection was faster in the low distractor probability location and slower in the high distractor probability location. Although the effect was only marginally significant, if at all, its magnitude was nearly constant across the three experiments (see Table 2). These results again support the view that the same priority maps underlie target selection (prioritization) and distractor filtering (deprioritization) mechanisms. However, the indirect effect generated by SL of distractor location was smaller compared to that generated by SL of target location, indicating some degree of asymmetry. Given the asymmetry, and regardless of its underlying sources, we were initially hesitant to conclude that the indirect effects elicited by SL of distractor location were real.

To more thoroughly assess whether the indirect effects elicited by SL of distractor (but also target) location were real and linked to the direct effects, we performed correlational analyses hinging on inter-individual variability of the two SL effects. We reasoned that, if the two effects were truly linked to one another, then the larger the direct effect in a given participant, the greater should also be the indirect effect in the same participant. Incidentally, variability across participants could reflect a variety of factors, including e.g., a different efficiency of the learning process, a different efficiency with which the learned statistical information can be used to exert attentional guidance, and so forth. At any rate,

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one might expect to find that SL will exert a variable influence on performance across participants, reflected by variable magnitude of the direct effect across participants. If the indirect effect is truly a by-product of the SL manipulation, then we should expect to find a positive correlation between the two effects, with larger indirect effects associated with larger direct effects in the individual participant, and vice versa for smaller direct effects. Correlation analyses confirmed this prediction. For both kinds of SL – that of target location and that of distractor location, the size of the indirect effect was positively correlated with the size of the direct effect. These results eliminate any residual doubt as to the existence of an indirect effect elicited by both kinds of SL, and especially SL of distractor location, and strengthen the notion that target selection and distractor filtering are likely guided by shared neural mechanisms, namely the same priority maps of space.

In sum, we found a tight association between the two forms of SL, yet some differences emerged. Specifically, although the size of the direct effect was comparable across experiments (see Table 2), the indirect effects were different in magnitude across experiments. For SL of target location, we consistently found an indirect effect that was twice as large as that found for SL of distractor location (see Table 2). We ruled out the possibility that such difference in magnitude was due to the different number of learning episodes between the two forms of SL. More specifically, the size of the indirect effect associated with SL of distractor location remained the same even when we almost doubled the SL epoch in Experiment 4. Therefore, it remains unclear what might be the reason for such asymmetry. One could hypothesize that the indirect effects generated by SL of distractor location were weaker compared to those generated by SL of target location because of the stronger impact on spatial priority maps of each episode of target selection compared to distractor filtering, though this possibility seems to be rejected by the observation that the direct effects were of roughly the same magnitude in the two cases. The reason of this asymmetry will therefore have to be firmly established with further experiments and ad-hoc modeling efforts.

7.4. Links to other forms of plasticity in spatial priority maps

An intriguing question concerning the learning-dependent alteration of spatial priority found in this study is its relationship with other forms of acquired spatial bias. In the last decade or so, there has been a surge of interest for exploring the impact of reward on attentional deployment (for reviews, see, e.g., Chelazzi et al., 2013; Anderson, 2016; Bourgeois et al., 2016). In a recent study, Chelazzi et al. (2014) investigated the impact of a monetary reward-based training regimen on the subsequent priority of spatial locations within the context of visual search. During a learning phase, participants performed a visual search task for geometrical shapes and received a monetary reward after each correct response, which could be high or low. Unbeknownst to them, each array location was associated with a different proportion of high vs. low rewards, with different locations associated with greater or smaller probability of high reward. At test, participants performed a different task in which they reported the identity of one or two targets (letters and digits) presented briefly amongst an array of non-targets. Results showed that, when a competition was present (two-target condition), the target stimulus presented at a location associated with higher probability to obtain a high reward during the training phase was more likely reported, presumably because of a higher priority acquired by that location. It will be especially important to directly compare with future studies the effects elicited by SL and reward-based learning. Jiang and colleagues (2015b) directly compared statistical and reward-based learning effects, and they demonstrated substantial differences in the efficacy of the two types of manipulation on spatial attention. Whereas spatial SL of target location produced robust effects, reward-based learning did not yield reliable changes in performance. Especially in view of the latter results, it will be very important to collect further evidence to establish differences and commonalities between probability cueing and reward-based treatments.

7.5. Conclusion

In sum, here we have demonstrated that spatial SL of target and distractor location is a strong source of attentional guidance, likely via plastic changes in one or more priority maps of space. The effects emerged relatively quickly within the learning epoch, they appeared to be location-specific and were robust even when inter-trial effects were controlled for. Importantly, both kinds of SL exerted their influence on attention independently from the participants' explicit knowledge of the applied manipulation; therefore, they can be said to guide attention implicitly. Crucially, the two forms of SL affected performance in a similar way and both were able to generate indirect effects. Such interaction (cross-talk) between target selection and distractor suppression mechanisms suggests at least partly shared underlying mechanisms. However, the indirect effects were asymmetric in size, with relatively stronger indirect effects produced by SL of target location.

Acknowledgements

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