Contrasting attentional biases in a saccadic choice task

Ómar I. Jóhannesson[1, *], Árni Kristjánsson[1,2] & Jérôme Tagu[1,3]

[1] Icelandic Vision Lab, Faculty of Psychology, School of Health Sciences, University of Iceland, Reykjavík, Iceland

[2] School of Psychology, National Research University Higher School of Economics, Moscow, Russian Federation

[3] EA 4139 Laboratory of Psychology, University of Bordeaux, Bordeaux, France

[*] Correspondence concerning this article should be sent to: Ómar I. Jóhannesson, Department of Psychology, University of Iceland, Sæmundargötu 2, 101 Reykjavík, Iceland, e-mail: oij1@hi.is

Conflict of interest

The authors report no conflict of interest

Data Availability

The datasets generated and analysed during the current study will be available from the corresponding author upon request.

Abstract

To gain insight into how human observers select items in the visual field we pitted two attentional biases against one another in a single free choice design. The first bias is the nasal-temporal asymmetry during free choice tasks, where observers tend to choose targets that appear in their temporal hemifield over targets appearing in their nasal hemifield. The second is the choice bias found in studies of attentional priming. When observers have to select between a stimulus that shares features with a preceding target and a stimulus sharing features with previous distractors, they have a strong tendency to choose the preceding search target and this bias increases the more often the same search is repeated. Our results show that both biases affect saccadic choice, but they also show that the nasal-temporal bias can modulate the strength of the priming effects, but not vice versa. The priming effect was stronger for stimuli appearing in the temporal than in the nasal hemifield, but the nasal-temporal bias was similar for primed and unprimed targets. Additionally, our findings are the first to show how search repetition leads to faster saccades. The observed difference between the effects of the NTA and priming biases may reflect the difference in neural mechanisms thought to be behind these biases and that biases at lower levels may outrank higher-level biases, at least in their effect on visual attention.

Introduction

While some objects in our visual field are important for behaviour in the present, others are not. The important objects typically require detailed visual processing and must therefore be projected onto the region with the highest acuity in the fovea. We can achieve this by making a saccade so that our centre of gaze falls on that object. How do we select these items of importance at any given moment? Visual attention serves a critical role in this, cutting down the clutter of irrelevant information, allowing us to focus on what is most important to us at any given time (Bundesen, 1990; Driver, 2001; Kristjánsson & Egeth, 2020). The physical properties of the visual environment (such as luminance) as well as higher order processes (for example our particular goals at a given moment) determine what we attend to and shift our gaze towards.

Interestingly these preferences can be biased by various factors (Desimone & Duncan, 1995; Kristjánsson, 2006) such as the location of the stimuli in the visual field and the identity of the stimuli that we have previously attended to. Here we investigate how such selection biases may interact. We focus on two biases of attention, one that has received renewed interest in recent years involving biases from differences in processing in the nasal and temporal hemifield (see Jóhannesson et al., 2018a for review) and a recently discovered choice bias from the priming of attention shifts (Brascamp et al., 2011; see Kristjánsson & Ásgeirsson, 2019, for review). Our aim is to come to a clearer understanding of these biases and answer questions such as whether they affect the same kind of process or whether they are independent of one another. The results could cast light upon at what levels of processing these selection biases operate and how processing at these different levels may interact.

Nasal-temporal asymmetries in choice

There are anatomical asymmetries between our nasal and temporal hemiretinae (see Jóhannesson et al., 2018a for review) such as asymmetric distributions of photoreceptors and ganglion cells (Anderson et al., 1991; Curcio & Allen, 1990; Osterberg, 1935; Perry et al., 1984). This anatomical asymmetry has been found to be reflected in behavioural effects (for example, Bompas & Sumner, 2008; Bompas et al., 2008; Rafal et al., 1991). To take an example, Posner and Cohen (1980) used a saccadic choice task where their observers were allowed to choose whether to saccade to targets that appeared simultaneously in the nasal or temporal visual hemifield with one of their eyes covered. Observers showed a clear preference for making saccades into the temporal (79%) over the nasal (21%) hemifield, presumably reflecting these anatomical asymmetries (the nasal hemiretina processes information in the temporal visual hemifield, and vice versa for the temporal hemiretina). Overall, Jóhannesson et al. (2018a) concluded in a review of the literature that the anatomical naso-temporal asymmetries (NTAs) cause behavioural asymmetries in

attentional orienting and in saccadic eye movements. For example, Berger and Henik (2000) found that attentional capture from an exogenous precue is stronger towards the temporal than the nasal hemifield. And in Rafal et al. (1991), cueing effects were stronger in the temporal than in the nasal hemifield and Rafal et al. (1989) reported NTAs for the so-called inhibition of return attentional effect.

Eye movements and attention shifts have often been thought to be highly correlated (Deubel & Schneider, 1996; Kowler et al., 1995; Kristjánsson et al., 2001; Rizzolatti et al., 1987; see Kristjánsson, 2011 for review). Hence, behavioural asymmetries have also been observed between the parameters of saccades directed to the nasal and temporal visual hemifields. For example, Honda (2002) found that 6 out of 12 participants responded faster to targets in the temporal hemifield but 2 showed the opposite effect. For the remaining 4 no differences in saccade latency were found between the hemifields. Kristjánsson et al. (2004) found the latency of prosaccades to be shorter when observers made saccades into the temporal, than into the nasal hemifield, but for antisaccades, this was reversed. Moreover, several studies have consistently found NTAs in saccadic peak velocity, that are higher for saccades into the temporal than into the nasal hemifield (e.g., Jóhannesson and Kristjánsson, 2013; Tagu et al., 2018a, 2018b). But, importantly for our purposes, this behavioural NTA has been found both for reactive and voluntary saccades. For example, it has been shown to occur for express saccades (Jóhannesson et al., 2018b; Koller & Rafal, 2019), that are thought to reflect bottom-up eye movement control, as well as for voluntary saccades such as when observers can freely choose which targets to saccade to (Bompas & Sumner, 2008; Bompas et al., 2008; Posner & Cohen, 1980). Note, however that nasal versus temporal differences in saccade latency are not always found (Bompas & Sumner, 2008, Jóhannesson et al., 2012). Saccadic choice tasks are considered to involve the highest level of voluntary eye movement control (see Huestegge et al., 2019), but the nasal/temporal bias in choice most likely reflects a lower-level bias, given the neural mechanisms involved.

Priming of visual search

When observers search for a particular target among distractors in a so-called visual search task, it mimics one of the most important functions of visual attention – the selection of task relevant objects from among the many potential targets in the typically cluttered visual environment. When observers search repeatedly for the same target, their search becomes faster (Maljkovic & Nakayama, 1994) and more accurate (Ásgeirsson et al., 2014; Sigurdardottir et al. 2008). It is as if observers become primed to the target characteristics (see Kristjánsson & Ásgeirsson, 2019 for review). This priming bias seems to be only partly under top-down control (see e.g. Ásgeirsson & Kristjánsson, 2019; Shurygina et al., 2019; Theeuwes & van der Burg, 2011), for example overriding observers' explicit goals. Maljkovic and Nakayama (1994) indeed showed that when observers have searched for a green target on three trials and

know that the target on the next trial will be red, search for the red target is still inefficient. This bias has nevertheless been thought to be adaptive since it can keep our focus on important tasks at any given moment (Kristjánsson & Campana, 2010).

A key study for our purposes was conducted by Brascamp et al. (2011). They investigated the influence of priming in visual search on choices when observers could freely choose a target diamond on "choice" trials following a number of search trials. The observers searched for a singleton target among distractors for a few trials in a row and subsequently judged whether the chosen diamond had a notch at right, left, top or bottom. The more often the same target and distractors in the search were repeated the shorter the search times became (see also Figure 1 in Kristjánsson and Campana (2010) and related discussion). Following such priming "streaks" Brascamp et al. found that attentional priming strongly determined target choice such that observers typically (on around 75% of trials) chose the item (of 2 possible ones) that had the colour of the preceding search target rather than the distractor colour. Conversely, and interestingly, the choice trials also affected response times on subsequent search trials.

Neural mechanisms

One of the interesting benefits of contrasting and comparing different biases of attentional choice is that these biases can reflect different neural mechanisms, potentially allowing insights into how these neural mechanisms may interact. The neural correlates of priming of visual search have been found to be well-known attentional networks in the parietal cortex and in the frontal eye fields (Bichot & Schall, 2002; Brinkhuis et al., 2020; Corbetta & Shulman, 2002; Kristjánsson et al., 2007; Rorden et al., 2011; Scolari et al., 2015), structures that are also involved in the saccade generation network (e.g., White & Munoz, 2011) and with areas connected with the primed feature in each case. On the other hand the neural mechanisms that are thought to be behind the saccadic choice NTA seem to be structural asymmetries in lower-level mechanisms such as in the retina (Curcio & Allen, 1990) that spread across the visual pathways, both through the retinotectal projections to the superior colliculi (Hubel et al., 1975; Itaya & Van Hoesen, 1983; Sylvester et al., 2007; Tigges & Tigges, 1981) and through geniculostriate projections to the LGN and V1 (Connolly & Van Essen, 1984; Toosy et al., 2001; Tychsen & Burkhalter, 1997; Williams et al., 1995; see Jóhannesson et al., 2018a for an overview). To trigger a saccade, both the geniculostriate and retinotectal pathways project to the superior colliculi which are considered to be involved in attentional orienting (Goldberg & Wurtz, 1972), especially as it relates to motor action (Krauzlis et al., 2013). The geniculostriate pathway also projects to other oculomotor structures such as the parietal and frontal eye fields. Overall, although there are differences, there are overlapping structures in the networks involved in priming of visual search and the NTA free choice bias, such as the frontal eye fields and the superior colliculi. This raises the question of whether the attentional biases in these two

effects could be related and might interact, and whether these potential interactions at the neuronal level could be observed in behavioural performance.

Current aims

While both priming and anatomical nasal/temporal differences lead to choice biases, there are some unanswered questions. Firstly, we do not know whether choice biases from priming (as in Brascamp et al., 2011) also occur for a saccadic choice task (no saccades were required in Brascamp et al. 2011). Secondly, we do not know how – or if – these two types of biases interact or modulate one another. This question is interesting since the two choice biases are thought to reflect the operation of different functional mechanisms and different neural systems. So, the second question is which bias will be stronger when their influence is contrasted. Or might performance even reflect some form of averaging of the two? If the primed colour appears in the temporal hemifield, then both biases should favour the same choice. But the more interesting question is what happens when they are in conflict such as when the primed target is in the nasal hemifield presumably leading to a bias towards the nasal hemifield but the NTA bias favours the temporal hemifield. We attempted to answer this question by pitting the two biases against each other in a single design.

What might happen when these two biases are contrasted? If the two biases are independent from one another and observed separately, then the priming effects would be of similar magnitude in the temporal and nasal hemifields, and the NTA-free-choice bias would be similar for primed and unprimed targets. Conversely, if the two biases interact with one another, then the magnitude of the priming effect might differ for the nasal and temporal hemifields, and the magnitude of the NTA-free-choice bias might differ for primed and unprimed targets. It is also possible that one of the two biases would be stronger than the other and would "erase" the weaker bias. For example, if the NTA-free-choice bias were stronger than the priming bias, we may observe a preference for temporal targets in all conditions, with no or weak priming, and vice versa if the priming effect were stronger.

Our basic paradigm was based on Brascamp et al. (2011). Observers performed a visual search for an oddly coloured disk (green or red) among two disks of the other colour (a task introduced by Bravo & Nakayama, 1992) with one eye closed with an eye-patch to ensure that the stimuli appeared either in observers' temporal or nasal hemifield (in binocular conditions, the nasal hemifield of one eye is the temporal hemifield of the other eye). We contrasted two sets of trial blocks – a *priming sequence* where the same search (e.g., red disk among green disks or vice versa) was repeated 2, 4 or 6 times before a *choice* trial, and a *switch sequence* where the search type always switched between trials (again 2, 4 or 6 trials) before the choice trial. In both conditions, the choice trial involved two targets, one in the nasal hemifield and the other in the temporal hemifield, one had the colour of the preceding target and the other

had the colour of the preceding distractors. Observers were told that they should make a saccade to either target and could freely choose which one they made a saccade to. We also measured baseline NTAs in a standard saccadic choice task without any priming manipulations.

Methods

Ethics

All aspects of the experiment were in line with the requirements of the local ethics committee and conformed to the ethical guidelines set out in the Declaration of Helsinki for testing human participants. All participants provided written, informed consent before they participated in the experiment.

Participants

There were 14 participants (12 females). Their average age was 24.1 years (SD = 2.4 years). All were students at the University of Iceland and received course credits for participating. All participants wore an eye patch over their left eye[1], so that the stimuli in the left and right visual hemifields were projected into the nasal and temporal hemifields, respectively.

Equipment

The movements of the right eye were tracked at 500 Hz with an EyeLink 1000+ (SR Research, Ontario, Canada). The stimuli were presented on a 24 inch monitor (model XL2411Z, BenQ, Taipei, Taiwan) with a resolution of 1920 x 1080 pixels running at 144 Hz. The distance from the eye to the screen was 57 cm. The computer used to control stimulus presentation had an "Intel Core i7" 4 GHz processor and 8 GB RAM running Windows 7 Professional 64-bit. PsychoPy (Peirce & MacAskill, 2018; Peirce et al., 2019) was used for programming the experimental displays. Head movements were restricted with a head and chin rest. We used the ColorCAL MKII colorimeter from Cambridge Research Systems to measure the CIE chromaticity coordinates (x, y) and luminance (Y) of the screen and stimuli.

Stimuli

The fixation stimulus in all parts of the experiment was a white dot (0.3 degrees of visual angle (dva) in diameter; x = 0.307, y = 0.295, Y = 47.290 cd/m^2) presented at screen centre on a black background (x = 0.271, y = 0.266, Y = 0.094 cd/m^2). All other stimuli had a diameter of 1 dva and appeared

[1] Past evidence has shown no left-right asymmetry in saccades that could potentially affect performance at a saccade choice task (see, e.g., Honda, 2002; Tagu, Doré-Mazars, & Vergilino-Perez, 2020; Vergilino-Perez et al., 2012), so although we only covered the left eye, we are quite confident that the left-right differences we observe in the current study reflect naso-temporal asymmetries in choice.

simultaneously with the disappearance of the fixation stimulus. The stimuli on the free choice trials (see Figure 1A) were white dots (x = 0.307, y = 0.295, Y = 47.290 cd/m^2), while the stimuli on the choice trials that were preceded by priming trials and switch trials were red (x = 0.645, y = 0.322, Y = 11.022 cd/m^2) and green (x = 0.309, y = 0.559, Y = 17.466 cd/m^2; Figure 1B)[2]. On all the choice trials the two stimuli appeared simultaneously at 8 dva to the left and right of the fixation stimulus. On half of the priming and half of the switch trials (that appeared before choice trials, see Figure 1B) one of the three stimuli was green (the target) and the two others were red (the distractors) while on the other half, this was reversed. The stimuli on the priming and switch trials were presented 8 dva away from the fixation stimulus, equally spread around an imaginary circle with an angle of 120° between them (see Figure 1B). These stimuli were randomly rotated by 45° around the fixation stimulus, always appearing 8 dva away from the centre of the screen but never on its horizontal meridian. This was to prevent stimuli from the search trials from potentially priming the locations of the choice stimuli.

[2] Although the difference in the luminance of the red and green stimuli is considerable it could not have affected the results because the distributions of the colours were perfectly balanced between all conditions in the experiment.

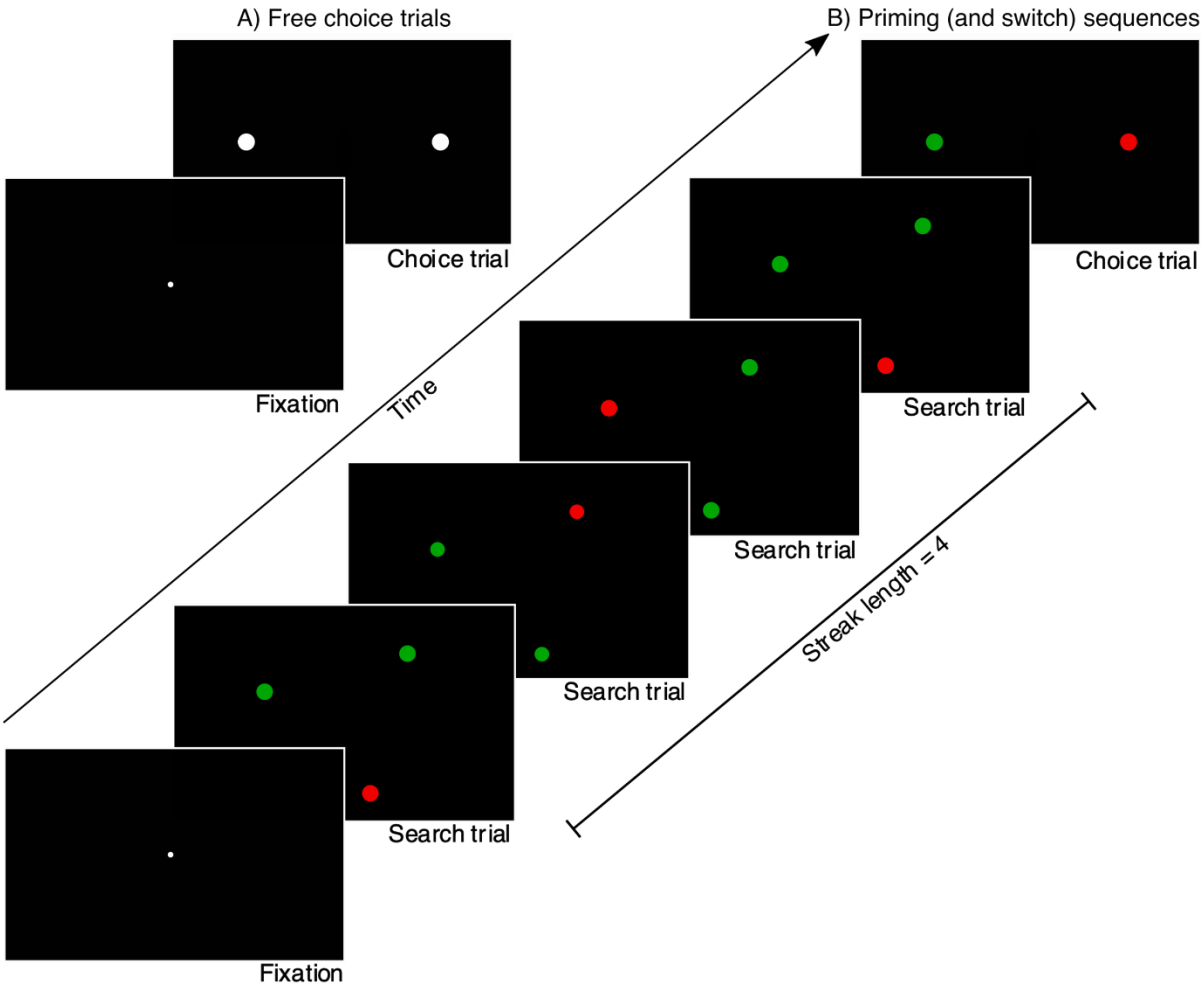

Fig. 1 *The experimental procedure. Panel A shows the procedure on the free choice trials. Panel B shows an example of a priming sequence, in this case with a streak length of 4. The switch sequences were similar with the exception that the target and the distractors swapped colours between each presentation. The size of the fixation dot was 0.3 dva and the size of all other stimuli was 1 dva. In the priming/switch trials the stimuli were randomly rotated in 45° steps (not shown in the figure) around the centre (radius = 8 dva) but they were never located on the horizontal meridian to prevent any potential influence of spatial priming from the priming and switch trials. See text for details.*

Procedure

General. Each session began with a 9-point calibration filling the screen. The experiment consisted of three main conditions: free choice trials (30 in 1 block), priming sequences and switch sequences (12 priming and 12 switch sequences in 4 blocks). The priming and the switch sequences consisted of one streak of priming trials (or one set of switch trials) and one choice trial. On the priming trials in the priming sequences, the colour of the target (e.g. red) and of the distractors (e.g., green, see Figure 1B) was kept constant for 2, 4 or 6 repetitions (i.e. the *streak lengths* were 2, 4 or 6). At the end of each streak of priming trials, a choice trial was presented. Therefore, one streak of priming trials and one choice trial

constitute a *priming sequence*. In the *switch sequences*, the structure was similar with the exception that the target-distractor colour combinations were always switched from one trial to the next. The switch sequences consisted of a *switch set* of 2, 4 or 6 trials after which a choice trial was presented. Priming and switch sequences were divided into 4 blocks composed of 4 repetitions of each of the 3 streak lengths of the priming sequences and 4 repetitions of each of the 3 switch sequences. The type of sequence (priming or switch) and the length of the sequences (2, 4 and 6) were randomly interleaved within each block. Participants could take a short break between the blocks, and a 9-point calibration procedure was executed before each block.

All trials began with the onset of a central fixation spot that was visible for a random period between 800 and 1400 ms. During this period, the system monitored fixation, and the participant was informed with an error message if fixation fell outside the boundaries (2 dva in diameter) around the fixation spot, and the fixation period was repeated, after which the stimuli were presented. On all trial types the maximum selection time was 2 secs and if the participant did not respond within this time limit the next trial was initiated. Before running the experiment, the experimental procedure was explained, and the participants were told that on all choice trials that they should saccade to one of the two stimuli that appeared on the screen and that they were free to saccade to the one they chose.

Free choice trials. After the fixation stimulus disappeared, two white dots appeared simultaneously, one in the nasal hemifield and the other in the temporal hemifield. The participants were told to saccade to the stimulus of their choice. Note that in this condition, neither the stimulus in the nasal or temporal hemifield was designated as the target.

Priming trial sequences. During the priming trials the target and distractor colours were constant within each streak length, and were repeated 2, 4 or 6 times. On half of the trials and for all streak lengths, the distractor colour was green, and the target was red (an *odd-one-out search*). For the other half of trials, this was reversed. The participants were told to saccade to the odd-one-out target as quickly and accurately as possible. At the end of each streak the choice stimuli were presented, one red and the other green. On half of the choice trials the stimulus was green in the nasal hemifield and red in the temporal hemifield. For the other half, this was reversed. Importantly, on half of the choice trials, the *primed* target appeared in the nasal hemifield and in the other half in the temporal hemifield. The primed stimulus therefore appeared in the nasal hemifield on 50% of the choice trials and in the temporal hemifield on 50% of the choice trials.

Switch trial sequences. The switch trial sequences were similar to the priming trial sequences (i.e. the length of the sequences was 2, 4 and 6 and below we refer to this as *number of switches*) with the exception that the colours of the stimuli were changed between each presentation. As such, in the switch trial sequences participants were only primed with 1 presentation, i.e., the colour of the target from the

last switch trial before the choice trial (see Kristjánsson et al., 2002 and Maljkovic & Nakayama, 1994; for examples of such 'switch' manipulations).

Data analyses

In our analyses, there were two main dependent variables, both based on data from the choice trials. The first one was the "priming proportion", a measure of the priming effect, that corresponded to the percentage of trials where the primed target (rather than the unprimed one) was selected, separately for each hemifield. In other words, the priming proportion is a measure of how often the chosen stimulus was a target on preceding search trials. The second main dependent variable was the "temporal proportion", which in contrast is a measure of the naso-temporal asymmetry and corresponds to the percentage of trials where the target in the temporal hemifield (as opposed to the one in the nasal hemifield) was selected, separately for primed and unprimed targets. In other words, the temporal proportion is a measure of how often the chosen stimulus was the one that was presented in the temporal hemifield.

We also analysed the selection times. Selection time refers to the time from when the display (priming, switch or choice trial) appeared until the participants' gaze entered a predefined boundary around the target (or the selected stimulus on the choice trials). The diameter of the boundary around the stimuli was 2 dva. The main factors on the choice trials were hemifield (nasal and temporal), streak lengths/number of switches (2, 4 or 6) and whether the colour of the selected stimulus was the same as on the preceding priming/switch trial (i.e. whether the selected stimulus was primed or not). In all analyses, we used the R statistical program (R Core Team 2017) running within the RStudio environment (RStudio Team 2017). To assess the significance of any differences between selection proportions for the nasal versus temporal hemifield on the free-choice trials we used paired *t*-tests[3] (R Core Team 2017). In all other selection analyses we used the glmer() function from the lme4 package (Bates et al. 2015) with random effects of participant on the intercept. When analysing the selection times we used the lmer() function (Bates et al. 2015) with random effects of participant on the intercept. When assessing the significance of any differences between levels of the relevant factors, we used the sliding contrasts (the contr.sdif() function of the MASS package; Venables and Ripley 2002), thus, avoiding the need for post-hoc tests. Before analysing data from each condition, we removed trials with no responses and with selection times that deviated more than ± 3 SD from the mean.

[3] It is not possible to use glmer() here, because there is no grouping variable that can be used as factor.

Results

Before analysing the data, we removed trials with no responses (i.e. selection times longer than 2000 ms; 32 of 7140 trials or less than 0.01%). It is common to exclude saccades with latencies shorter than 80 ms because they are considered to be anticipatory (see e.g. Bompas et al. 2008; Delinte et al. 2002; Fischer and Weber 1992). Our measure of the saccadic responses includes the duration of the saccades. We therefore removed trials where the selection times were shorter than 80 ms (7 of 7140 or less than 0.01%).

Naso-temporal asymmetry on choice trials

Free choice trials. For the choice trials, we removed 6 trials (1.3%) where selection times were outside our criteria. On the remaining trials the participants selected the temporal and nasal hemifields on 62% and 38% of the trials, respectively, see Figure 2a. This difference of 24 percentage points was significant (paired-$t(13) = -2.57$, $p = .023$). When looking at individual differences we found that one participant selected the nasal hemifield stimuli more often than the temporal hemifield stimuli, two selected the hemifields equally often. The remaining 11 participants selected the temporal hemifield more often than the nasal hemifield, including two individuals who only selected the temporal hemifield.

Choice trials within priming sequences. We removed 13 trials with selection times outside our criteria (1.9%). After this removal, the selection proportion for the temporal hemifield was 56.9% (43.1% for the nasal hemifield, see Figure 2a). In the logistic random effect regression model the dependent binominal variable was whether the temporal hemifield was selected (1) or not (0) and the factors were hemifield (i.e., whether the primed colour appeared in the temporal or nasal hemifield) and streak length (2, 4 and 6). The difference between the hemifields was significant ($p < .001$). For streak length 2 the temporal hemifield was selected on 59.1% of trials and 52.3% for streak length 4 (the difference between streak lengths was not significant, $p = .123$). For streak length 6 temporal hemifield stimuli were selected on 59.3% of trials, significantly higher than for streak length 4 ($p = .045$). The interaction between hemifield and streak length was not significant (both ps > .11). One participant selected stimuli in each hemifield equally often, three selected nasal hemifield stimuli more frequently than temporal hemifield stimuli but all other participants selected temporal stimuli more often than nasal ones. For more detailed information about the results see Table A1 in appendix A.

Choice trials within switch sequences. Trials with selection times outside our criteria were 13 (1.9% of the total trials). After removing the 13 trials the selection proportions for the temporal and the nasal hemifield were 60% and 40%, respectively, see Figure 2a. Because the number of switches is irrelevant to the main questions, we only analysed the effect of hemifields and found that the above reported difference was significant ($p = .034$). Four participants selected the nasal hemifield stimulus more often than the stimulus in the temporal hemifield, but other participants selected the temporal hemifield stimuli more often than the nasal ones.

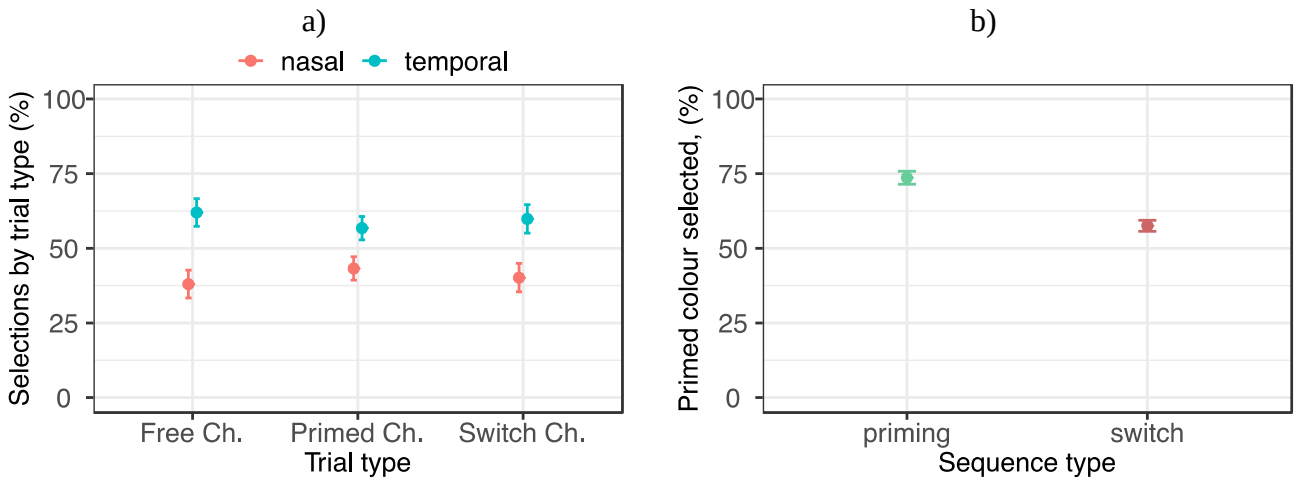

Fig. 2 *Selection proportions. Panel* ***a*** *shows the selection proportions for the hemifields as a function of choice trial types. Note that on the free choice trials (Free Ch.) no priming occurred before the two stimuli were presented. On the primed choice trials (Primed Ch.) one of the colours had been presented 2, 4 or 6 times on the previous priming trials and on the switch trials (Switch Ch.), the chosen colour had been presented only once. Panel* ***b*** *shows the selection proportions following the priming and switch sequences. See main text for further details. The error bars show the within-condition SEMs.*

All choice trials. To assess the differences between choice trial types, we combined the choice trials and analysed the data with logistic random effects regression. In this model the dependent variable was – as before – whether the temporal hemifield was selected or not. The factor was choice trial type (free choice, primed choice and switch choice), but no significant differences were found (both *p*s > .09; see Figure 2a).

Priming effects on choice trials

Priming effects. To assess the effect of priming, *per se*, independent of hemifield and repetitions, we contrasted selection ratios of the primed colour between the choice trials of the priming and switch sequences. In these, and the following analyses, we coded the number of switches on the switch choice trials as streak length 1 (on these trials, priming was induced with the colour of the target from the last switch trial before the choice trial) and did not use the data from the free choice trials because these trials were not preceded by any search trials (see figure 1A). The selection *proportion* for the primed colour on the primed choice trials was 73.6% but 57.6% on switch choice trials (see Figure 2b). A random logistic regression with trial type as factor and selection *proportions* as dependent variable revealed a significant difference ($p < .001$).

Priming temporal and nasal hemifields. To investigate the effect of hemifield and streak length on priming we ran a logistic regression where the dependent variable was whether the primed colour (i.e., the last observed colour) was selected (1) or not (0) with hemifield (nasal and temporal) and streak length as factors (1, 2, 4 and 6). The results showed that the difference between hemifields was significant ($p < .001$) meaning that the primed colour was selected more often in the temporal than the nasal hemifield.

Note however that for both hemifields, the selection proportions are very similar for streak length 4 (see Figure 3). The difference between streak length 1 (the data from the switch choice trials) and 2 was significant (p = .008) but no other differences between the different streak lengths were significant (both ps > .16). Although the effect of streak length does not significantly increase after streak length 2, Figure 3 shows that the effect of streak length 4 is similar to the effect of streak length 2 and the effect of streak length 6 is numerically larger than of streak length 4. This indicates that the effect of streak lengths 4 and 6 differ significantly from streak length 1. No interaction effects were significant (all ps > .057). What figure 3 reveals in other words, is that the primed target was selected significantly more often in the temporal hemifield than in the nasal one. This indicates that the priming effect is stronger in the temporal than the nasal hemifield, but the results also show that the time course of the priming as a function of search repetitions is similar within both hemifields (Figure 3). For more detailed information about the results see Table A2 in appendix A.

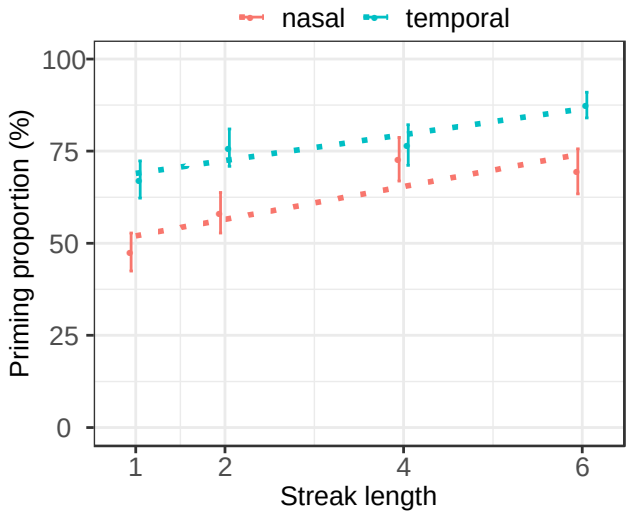

Fig. 3 *Selections of the primed colour. The figure shows the selection proportion of the primed colour as a function of hemifield and streak length. The cyan data show the proportion of all the choice trials where the temporal stimulus was chosen, which corresponded to the primed stimulus. Similarly, the magenta data show the proportion of all the choice trials where the nasal stimulus was chosen, which corresponded to the primed stimulus. Note that when the primed colour was not selected, the unprimed colour in the same hemifield was selected. The dotted lines represent linear fits, and the error bars represent the within-condition SEMs*

Free choice bias for primed and unprimed colours. To assess whether priming affects the NTA free choice bias we ran a logistic regression with selected hemifield (temporal = 1 and nasal = 0) as the dependent variable and streak lengths (1, 2, 4 and 6; streak length 1 involves the switch choice trials) and whether the selected stimulus had been primed (1) or not (0) as factors. Neither the effects of priming (p = .061) nor streak length were significant (all ps > .058) and no interaction was significant (all ps > .32). This is illustrated in Figure 4. We note that in Figure 3 the priming patterns for streak length 4 deviate from the general pattern in that figure and in Figure 4, the deviation is even larger but the reasons for this are unknown. In other words, Figure 4 shows that the NTA free choice bias (observed in Figure 2a) seems to be similar for both primed and unprimed targets and does not change as a function of search repetitions. For more detailed information about these results see Table A3 in appendix A.

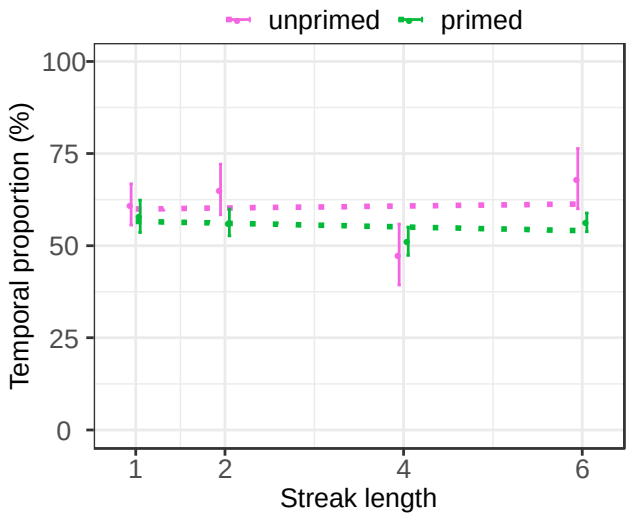

Fig. 4 *Selections of the temporal stimulus. The figure shows the selection proportions for temporal hemifield stimuli as a function of the streak length (i.e., repetitions of the same preceding search type). The purple data show the proportion of all the choice trials where the unprimed stimulus was chosen, which corresponded to the temporal stimulus. Similarly, the green data show the proportion of all the choice trials where the primed stimulus was chosen, which proportion corresponded to the temporal stimulus. Note that when the primed colour in the temporal hemifield was not selected, the primed colour in the nasal hemifield was selected (and vice versa for the unprimed colour). The dotted lines represent linear fits, and the error bars represent the within-condition SEMs.*

Selection times on choice trials

Free choice trials. The average selection time for the nasal hemifield was 299 ms (SD = 108 ms) while for the temporal hemifield it was 293 ms (SD = 120 ms). The difference was not significant (t = 0.834). The dependent variable in the random effects model was the selection time with selected hemifield (nasal or temporal) as factor.

Choice trials in priming sequences. The average selection times for the nasal hemifield were 348 ms (SD = 87 ms) and 342 ms in the temporal hemifield (SD = 98 ms). The differences as a function of hemifield and streak length were small (< 10 ms) and no effects were significant (all ts <= 0.6). In the random effects model the selection times were the dependent variable with hemifield and streak length as factors.

Choice trials in switch sequences. The selection times in both hemifields were the same (359 ms) but the SD for the nasal hemifield was 88 ms while for the temporal hemifield it was 109 ms. A similar random effects model as before revealed no significant effects (all ts < 1.0).

Combined choice trials. The final step in the analyses of the selection times on the choice trials was to compare selection times between trial types (see Figure 5, panel a). The results from a random effects model with selection times as the dependent variable and contrast coded hemifield and trial type showed that the main effect of hemifield was not significant (t = – 0.55). The selection times were significantly longer for the primed choice than the free choice trials (t = 7.82) and the selection times on the switch choice trials significantly longer than for the primed choice trials (t = 2.56). The interactions between hemifield and trial type were not significant (both ts <= 0.7).

Selection times on search trials as a function of search repetition

We also analysed selection times on search trials as a function of search repetition. When we analysed data from search trials within our priming sequences, the choice trials were excluded, and we used a

random effects model with selection time as the dependent variable and contrast coded streak length (or number of repetitions) as factors. Before analysing the selection times, we removed 51 trials (1.9%) that were outside our criteria. The average selection times were 366 ms (SD = 104 ms). When comparing the selection times between streak lengths we found that they were significantly shorter between streak lengths 4 and 6 (t = – 2.83) but not between streak lengths 2 and 4 (t = 0.05), see Figure 5, panel b. We also looked at the effect of repetitions within each streak length and in the whole data set[4]. For streak length 2 the selection times were significantly shorter (t = – 3.47) when observers responded to the second presentation than the first one. For streak lengths 4 and 6 we found no significant effects of repetition (all ts <= |1.56|).

In the whole primed data set we found that the selection times were significantly shorter when observers responded to the second presentation (t = – 2.88) than the first presentation and when they responded to the fifth presentation compared to the fourth one (t = – 2.25). No other differences were significant (all other ts <= |1.16|), see Figure 5, panel c. We also compared the average selection time within each streak length against the estimated average selection time (the intercept) and found that it was significantly reduced in all streak lengths with respect to the estimated mean (all ts > 2.6). In sum, we found a small but consistent and significant decrease in selection times the more often the same search was repeated.

Selection times on search trials within switch sequences

For this analysis, we excluded the choice trials and used a random effects model with selection times as the dependent variable and used the contrast coded numbers of switches (2, 4 and 6) as factor. On the switch trials, the colour of the target constantly changed between search trials, so there were no actual repetitions. We removed 50 trials (1.9% of the data) that were outside our criteria and after that the average selection time was 389 ms (SD = 115 ms). When the number of switches was 2 the average selection time was 378 ms (SD = 118 ms), when they were 4, the average selection time was 398 ms (SD = 116 ms) and when the number of switches was 6, the average selection time was 388 ms (SD = 113 ms). The difference between 2 and 4 switches was significant (t = 3.15) and also between 4 and 6 switches (t = – 2.20), see Figure 5, panel b. Although these differences were significant, they are hard to interpret as they go up and then down as a function of the number of switches in each set.

[4] When the effects of repetition in the whole data set are measured, it is important to note that the same colour combination is repeated twice, occurring in each of the three streak lengths; 4 repetitions occur for streak lengths 4 and 6 repetitions occur only when the streak length is 6. Therefore, there is more data behind 2 repetitions than 4 and more data behind 4 repetitions than 6 repetitions.

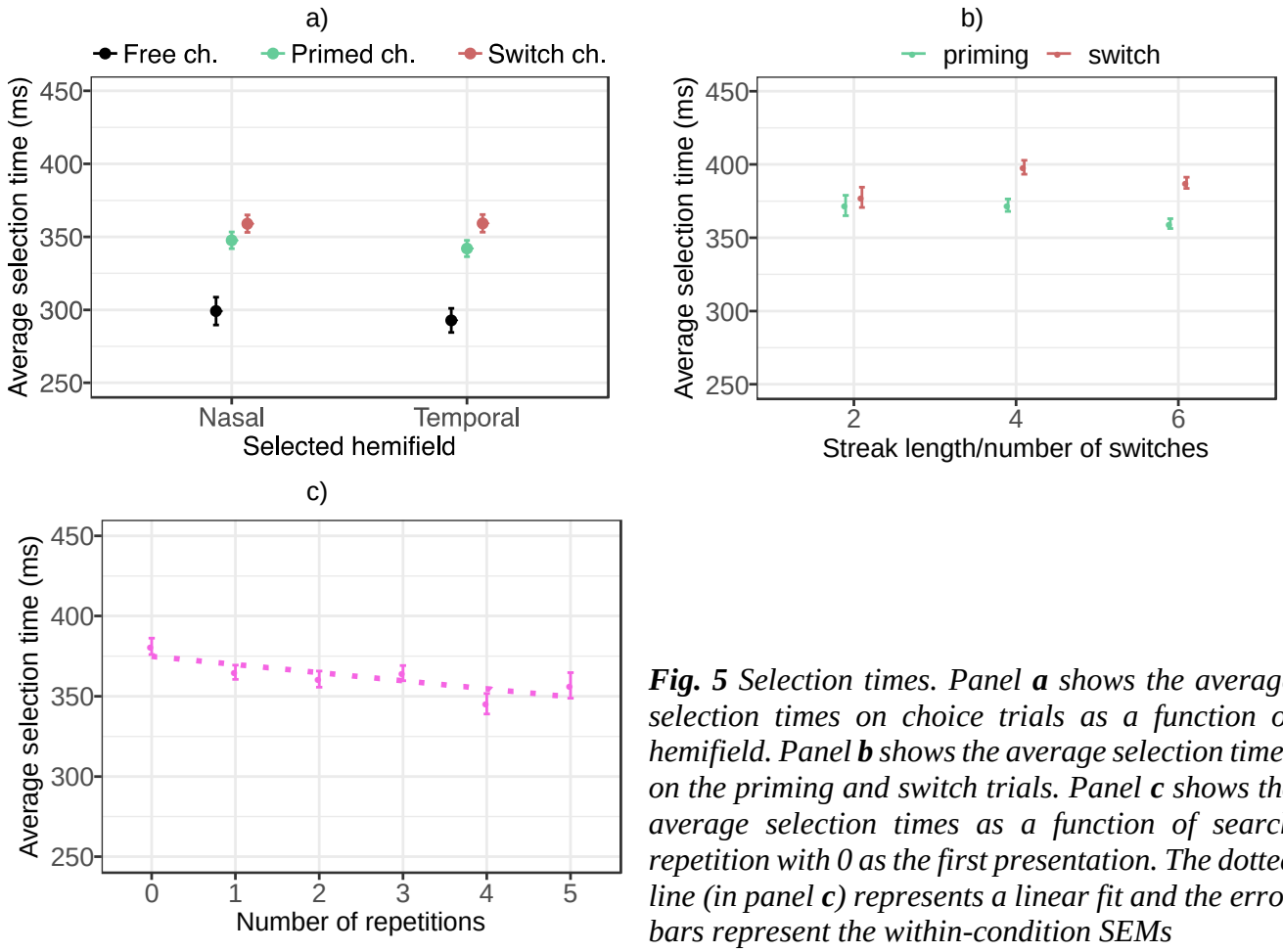

Fig. 5 *Selection times. Panel* ***a*** *shows the average selection times on choice trials as a function of hemifield. Panel* ***b*** *shows the average selection times on the priming and switch trials. Panel* ***c*** *shows the average selection times as a function of search repetition with 0 as the first presentation. The dotted line (in panel* ***c****) represents a linear fit and the error bars represent the within-condition SEMs*

Discussion

We pitted two attentional selection biases against each other, the nasal/temporal free choice bias and the priming bias. To this aim, we used a simple design where search trials that were used to induce priming effects were interleaved with choice trials. Importantly, the results in the free choice condition replicated the standard NTA free-choice bias: when participants had to choose between two perceptually identical stimuli, one in the temporal and one in the nasal hemifield, they were more likely to choose the stimulus in the temporal, than in the nasal hemifield as found in previous experiments (Bompas & Sumner, 2008; Bompas et al., 2008; Posner & Cohen, 1980). Moreover, when we contrasted the choice trials from the priming sequences and switch sequences, we replicated the standard priming bias, i.e., observers were overall more likely to choose the colour that had been primed than the unprimed colour, which is consistent with the choice-from-priming findings of Brascamp et al. (2011). Their result was consistent with the general finding that repeated ("primed") targets are found more quickly and accurately than unprimed targets (Ásgeirsson et al., 2014; Maljkovic and Nakayama, 1994; Sigurdardottir et al., 2008). Notably, our results go beyond those of Brascamp et al. in that the priming bias was also seen in a task

that required saccadic eye movements. This means that repetition of search determines saccade selection of targets that observers are free to select between. We also found that saccadic selection time decreased as the same search was repeated. This reinforces the conclusions of McPeek et al. (1999) and Shurygina et al., (2019) who found that repeated search in a pop-out search task speeded saccades, arguing that this decrease in selection time reflects that saccades are facilitated by a short-term memory system, in line with the implicit short-term memory system proposed by Nakayama et al. (2004).

When studied separately, we therefore overall replicated the two standard biases (Figure 2). Note that this replication of the standard biases was an important and necessary step before testing our main question, namely whether the two biases compete and modulate each other when they are studied simultaneously. Specifically, our results show that when the two biases are studied simultaneously, the NTA free choice bias modulates the priming bias. Indeed, although the NTA free choice bias in selection proportion was observed on choice trials from all conditions and did not differ for primed and unprimed colours (Figure 4), the priming effect depended on which hemifield the target appeared in (Figure 3). In other words, our results importantly show that the priming effect is modulated by the NTA (i.e., the two best-fit-lines in Figure 3 are significantly different) while there is no evidence that the NTA free choice bias is modulated by the priming effect (i.e., the two best-fit-lines in Figure 4 are not significantly different).

At the neural level, the modulation between the two biases could reflect activity in common structures in their neurophysiological bases, such as the superior colliculi or frontal eye fields. The NTA free choice bias is thought to reflect asymmetries found very early in the visual system between inputs from the nasal and temporal hemiretinae (Curcio & Allen, 1990) that spread across the visual pathways and oculomotor network (see Jóhannesson et al., 2018a, for review). On the other hand, the priming bias probably does not involve such early visual structures, as its neural correlates mainly involve parietal and frontal structures (Brinkhuis et al., 2020; Corbetta & Shulman, 2002; Kristjánsson et al., 2007; Rorden et al., 2011; Scolari et al., 2015; Westerberg et al., 2020). As such, we may speculate that when the priming bias is introduced in the visual system, the NTA bias has already had its influence. Input from the nasal hemiretina (i.e., visual information from the temporal hemifield) is therefore favoured. Timing differences in the neural correlates of the two attentional biases might explain why we found that the priming bias depends on whether the stimuli are in the temporal or nasal hemifield, but that the NTA free choice bias appears to be independent of whether the stimulus colour had been primed or not.

One might however wonder why such timing differences in neural correlates would not induce differences in saccadic response times. Indeed, the analysis of selection times in choice trials revealed only a priming effect, where the saccadic latencies were shorter for primed choice trials than for choice trials in switch sequences, but there was no latency difference between saccades directed to nasal and

temporal stimuli. Note however that many studies have failed to observe any NTAs in saccade latency (e.g., Bompas et al., 2008; Honda, 2002; Jóhannesson et al. 2012; Rafal et al., 1991; Tagu et al., 2018a, 2018b), and the only studies reporting consistent NTAs in saccade latencies have involved express saccades (Jóhannesson et al., 2018b; Koller and Rafal, 2019). The absence of NTA in the latency of other saccade types is thought to reflect the fact that the NTA is masked by the numerous top-down influences that affect saccade latencies (see Galley, 1989; Bompas et al., 2008; Jóhannesson et al., 2018a; Tagu et al., 2018a for similar interpretations). Note that attentional priming is here assumed to be one aspect of these top-down influences. In other words, our results suggest that although the NTA choice bias seems to win over the priming bias on selection *proportions*, the relation seems to reverse for selection times where the priming bias overrides the NTA free choice bias. Overall, this indicates that the saccade latency results may reflect different processing levels than the asymmetry in choice.

Conclusions and future directions

Here we asked, firstly, whether choice biases from priming (as were found in Brascamp et al., 2011) also occur for a saccadic choice task. We found that observers chose to saccade to the primed target on 65.6% of trials. Secondly, we asked how the choice bias from priming would interact with the NTA in choice observed in many previous studies (see Jóhannesson et al., 2018a for review). While we replicated the standard NTA free-choice bias in that observers preferred to saccade to temporal hemifield targets, we also found that the NTA free choice bias interfered with the priming bias. Although the nasal-temporal asymmetry in saccadic choice tasks was observed on choice trials from all conditions, the priming effect depended on which hemifield the choice target appeared in, being stronger for stimuli in the temporal hemifield.

Finally, we conclude that the free choice bias modulates the priming effect but that priming does not seem to significantly modulate the free choice bias. If there were no free choice bias, the primed colour would be selected equally often in the nasal and the temporal hemifield. But as Figure 3 clearly shows, that is not the case. The primed colour is selected significantly more often in the temporal, than in the nasal hemifield. This suggests that the free choice bias adds to the priming effect in the temporal hemifield. However, it seems that the converse does not hold: priming effects do not seem to significantly modulate the free choice bias because the selection of the temporal hemifield is not affected by priming as Figure 4 shows. Importantly, we have therefore identified an asymmetric relationship between two attentional biases, that co-exist and compete with each other, presumably both at the neural and behavioural levels. Attentional biases are however known to show individual differences at the behavioural level (for a review, see e.g., Jóhannesson et al., 2018a). Now that we have cast light on how NTA free choice and priming biases are related, future studies involving larger samples may investigate

whether individual differences in NTA free choice bias could modulate the priming bias, and vice versa. Moreover, future studies may address potential competition with other attentional biases, such as whether spatial priming biases (Kristjánsson & Ásgeirsson, 2019) and biases towards previously attended locations in the visual scene (Jonikaitis, Klapetek & Deubel, 2017) interact with the NTA free-choice and (feature) priming biases. Here, we wanted to focus on the competition between NTA free choice and priming biases, and our paradigm was therefore designed to avoid any spatial priming (i.e., stimulus locations of search and choice trials never coincided). Hence, future work may examine whether spatial priming also modulates the NTA free-choice bias and the (feature) priming bias.

References

Anderson SJ, Mullen KT, Hess RF (1991) Human peripheral spatial resolution for achromatic and chromatic stimuli: limits imposed by optical and retinal factors. J Physiol 442(1):47–64. http://doi.org/10.1113/jphysiol.1991.sp018781

Ásgeirsson ÁG, Kristjánsson Á (2019) Attentional priming does not enable observers to ignore salient distractors. Visual Cogn 27(5-8):595-608

Ásgeirsson ÁG, Kristjánsson Á, Bundesen C (2014) Independent priming of location and color in identification of briefly presented letters. Atten Percept Psychophys 76:40-48

Bates D (2010) lme4: mixed-effects modelling with R. http:// lme4.r-forge.r-project.org/book/

Berger A, Henik A (2000) The endogenous modulation of IOR is nasal-temporal asymmetric. J Cogn Neurosci 12(3):421-428

Bichot NP, Schall J D (2002) Priming in macaque frontal cortex during popout visual search: feature-based facilitation and location-based inhibition of return. J Neurosci 22(11):4675–4685

Bompas A, Sumner P (2008) Sensory sluggishness dissociates saccadic, manual, and perceptual responses: An S-cone study. J Vis 8(8):1–13

Bompas A, Sterling T, Rafal RD, Sumner P (2008) Naso-temporal asymmetry for signals invisible to the retinotectal pathway. J Neurophysiol 100(1):412–421

Brascamp JW, Blake R, Kristjánsson Á (2011) Deciding Where to Attend: Priming of Pop-Out Drives Target Selection. J Exp Psychol Human 37(6):1700–1707. http://doi.org/10.1037/a0025636

Bravo MJ, Nakayama K (1992) The role of attention in different visual-search tasks. Percept Psychophys 51(5):465–472

Brinkhuis MA, Kristjánsson Á, Harvey BM, Brascamp, JW (2020) Temporal Characteristics of Priming of Attention Shifts Are Mirrored by BOLD Response Patterns in the Frontoparietal Attention Network. Cereb Cortex 30(4):2267–2280

Bundesen C (1990) A theory of visual attention. Psychol Rev 97(4):523

Connolly M, Van Essen, D (1984) The representation of the visual field in parvicellular and magnocellular layers of the lateral geniculate nucleus in the macaque monkey. J Comp Neurol 226(4):544–564

Corbetta M, Shulman GL (2002) Control of goal-directed and stimulus-driven attention in the brain. Nature Rev Neurosci 3(3):201–215

Curcio CA, Allen KA (1990) Topography of ganglion cells in human retina. J Comp Neurol 300(1):5–25

Delinte A, Gomez C, Decostre M, Crommelinck M, Roucoux A (2002) Amplitude transition function of human express saccades. Neurosci Res 42:21–34

Desimone R, Duncan J (1995) Neural mechanisms of selective visual attention. Annu Rev Neurosci 18(1):193–222

Deubel H, Schneider WX (1996) Saccade target selection and object recognition: Evidence for a common attentional mechanism. Vis Res 36(12):1827–1838

Driver J (2001) A selective review of selective attention research from the past century. Brit J Psychol 92 (1):53–78

Fischer B, Weber H (1992) Characteristics of "anti" saccades in man. Exp Brain Res 89(2):415–424

Galley N (1989) Saccadic eye movement velocity as an indicator of (de) activation: A review and some speculations. J Psychophysiol 3:229–244

Goldberg ME, Wurtz RH (1972) Activity of superior colliculus in behaving monkey. II. Effect of attention on neuronal responses. J Neurophysiol 35(4):560–574

Honda H (2002) Idiosyncratic left-right asymmetries of saccadic latencies: Examination in a gap paradigm. Vis Res 42(11):1437–1445

Hubel DH, LeVay S, Wiesel TN (1975) Mode of termination of retinotectal fibers in macaque monkey: An autoradiographic study. Brain Res 96(1):25–40

Huestegge L, Herbort O, Gosch N, Kunde W, Pieczykolan A (2019) Free-choice saccades and their underlying determinants: Explorations of high-level voluntary oculomotor control. J Vis 19(3):1–15, https://doi.org/10.1167/19.3.14

Itaya SK, Van Hoesen GW (1983) Retinal projections to the inferior and medial pulvinar nuclei in the old-world monkey. Brain Res 269(2):223–230

Jonikaitis, D., Klapetek, A., & Deubel, H. (2017). Spatial attention during saccade decisions. *J Neurophysiol*, *118*(1), 149-160.

Jóhannesson ÓI, Ásgeirsson ÁG, Kristjánsson Á (2012) Saccade performance in the nasal and temporal hemifields. Exp Brain Res 219(1):107–120. DOI 10.1007/s00221-012-3071-2

Jóhannesson ÓI, Edelman JA, Sigurþórsson BD, and Kristjánsson Á (2018b) Effects of saccade training on express saccade proportions, saccade latencies, and peak velocities: an investigation of nasal/temporal differences. Exp Brain Res 236(5):1251–1262. DOI: 10.1007/s00221-018-5213-7

Jóhannesson ÓI, Kristjánsson Á (2013) Violating the main sequence: asymmetries in saccadic peak velocities for saccades into the temporal versus nasal hemifields. Exp Brain Res 227(1):101–110. http://doi.org/10.1007/s00221-013-3490-8

Jóhannesson ÓI, Tagu J, Kristjánsson Á (2018a) Asymmetries of the visual system and their influence on visual performance and oculomotor dynamics. European J Neurosci 48(11):3426–3445. DOI:10.1111/ejn.14225

Kowler E, Anderson E, Dosher B, Blaser E (1995) The role of attention in the programming of saccades. Vis Res 35(13):1897–1916

Koller K, Rafal RD (2019) Saccade latency bias toward temporal hemifield: Evidence for role of retinotectal tract in mediating reflexive saccades. Neuropsychologia 128:276–281. https://doi.org/10.1016/j.neuropsychologia.2018.01.028

Krauzlis RJ, Lovejoy LP, Zénon A (2013) Superior colliculus and visual spatial attention. Annu Rev Neurosci 36(1):165–182. https://doi.org/10.1146/ annurev-neuro-062012-170249

Kristjánsson Á (2006) Rapid learning in attention shifts: A review. Visual Cogn 13(3):324–362

Kristjánsson Á (2011) The intriguing interactive relationship between visual attention and saccadic eye movements In L Liversedge, I D Gilchrist, S Everling (Eds), Oxford handbook of eye movements (Vol. 1, 1st ed, pp. 455–470). Oxford, UK: Oxford University Press

Kristjánsson Á, Ásgeirsson ÁG (2019) Attentional Priming: Recent insights and current controversies. Curr Opin Psychol, 29:71–75

Kristjánsson Á, Campana G (2010) Where perception meets memory: A review of repetition priming in visual search tasks. Atten Percept Psychophys 72(1):5–18. http://doi.org/10.3758/APP.72.1.5

Kristjánsson Á, Chen Y, Nakayama K (2001) Less attention is more in the preparation of antisaccades, but not prosaccades. Nature Neurosci 4:1037–1042

Kristjánsson Á, Egeth H (2020) How feature integration theory integrated cognitive psychology, neurophysiology, and psychophysics. Atten Percept Psychophys 82:7–23

Kristjánsson A, Vandenbroucke M, Driver J (2004) When pros become cons for anti-versus prosaccades: Factors with opposite or common effects on different saccade types. Exp Brain Res 155(2):231–244

Kristjánsson Á, Vuilleumier P, Schwartz S, Macaluso E, Driver J (2007) Neural basis for priming of pop-out during visual search revealed with fMRI. Cereb Cortex 17(7):1612–1624

Kristjánsson Á, Wang D, Nakayama K (2002) The role of priming in conjunctive visual search. Cognition 85(1):37–52. http://doi.org/10.1016/S0010-0277(02)00074-4

Maljkovic V, Nakayama K (1994) Priming of pop-out: I. Role of features. Memory Cogn 22(6):657–672

McPeek RM, Maljkovic V, Nakayama K (1999) Saccades require focal attention and are facilitated by a short-term memory system. Vis Res 39(8):1555–1566. http://doi.org/10.1016/s0042-6989(98)00228-4

Nakayama K, Maljkovic V, Kristjansson A (2004) Short-Term Memory for the Rapid Deployment of Visual Attention. In: Gazzaniga MS (ed) The cognitive neurosciences. MIT Press, pp 397–408

Osterberg G (1935) Topography of the layer of rods and cones in the human retina. Copenhagen, Denmark: Nyt nordisk forlag

Peirce J, Gray JR, Simpson S, MacAskill M, Höchenberger R, Sogo H, ... Lindeløv JK (2019) PsychoPy2: Experiments in behavior made easy. Behav Res Methods 51(1):195–203

Peirce J, MacAskill M (2018) Building experiments in PsychoPy. London: Sage

Perry VH, Oehler R, Cowey A (1984) Retinal ganglion cells that project to the dorsal lateral geniculate nucleus in the macaque monkey. Neurosci 12(4):1101–1123

Posner M, Cohen Y (1980) Attention and the control of movements. In G E Stelmach J Requin (Eds), Tutorials in motor behavior (pp 243–258). Amsterdam, Netherlands: Elsevier/North-Holland

R Core Team (2020) R: a language and environment for statistical computing. R foundation for statistical computing, Vienna, Austria. https://www.R-project.org. Accessed 29 Feb 2020

Rafal RD, Calabresi PA, Brennan CW, Sciolto TK (1989) Saccade preparation inhibits reorienting to recently attended locations. J Exp Psychol Human 15(4):673–685. https://doi. org/10.1037//0096-1523.15.4.673

Rafal RD, Henik A, Smith J (1991) Extrageniculate contributions to reflex visual orienting in normal humans: A temporal hemi- field advantage. J Cogn Neurosci 3(4):322–328

Rizzolatti G, Riggio L, Dascola I, Umiltá C (1987) Reorienting attention across the horizontal and vertical meridians: Evidence in favor of a premotor theory of attention. Neuropsychologia 25(1):31–40

Rorden C, Kristjánsson Á, Revill KP, Saevarsson S (2011) Neural correlates of inter-trial priming and role-reversal in visual search. Front Hum Neurosci 5:1–8. http://doi.org/10.3389/fnhum.2011.00151

RStudio Team (2020) RStudio: integrated development for R. RStudio Inc., Boston, MA. http://www.rstudio.com. Accessed 29 Feb 2020

Scolari M, Seidl-Rathkopf KN, Kastner S (2015) Functions of the human frontoparietal attention network: Evidence from neuroimaging. Current Opinion in Behavioral Sciences 1:32–39

Shurygina O, Kristjánsson Á, Tudge L, Chetverikov A (2019) Expectations and perceptual priming in a visual search task: Evidence from eye movements and behavior. J Exp Psychol Human 45(4):489

Sigurdardottir HM, Kristjánsson Á, Driver J (2008) Repetition streaks increase perceptual sensitivity in visual search of brief displays. Visual Cogn 16(5):643–658. http://doi.org/10.1080/13506280701218364

Sylvester R, Josephs O, Driver J, Rees G (2007) Visual fMRI responses in human superior colliculus show a temporal-nasal asymmetry that is absent in lateral geniculate and visual cortex. J Neurophysiol 97(2):1495–1502. https://doi.org/10.1152/ jn.00835.2006

Tagu J, Doré-Mazars K, Vergilino-Perez D (2020) Saccade accuracy as an indicator of the competition between functional asymmetries in vision. Exp Brain Res 238(2):411–425. https://doi.org/10.1007/s00221-019-05717-6

Tagu J, Doré-Mazars K, Vergne J, Lemoine-Lardennois C, Vergilino-Perez D (2018a) Recentering bias for temporal saccades only: Evidence from binocular recordings of eye movements. J Vis 18(1):1–16. https://doi.org/10.1167/18.1.10

Tagu J, Doré-Mazars K, Vergne J, Lemoine-Lardennois C, Vergilino-Perez D (2018b) Quantifying eye dominance strength – New insights into the neurophysiological bases of saccadic asymmetries. Neuropsychologia, 117:530–540. https://doi.org/10.1016/j.neuropsychologia.2018.07.020

Theeuwes J, Van der Burg E (2011) On the limits of top-down control of visual selection. Atten Percept Psychophys 73(7):2092

Tigges J, Tigges M (1981) Distribution of retionfugal and corticofugal axon terminals in the superior colliculus of squirrel monkey. Invest Ophth Vis Sci 20:149–158

Toosy AT, Werring DJ, Plant GT, Bullmore ET, Miller DH, Thompson AJ (2001) Asymmetrical activation of human visual cortex demonstrated by functional MRI with monocular stimulation. Neuroimage 14(3):632–641

Tychsen L, Burkhalter A (1997) Nasotemporal asymmetries in V1: Ocular dominance columns of infant, adult, and strabismic macaque monkeys. J Comp Neurol 388(1):32–46

Venables WN, Ripley BD (2002) Modern applied statistics with S. 4th edn. Springer, New York. ISBN 0-387-95457-0

Vergilino-Perez D, Fayel A, Lemoine C, Senot P, Vergne J, Doré-Mazars K (2012) Are there any left-right asymmetries in saccade parameters? examination of latency, gain, and peak velocity. Invest Ophthalmol Vis Sci 53(7):3340–3348. https://doi.org/10.1167/iovs.11-9273

Westerberg JA, Maier A, Schall JD (2020) Priming of Attentional Selection in Macaque Visual Cortex: Feature-Based Facilitation and Location-Based Inhibition of Return. Eneuro 7(2). http://doi.org/10.1523/ENEURO.0466-19.2020

White BJ, Munoz DP (2011) The superior colliculus. In S P Liversedge, I D Gilchrist, S Everling (Eds), The Oxford Handbook of Eye Movements (pp195–213). New York: Oxford University Press

Williams C, Azzopardi P, Cowey A (1995) Nasal and temporal retinal ganglion cells projecting to the midbrain: Implications for “blindsight”. Neuroscience 65(2):577–586

Appendix A

Table A1. *Summary of the nasal temporal asymmetry. Descriptive statistics and results of the statistical tests in all the choice trials.*

Trial type	Streak length	Nasal %	Temporal %	*p*-value
Free choice trials[1]	None	38.0	62.0	.023
Choice trials in priming sequences	All	43.1	56.9	< .001
Choice trials in priming sequences	2	40.9	59.1	NA
Choice trials in priming sequences	4	47.7	52.3	NA
Choice trials in priming sequences	4 – 2	6.8	– 6.8	.123
Choice trials in priming sequences	6	40.7	59.3	NA
Choice trials in priming sequences	6 – 4	– 7.0	7.0	.045
Choice trials in priming sequences	Interaction	NA	NA	> .110
Choice trials in switch sequences	1	40.0	60.0	.034

[1] paired-$t(13) = -2.57$, $p = .023$

Table A2. *Summary of the priming effects. Descriptive statistics and results of the statistical tests in the choice trials in the combined primed and switch sequences. The table shows that the difference between hemifields (the main effect of hemifield) was significant and the effect of priming was stronger in streak length 2 than in streak length 1. Furthermore, the effect of priming increased similarly in both hemifields between streak length 1 and 2. Streak lengths 4 and 6 did not have significant effects. Therefore, it can be concluded that the difference between the hemifields was always significant.*

	Nasal		Temporal		
Streak length	Primed %	Unprimed %	Primed %	Unprimed %	*p*-value
All[1] (main effect)	62.0	38.0	77.2	22.8	<.001
1	47.6	52.4	67.6	32.4	NA
2	58.2	41.8	77.1	22.9	NA
2 – 1[2]	10.6	– 10.6	9.5	– 9.5	.008
4	72.5	27.5	76.6	23.4	NA
4 – 2[2]	14.3	– 14.3	– 0.5	0.5	.161
6	69.7	30.3	87.5	12.5	NA
6 – 4[2]	– 2.8	2.8	10.9	– 10.9	.182
All interaction	NA	NA	NA	NA	>= .057

[1] the *p*-value is from the statistical test comparing the hemifields

[2] the *p*-value is from the statistical test comparing one streak length to another

Table A3. *Selections of the temporal stimulus. Descriptive statistics and results of the statistical tests in the choice trials in the combined primed and switch sequences. The table shows that neither the effect of priming nor the effect of streak length was significant. Therefore, it can be concluded that the priming effect does not alter the free choice bias.*

	Nasal		Temporal		
Streak length	Primed %	Unprimed %	Primed %	Unprimed %	*p*-value
All[1]	44.7	37.7	55.3	62.3	.061
1	42.0	38.6	58.0	61.4	NA
2	43.6	36.5	56.4	63.5	NA
2 – 1[2]	1.6	– 2.1	– 1.6	2.1	.899
4	48.8	46.4	51.2	53.6	NA
4 – 2[2]	5.2	9.9	– 5.2	– 9.9	.118
6	44.3	29.2	55.7	70.8	NA
6 – 4[2]	– 4.5	– 17.2	4.5	17.2	.058
All interaction	NA	NA	NA	NA	>= .329

[1] the *p*-value is from the statistical test comparing the primed and unprimed selections

[2] the *p*-value is from the statistical test comparing one streak length to another