Evidence for distinct mechanisms underlying attentional priming and sensory memory for bistable perception

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Attentional selection in visual search paradigms and perceptual selection in bistable perception paradigms show functional similarities. For example, both are sensitive to trial history: They are biased toward previously selected targets or interpretations. We investigated whether priming by target selection in visual search and sensory memory for bistable perception are related. We did this by presenting two trial types to observers. We presented either ambiguous spheres that rotated over a central axis and could be perceived as rotating in one of two directions, or search displays in which the unambiguously rotating target and distractor spheres closely resembled the two possible interpretations of the ambiguous stimulus. We interleaved both trial types within experiments, to see whether priming by target selection during search trials would affect the perceptual outcome of bistable perception and, conversely, whether sensory memory during bistable perception would affect target selection times during search. Whereas we found intertrial repetition effects among consecutive search trials and among consecutive bistable trials, we did not find cross-paradigm effects. Thus, even though we could ascertain that our experiments robustly elicited processes of both search priming and sensory memory for bistable perception, these same experiments revealed no interaction between the two.

Introduction

A central function of the visual system is to identify relevant items in a given scene, and to prioritize neural analysis of those items through the process of attention allocation. A good example is provided by visual search, where observers make a selection between relevant and irrelevant objects or object-features. The ability to effectively allocate attention is not static, but develops with experience. For instance, research during the past few decades has consistently shown implicit intertrial priming effects in visual search (Kristjánsson & Campana, 2010). Specifically, when observers are asked to respond to a target that is unique among display elements, response times decrease as a function of the number of repetitions of target features, or distractor features, over trials, indicating that observers are increasingly biased towards recently selected features and objects (Lamy, Carmel, Egeth, & Leber, 2006; Maljkovic & Nakayama, 1994; Sigurdardottir, Kristjánsson, & Driver, 2008). These effects have been shown to decay over the course of five to eight trials regardless of interstimulus interval durations, which can last for several seconds up to a minute (Maljkovic & Nakayama, 1994).

Another key function of the visual system is to interpret visual input by parsing it into meaningful components. This interpretative function can be seen at work during the perception of ambiguous stimuli that can be interpreted in two ways, and the observer perceives the two interpretations in alternation. Just like visual search, the perception of ambiguous stimuli is subject to prior exposure. Specifically, when an ambiguous stimulus is presented several times in succession, perception on a given presentation is biased toward the interpretation that was perceived during preceding presentations (Brascamp et al., 2008; Leopold, Wilke, Maier, & Logothetis, 2002; Maier, Wilke, Logothetis, & Leopold, 2003). This sensory memory relies on the repetition of visual features rather than on a behavioral response (Brascamp, Knapen, Kanai, van

Ee, & van den Berg, 2007; Pastukhov, Füllekrug, & Braun, 2013). Moreover, sensory memory that is formed during bistable perception can last for several seconds (Maier et al., 2003)—in fact, it is strongest if ambiguous displays are interleaved with blank periods of several seconds (Leopold et al., 2002), and increases in strength with longer periods of perceptual dominance (Brascamp, Pearson, Blake, van den Berg, 2009).

Several authors have suggested that there may be a close association between attentional selection among input elements on the one hand and perceptual selection among interpretations on the other (Brascamp & Blake, 2012; Dieter & Tadin, 2011; Knapen, Brascamp, Adams, & Graf, 2009; Leopold & Logothetis, 1999; Ooi & He, 1999; Paffen & Alais, 2011; Sterzer, Kleinschmidt, & Rees, 2009). Apart from more general suggestions of parallels between bistable perception and attention, there are more specific indications that the history effects that play a role in the two contexts may be related. For example, search priming has been shown to have distinct perceptual consequences, overcoming masking (Ásgeirsson, Kristjánsson, & Bundesen, 2014) and releasing visual stimuli from crowding (Kristjánsson, Heimisson, Róbertsson, & Whitney, 2013). Further evidence indicates that allocation of attention can bias bistable perception (Chong & Blake, 2006; Kristjánsson, 2009; Mitchell, Stoner, & Reynolds, 2004; see also Tanaka & Sagi, 1998), for instance when the cueing of attention to specific elements of the visual input affects the outcome of perceptual conflict during binocular rivalry (Chong & Blake, 2006; Mitchell et al., 2004). On the other hand, there are also notable differences between history effects for target selection and perceptual selection. In addition to the differences in time dependence that we mentioned above, there are also spatial differences, with the spatial range of sensory memory for bistable stimuli being quite limited (Chen & He, 2004; Knapen et al., 2009), whereas search priming is not strongly location-specific (e.g., Maljkovic & Nakayama, 1994). Recent evidence shows that perception of unambiguous stimuli can be biased by previously attended stimuli over a broader distance, but it is not clear whether this bias generalizes to bistable perception (Fischer & Whitney, 2014). A further possible difference is that sensory memory for ambiguous stimuli, but not search priming, is strongly dependent on the degree of perceptual ambiguity of the earlier stimulus that leaves the memory (Pearson & Brascamp, 2008). It is an open question how the intricate dependencies of sensory memory on stimulus properties (Pastukhov et al., 2013; Pastukhov, Lissner, & Braun, 2014) and on intervening events (Kanai, Knapen, van Ee, & Verstraten, 2007; Maier et al., 2003), compare to such dependencies of search priming (Thomson & Milliken, 2012).

In light of this combination of suggestive parallels but also clear differences, our aim is to further investigate the relation between history effects in bistable perception and attention allocation. Specifically, we ask two questions. First, does the priming elicited by visual search trials induce a bias in the perception of a subsequently presented ambiguous stimulus? And, second, does the sensory memory that is formed by the perception of ambiguous stimuli affect response times during a subsequent visual search trial? Based on the earlier cueing paradigms by Mitchel and others (2004) and Chong and Blake (2006), we hypothesize that mechanisms invoked by attention allocation during visual search are also used to resolve ambiguity when observing a bistable figure. Our results will provide insight into the extent to which target-distractor priming and sensory memory of bistable stimuli reflect the operation of shared mechanisms of the visual system.

Experiment 1

In Experiment 1 we tested whether priming elicited by visual search could affect perception of an ambiguous figure. We used a search display where both the target object and the distractor objects were animations of a sphere rotating around its central axis (Figure 1a). Critically, although these objects were unambiguous, they closely resembled the two perceptual interpretations of an ambiguous sphere, seen to be rotating in either of these two directions (Nawrot & Blake, 1989; Wallach & O'Connell, 1953). By interleaving these search displays with presentations of the ambiguous sphere, we could measure, both whether prior search for a particular target affected subsequent search for the same target (visual search priming), and whether prior search for a particular target affected subsequent perception of the ambiguous stimulus. The latter pattern would constitute a form of across-paradigm priming, supporting the notion that priming in visual search and sensory memory during bistable perception have an overlapping neural basis.

Methods

Participants

Ten subjects participated in Experiments 1 and 2. Five of these, including the third author of this paper, were colleagues, experienced with psychophysics tasks. These observers participated for free, whereas the remaining observers received 7.50 Euro per hour or student credits. Observers signed informed consent, and all experiments were conducted in agreement with
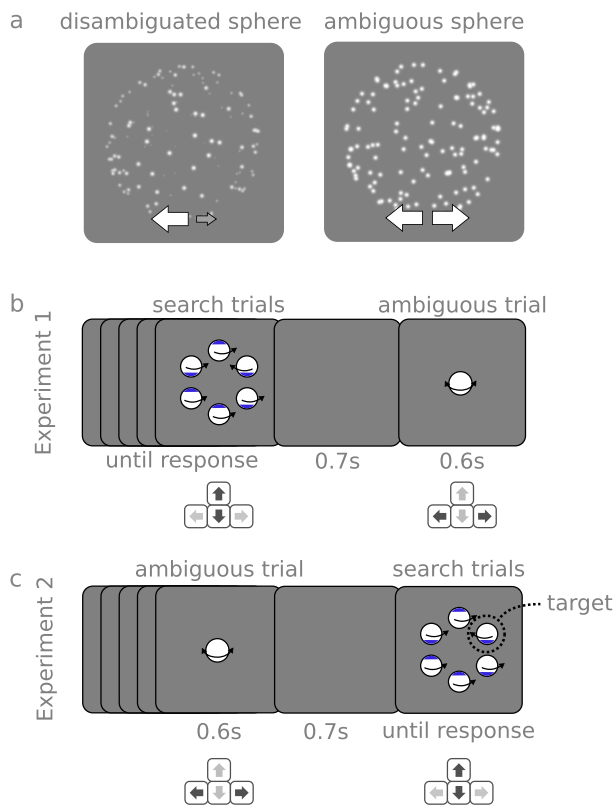
Figure 1. Experiment design. The upper two panels display disambiguated and ambiguous spheres used in Experiments 1 and 2 (not drawn to scale). In Experiment 1, series of search trials were interleaved with bistable trials. Conversely, in Experiment 2 series of bistable trials were interleaved with search trials. During a search trial observers reported the location of the blue shaded end of the sphere, either by pressing the up or down arrow keys, when the sphere rotated around its vertical central axis, or the left or right arrow keys, when the sphere rotated around its horizontal central axis. During bistable trials, observers reported their perceived rotation direction either by pressing left and right arrow keys when the sphere rotated around its vertical central axis, or the up or down arrow keys when the sphere rotated around its horizontal central axis.

the ethics guidelines of Utrecht University and in accordance with the Declaration of Helsinki.

Stimuli and apparatus

Stimuli were created in Python and Psychopy, which was also used for stimulus presentation (Peirce, 2008). The stimuli were presented on a 60 Hz, 1024 × 768 pixel, 40.5-cm wide CRT monitor 70 cm away from the observer. Observers placed their head in a chinrest to maintain a constant distance from the screen throughout the experiment. The rotating sphere (Figure 1a) animations consisted of orthographic projections (radius: 2.4° of visual angle [VA]) of transparent spheres whose surfaces were covered in 128 randomly positioned white dots (luminance: 70.10 cd/m^2, radius: 0.24° VA). Each dot was then masked using a Gaussian kernel (*SD*: 0.04° VA). The simulated spheres rotated at 0.17 cycles per second, and the stimuli were presented on a gray background (10.45 cd/m^2).

All experiments included two kinds of displays. For the first type of display, which contained a single sphere presented at fixation, no depth cue distinguished whether this sphere's left-moving surface or its right-moving surface was closer to the observer. This condition resulted in bistable perception, with the sphere being perceived as rotating in one of two possible directions around its rotation axis. The second type of display consisted of a search array containing six spheres that were disambiguated using both dot size and dot luminance. Specifically, dot-size scaled linearly with simulated depth, from 0.24° of visual angle at the closest point to 0.12° of visual angle at the farthest point, and luminance changed with simulated depth from 70.10 to 14.99 cd/m^2. The search array contained one target sphere, defined by the fact that its rotation direction was opposite to that of the other five spheres. These spheres were placed circularly around fixation at an eccentricity of 5° VA. The angular position around fixation was randomized on each display, with equal distance between each sphere. Although the dots of all spheres were generally white, dots on one of the polar ends of each sphere in a search display were blue (7.97 cd/m^2 for near dots, and 9.21 cd/m^2 for far dots), for task-related reasons (see below). The blue dots covered one pole that corresponded to 15% of the sphere's diameter. On three random spheres the poles facing one end were colored blue whereas on the other half of the spheres the poles facing the opposite end were colored blue (Figure 1b).

Procedure

In a pilot experiment, many observers reported a single perceived rotation direction during bistable trials throughout the experiment. An absolute preference for a single interpretation renders us unable to dissociate sensory memory from a predisposed preference for a single interpretation. By eliminating such a strong preference, we should be better able to dissociate sensory memory from a predisposed preference. We therefore conducted a short experiment prior to Experiments 1 and 2 to address this issue. We expected that the strength of a preference for a single interpretation would vary between differently oriented rotation axes. We therefore selected the axis angle with the best balance between both possible rotation directions for use in Experiments 1 and 2. Each observer participated in four blocks of 150 trials with four different orientations in the following order: (a) rotation around

its central vertical axis; (b) rotation around its central horizontal axis; (c) rotation around its vertical axis tilted 45° counterclockwise; and (d) rotation around its vertical axis tilted 45° clockwise. The spheres were presented in this order so that the rotation axes were maximally dissimilar between consecutive blocks to minimize contamination from rotation direction between blocks. Additionally, we included a one-minute continuous presentation of the sphere after each block and asked observers to indicate perceptual switches with a button press. This is an effective way to eliminate sensory memory after intermittent presentation of bistable stimuli (Brascamp et al., 2008).

In Experiment 1, observers performed a search task and were asked to identify the odd-rotating sphere by reporting the location of its blue-shaded polar end (Figure 1b and 1c), providing a response that was unrelated to the sphere's rotation direction (e.g., up or down vs. left or right), eliminating the possibility that repetition effects could be ascribed to motor response priming (Lamy, Yashar, & Ruderman, 2010). The trial sequence of this experiment was organized as follows. Series of one to five search trials were interleaved with individual trials on which an ambiguous sphere was presented, hereafter termed "bistable trials." Sixty series of each length were shown in random order, resulting in a total of 900 search trials and 300 bistable trials. Target and distractor rotation directions remained constant throughout a series of search trials, but were randomly reassigned following each bistable trial. On search trials the stimuli stayed on the screen until a response was provided, whereas the bistable trials had a fixed duration of 0.6 s. In the latter case, a shorter fixed duration was chosen to minimize the possibility that the interpretation of the ambiguous sphere would switch within a single presentation (Leopold et al., 2002). All trials were preceded by a fixation display with a central dark gray 9.6 cd/m² dot, presented for 0.7 s. The fixation dot remained visible throughout the experiment and was displayed so it appeared to be behind the ambiguous spheres. We instructed observers to maintain fixation throughout the experiment. Observers were allowed to provide a response while the bistable sphere was visible and during the fixation display that followed. They could correct their response to a bistable trial and only the last response was recorded as the perceived rotation direction.

Analysis

Most observers showed an overall gradual reduction in response time on search trials over the course of the experiment, presumably reflecting a learning effect. This slow change is not indicative of search priming, because search priming is specific to target and distractor identities, which changed back and forth throughout. Given our focus on search priming, we adjusted search response times for each experiment and each observer by fitting a linear curve to all sequential search response times and subtracting that curve's slope from the raw data. Search trials with incorrect responses or response times under 200 ms or response times over four standard deviations above the mean response time were excluded from the dataset. Finally, to reduce between-subject variance, search response times were normalized to individual median search response times in all experiments, by dividing by the observer's median response time.

Some observers had a strong preference for a single rotation direction during bistable trials, in spite of our efforts to minimize this preference (see above). A very strong bias may be interpreted as a perceptual bias rather than sensory memory. We therefore excluded two observers who gave the same response on at least 95% of bistable trials. Our final analysis for Experiment 1 included eight out of 10 observers. Across these observers, the proportion of bistable trials on which they reported their preferred percept was 61% ($SD = 12\%$).

Results and discussion

We first measured within-paradigm search priming by looking at response times within a series of target repetitions. Figure 2a displays normalized median response times (y axis) against the number of consecutive trials that immediately preceded the current trial (x axis) and on which the rotation directions of target and distractors were the same as on the current trial. The figure shows that response times decreased gradually as a function of target (and distractor) repetition. A repeated-measures analysis of variance (ANOVA) revealed a significant effect of target repetition on response times, $F(4, 28) = 4.95$, $p < 0.01$. Posthoc, we calculated Spearman's rank correlation coefficients for response times against the number of target repetitions for each observer and found that rho-values across observers were significantly lower than zero, $t(7) = -4.18$, $p < 0.01$. This confirmed that response times decreased with target repetition, showing that our design elicited search priming.

We report Bayes factors (*BF*) for all t tests that we performed, which can allow a stronger interpretation in cases where the null hypothesis cannot be rejected. Typically, a Bayes factor larger than 3 provides substantial evidence for the alternative hypothesis, whereas a Bayes factor smaller than 1/3 provides substantial evidence in favor of the null hypothesis (Dienes, 2014). For the above t test, a Bayes factor
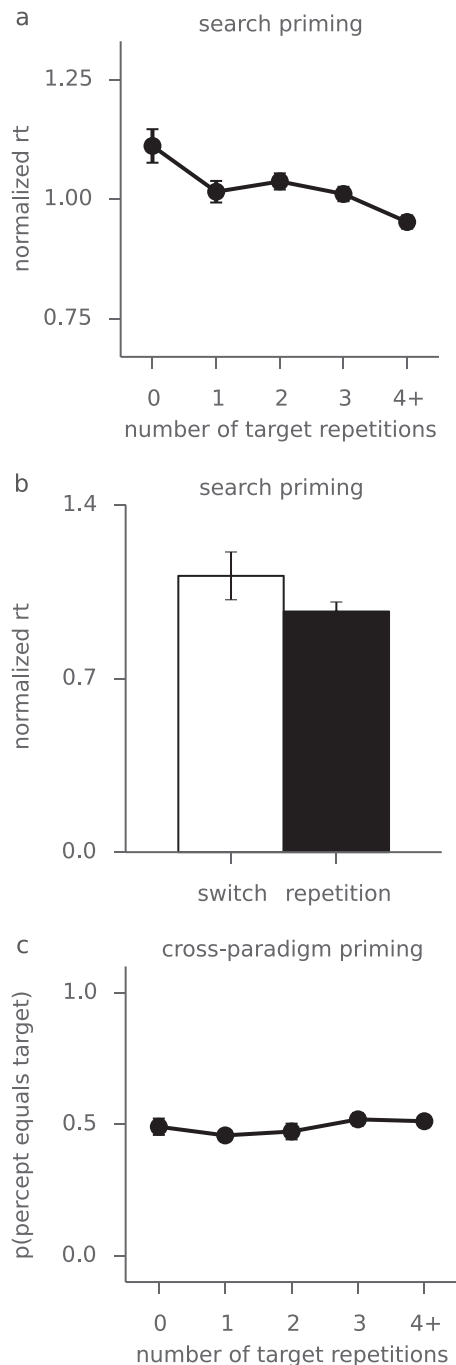
Figure 2. Panel (a) shows the average across observers of median response times (rt), normalized to the median for each observer, as a function of the number of trials in which the target rotation direction repeated. Panel (b) displays the average across-observer median response times on search trials, immediately following a bistable trial, where target and distractor rotations switched versus repeated with respect to the previous search trial. Panel (c) displays the proportion of trials where perceived rotation corresponded to the target rotation direction of the immediately preceding search trial, as a function of the number of consecutive search trials in which →

analysis supported the conclusion of nonzero rho values ($BF = 13.13$).

A second analysis focused exclusively on search trials that immediately followed a bistable trial. We compared search trials on which target and distractor rotation directions switched relative to the most recent search trial (i.e., relative to the search trial immediately preceding the intervening bistable trial) to search trials on which target and distractor rotation directions repeated. Figure 2b displays median response times for switched and repeated targets. Response times when target and distractor rotation directions repeated were significantly shorter compared to when target and distractor rotation directions switched, $t(7) = 4.17$, $p < 0.01$; $BF = 13.06$. This second analysis shows that search priming occurs across an intervening bistable trial. The mnemonic signal that is responsible for this priming therefore survives an intervening bistable trial. This provides an ideal starting point for addressing our next question, namely whether this signal may also affect perception during bistable trials.

To investigate this, we calculated the proportion of bistable trials on which the perceived rotation direction of ambiguous spheres corresponded to the rotation direction of the preceding target. Analogous to the analysis of Figure 2a, we calculated this proportion separately, as a function of the number of consecutive trials preceding bistable trials where target and distractor rotation direction repeated (Figure 2c). We performed a repeated-measures ANOVA and found that the proportion of perceived rotation directions corresponding to the preceding target rotation direction did not change for different numbers of target repetitions, $F(4, 28) = 0.94$, $p = 0.46$. In addition, the proportion of perceived rotation directions that corresponded to the preceding target rotation direction was not different from 0.5, regardless of the number of target repetitions, $t(7) = 0.06$, $p = 0.95$; $BF = 0.34$. Note that the Bayes factor of close to 1/3 adds further weight to this null result.

The results indicate that visual search priming does not influence the perception of ambiguous stimuli, suggesting that priming of visual search is distinct from sensory memory for bistable perception. If these forms of priming are truly independent, and can exist simultaneously, then one might also expect our experiment to preserve a strong sequential dependence between perception on consecutive bistable trials, in spite of the fact that these trials were separated by

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the current target rotation did not change. Each first value on the x axis reflects the initial trial in a series of repeated target rotation directions, hence 0 repetitions. We collapsed all trials with four or more search repetitions. Error bars show standard errors of the mean.

multiple search trials here. We calculated the proba-bility that perceived rotation direction on a given bistable trial corresponds to the perceived rotation direction on the previous bistable trial as a function of the number of consecutive preceding trials in which perceived rotation repeated. A repeated-measures ANOVA showed that this probability changed with the number of preceding same percept repetitions, $F(4, 28) = 20.23$, $p < 0.001$. Posthoc, we calculated Spearman's rank correlation coefficients per observer and found that rho-values were significantly greater than zero across observers, $t(7) = 9.22$, $p < 0.001$; $BF = 634.53$. In other words, observers were increasingly more likely to perceive the same rotation direction on subsequent trials after each repeated percept. This demonstrates that perception during bistable trials, although not detectably affected by target rotation direction during immediately preceding search trials, depended on perceived rotation direction during bistable trials further in the past. This result again suggests that visual search priming and sensory memory for bistable perception reflect independent forms of history effects.

Experiment 2

With Experiment 1 we measured whether search priming can affect perception during bistable trials. Experiment 2 was designed to assess the converse, whether perception during earlier bistable trials can affect response times during visual search. Accordingly, Experiment 2 was exactly like Experiment 1, except that individual search trials now sparsely interleaved longer sequences of bistable trials (Figure 1c).

Methods

The same observers participated in Experiment 2 as in Experiment 1. The stimuli were identical to the stimuli used in Experiment 1. We presented series of one to five bistable trials—a total of 60 series of each length. Each series of search trials was followed by a bistable trial (1,200 trials per observer).

Similar to Experiment 1, we found that some observers had a strong bias toward one of two possible interpretations of the ambiguous sphere. For reasons explained earlier, we excluded three subjects who reported the same perceived rotation on 95 percent of all bistable trials. In total seven out 10 observers were included for further analysis. The proportion of trials on which the remaining observers reported their preferred percept was 63% (*SD*: 16%).
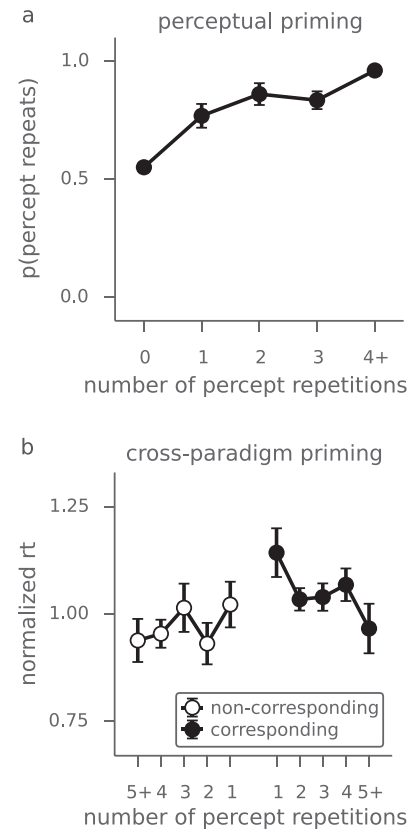

Figure 3. Results of Experiment 2. Panel (a) displays the proportion that perceived rotation on the next bistable trial corresponds to the perceived rotation on the current bistable trial on the *y* axis. The *x* axis represents the number of consecutive bistable trials that immediately preceded the current trial in which perceived rotation corresponded to the current trial. Here, 0 indicates the first trial in a sequence of consecutive bistable trials in which the perceived rotation direction did not change. Bistable trials in which the number of preceding bistable trials with identical perceived rotation directions exceeded four were collapsed into one bin. Panel (b) shows response times on interleaved search trials as a function of the number of bistable trials, that immediately preceded the search trial, in which perceived rotation corresponded (solid black dots), or did not correspond (white dots) to the target rotation direction. The numbers on the *x* axis indicate the number of consecutive bistable trials in which perceived rotation direction did not change, binned in percentiles of 20%. All error bars represent standard errors of the mean.

Results and discussion

We first measured sensory memory, by calculating the probability that perceived rotation direction repeats from one trial to the next. Figure 3a shows that this probability increases, as a function of the number of consecutive bistable trials in which the same rotation direction was perceived. A one-way repeated-measures ANOVA showed that the probability that perceived

rotation repeats in the next trial was indeed significantly affected by the number of consecutive trials in which the current perceived rotation repeated, $F(4, 24) = 32.54$, $p < 0.001$. We then calculated a Spearman's rank correlation coefficient for each observer. A two-tailed t test revealed that rho-values across observers were significantly greater than zero, suggesting that the probability of percept repetition increased with preceding percept repetitions, $t(6) = 18.062$, $p < 0.001$; $BF = 6909.98$, confirming significant intertrial effects of sensory memory between consecutive bistable trials. Note that the repetition probability after the first bistable trial following a perceptual switch is indicated by the first point on the x axis in Figure 3a. This probability was slightly larger than chance, $t(6) = 2.41$, $p = 0.05$; $BF = 1.9$, indicating that sensory memory was formed after a single trial. Note, however, that the Bayes factor suggests that this is not a reliable effect.

Next, we tested whether perception during bistable trials also affected subsequent search trials by analyzing separately search trials where target rotation corresponded to the perceived rotation during the immediately preceding bistable trial (black dots in Figure 3b), and search trials where this was not the case (white dots in Figure 3b). For both these kinds of search trials we then binned all response times, depending on the number of consecutive preceding bistable trials on which the same rotation direction was perceived (bin rank numbers indicated on the x axis of Figure 3b). The figure shows that response times were slightly higher when the target's rotation direction and perceived rotation direction on the immediately preceding bistable trial corresponded. Note that the direction of this difference in response times is opposite to what we would expect if a bias toward a given target rotation direction reflects a mechanism that also underlies a perceptual bias for a given rotation direction during bistable perception. Additionally, the figure shows no clear dependence on the number of consecutive repetitions of the same perceived rotation direction preceding the current trial (the curves' slopes). This was confirmed with a two-way repeated-measures ANOVA with the correspondence of the target's rotation direction and perceived rotation direction as one factor and the number of consecutive perceived rotation repetitions as a second factor. The main effect of perceived and target rotation correspondence was not significant, $F(1, 6) = 5.31$, $p = 0.06$, nor was there a significant main effect of the number of perceived rotation repetitions, $F(4, 24) = 1.96$, $p = 0.13$, or an interaction between perceived and target rotation direction correspondence, and the number of perceived rotation repetitions, $F(4, 24) = 0.29$, $p = 0.88$. In other words, we found no evidence that sensory memory affected search response times. In agreement with Experiment 1, this suggests that sensory memory for

perceived rotation during bistable perception is independent of search priming.

In spite of this lack of an effect in the ANOVA analysis, for consistency we compared response times on trials in which the target rotation direction either corresponded, or did not correspond to the immediately preceding response on a bistable trial. Here we again found no evidence that observers responded faster when the perceived and target rotation directions corresponded, $t(6) = 2.96$, $p = 0.03$; $BF = 3.31$ (a result which suggests an effect but in the direction opposite to our hypothesis). If the two forms of history effects are independent, priming effects between search displays, irrespective of intervening bistable trials, may have occurred in parallel to history effects between bistable trials. To test this, we calculated median response times as a function of the number of preceding consecutive search trials on which target rotation direction was the same as on the current trial and conducted a one-way repeated-measures ANOVA. We found no effects of target repetition on response times, $F(4, 24) = 0.94$, $p = 0.46$, suggesting that no priming by search occurred with interleaved series of bistable trials, possibly because these search trials were spaced quite far apart in time. Note that the absence of search priming leaves room for response times to be affected by sensory memory, if the two forms of history effects were not independent.

Reanalysis of Experiments 1 and 2

One last possibility that we address is whether the way we define priming may explain the absence of a paradigm interaction. Consider search priming as we evaluated it in the analysis of Figure 2. After each change in target rotation direction, we counted the number of same-target repetitions and used this number as an index of accumulated priming. In other words, all trial history that preceded a target change was not taken into account in this analysis. Ignoring trial history could pose a limitation, because it is likely that priming toward one rotation direction, especially following a long sequence of repetitions of that target rotation direction, is not completely eliminated directly after a switch.

Rather, the decay of priming and of sensory memory is plausibly a more gradual process (Brascamp, Pels, & Kristjánsson, 2011; Maljkovic & Martini, 2005; Maljkovic & Nakayama, 1994). If that is the case, we may expect different levels of priming toward a certain rotation direction when a switch follows a long repetition sequence compared to when it follows a shorter repetition sequence. A similar consideration applies to sensory memory, which does not disappear

after each perceptual switch (Brascamp et al., 2008; Pastukhov & Braun, 2008), yet the analysis method we used for Figure 2 was blind to all history preceding each switch. In other words, the model of sensory memory we employed may lack important information about trial history and, as such, the power of our previous analyses may have been limited. An additional analysis addressed this by taking into account trial history preceding switches in perception or in target rotation direction, potentially allowing more precise prediction of the current internal state of priming or sensory memory, and a better ability to identify associated effects on response time and perception, both within and across paradigms.

Methods

For Experiment 1, we first created a model aimed at predicting within-paradigm search priming that resulted from target repetition. We assumed that priming for a given target rotation direction gradually accumulated with every repetition of that target rotation direction, and gradually decayed whenever the other target was presented. For within-paradigm search priming, we assumed that response times followed an exponentially decaying function as a function of target repetition. There is good evidence supporting the general assumption that exponential build-up and decay can reasonably approximate the time course of priming (Maljkovic & Martini, 2005; Martini, 2010). What is unknown, however, is how fast or slow this build-up and decay progressed for the observers in this experiment. In other words, the exponential's time constant needed to be determined. To do this we used an iterative approach. Specifically, we defined priming strength as a differential equation:

$$y_{t+1} = y_t + \frac{c_t - y_t}{\tau} \qquad (1)$$

where y is the level of priming, t is the current trial index, c represents target rotation direction (i.e., 0 for leftward and 1 for rightward), and τ is the constant that represents the speed of priming progression. We assumed that reaction times in response to leftward rotating targets are proportional to y, whereas reaction times to rightward rotating targets are proportional to $1 - y$. In other words, levels of y approaching 1 indicate priming toward the rightward rotation direction, and values that approach 0 indicate priming toward the leftward rotation direction. For each observer, we calculated a range of hypothetical priming levels y for each search trial in the experiment, by using a range of potential values of τ (1 to 21 with a step size of 0.1). We then correlated these priming levels to the response times that were actually observed. We then defined the best

model (Figure 4a) by selecting the value of τ that produced the largest Pearson correlation coefficient (Figure 4b) between priming level and reaction time. If the selected model was a good predictor of response time, this would suggest the model's variable y accurately tracks the internal state of search priming, so we then used this same variable y to predict perceived rotation direction for the bistable trials that were interleaved. Specifically, we tested whether variable y correlated positively with the probability of perceiving rightward rotation, as would be expected if the internal signal responsible for search priming also biased perception. For Experiment 2 we used a fully analogous approach, but now determined the time constant of sensory memory on the basis of bistable trials only. The model that best fit the data from bistable trials was then selected to predict search response times on interleaved search trials (Figure 4c and 4d).

Results and discussion

We found that, for most observers, the search priming model was a good predictor of search response time data in Experiment 1 (Figure 5a). Correlation coefficients of the model and response times were greater than zero across observers (one sample t-test): $t(7) = 3.08$, $p = 0.02$; $BF = 4.2$. In one sense this is not surprising, because the model's time constant was selected on the basis of these data. Nevertheless, it does mean that the model's priming variable accurately tracks the state of priming caused by search trials, so that this variable should also predict perception if perception is influenced by this form of priming. However, the model did not predict perceived rotation during bistable trials in Experiment 1, as the lack of correlation between the model's priming variable and the probability of perceiving one or the other rotation direction shows (Figure 5c). The absence of a correlation was borne out in statistics (one sample t test): $t(7) = -0.35$, $p = 0.74$; $BF = 0.35$. Figure 5e displays these correlations for individual observers in Experiment 1. For each observer, the across-paradigm fit results are plotted on the y axis, against the within-paradigm results on the x axis. The converse approach yielded very similar results (Figure 5b and 5d): When basing our model on bistable trials we were able to predict perception on bistable trials quite accurately for Experiment 2, $t(7) = 15$, $p < 0.001$; $BF = 10,803.09$, yet we could not predict response times on the interleaved search trials, $t(7) = -1.76$, $p = 0.12$; $BF = 0.99$. Note, however, that the Bayes factor of the latter analysis indicates that we should be careful to accept this null-hypothesis. Figure 5f plots the correlation coefficients for the across-paradigm fits (y axis), against those for
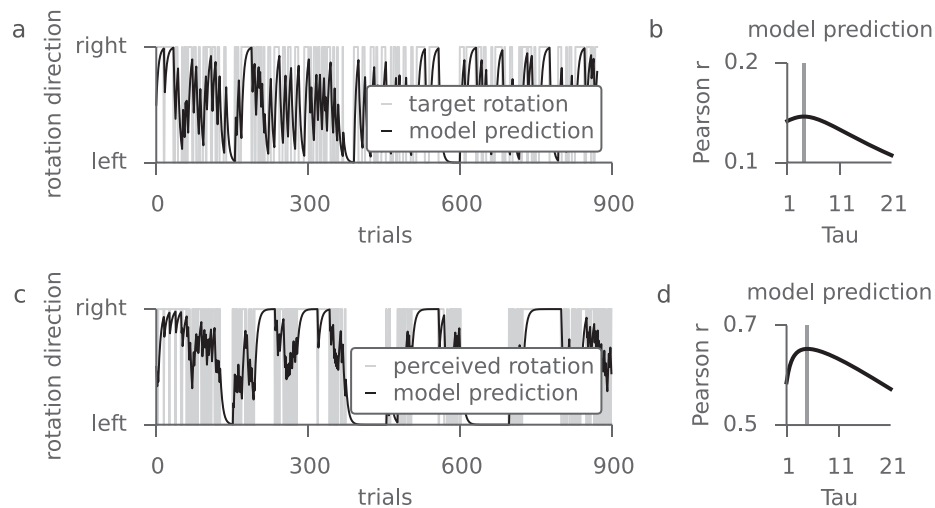
Figure 4. The modelled priming and sensory memory signals for Experiment 1 and 2, for a typical observer. Panel (a) displays the modelled priming signal as a black line for all search trials. Larger values on the *y* axis indicate a bias toward rightward rotation that predicts shorter response times on trials where the target rotated rightward versus leftward, and vice versa for lower values on the *y* axis. The gray line reflects target rotation directions throughout the entire experiment. Panel (c) displays the modelled sensory memory signal as a black line for all bistable trials. The gray line reflects perceived rotations on bistable trials during the entire experiment. Panel (b) and (d) show Pearson correlation coefficients for different values of τ, for both models. Peak values were selected to compute the priming signals.

the within-paradigm fits (*x* axis), for each observer in Experiment 2.

To summarize, using a different approach, that takes trial history into account even when it precedes a switch in target rotation direction or perceived rotation, we found no effect of priming of visual search on bistable perception, nor an effect of sensory memory on search performance. In sum, the results of Experiments 1 and 2 show within-paradigm history effects but no effects across-paradigm, providing no evidence that priming of attentional selection and sensory memory for perceptual selection are related.

Experiment 3

The preceding experiments suggest that "history effects" does not occur between paradigms. However, before drawing such a conclusion, we first addressed one additional methodological factor that might play a role. Specifically, Experiment 1 revealed within-paradigm priming effects on search response times and effects of bistable trials on bistable perception. This poses a problem if interparadigm priming, although present, is much weaker than within-paradigm priming. It is possible that the within-paradigm perceptual priming that we demonstrated in Experiment 1 was so dominant that it fully determined subsequent perception, in spite of the simultaneous presence of priming caused by intervening search trials.

We therefore ran a different variant of Experiment 1, systematically varying the degree of ambiguity of the sphere that was presented on bistable trials. Specifically, on separate trials we included depth cues of varying strength, rendering the sphere either fully ambiguous, fully unambiguous, or somewhere in between. The purpose was twofold: First, by encouraging different perceived rotation directions on separate trials, we limited the build-up of sensory memory for one specific rotation direction. Second, the presence of depth cues of various strengths prevented the probability of perceiving a given rotation direction from saturating to 0 or 1 under the influence of any sensory memory that still formed, thus leaving room for detecting small effects of the interleaved search trials on perceived rotation direction. In other words, this experiment allowed us to test for across-paradigm interaction from search trials onto perception during bistable trials, with minimal interference of sensory memory from bistable trials.

Methods

Spheres that rotated around their central vertical axis, similar to the ones in Experiments 1 and 2 were presented, but with depth cues added on the spheres on bistable trials. Specifically, to provide a depth cue, we altered the sphere's dot size and luminance as we did for the target and distractor spheres of Experiments 1 and 2, while in addition we applied a perspective depth
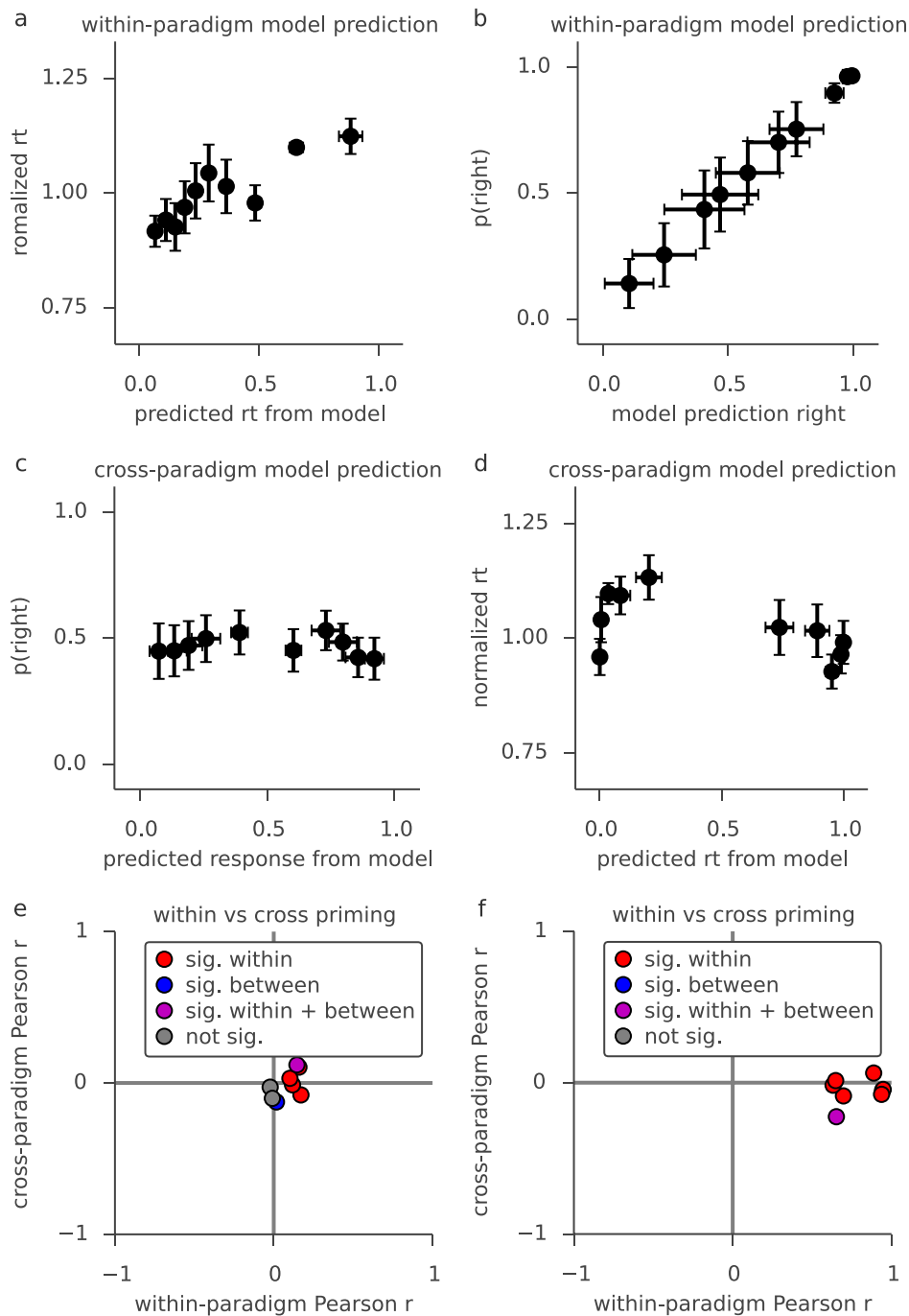
Figure 5. Results of our Reanalysis of Experiments 1 (left column) and 2 (right column). The first row of panels shows how well the model fits the within-paradigm data, and the second row shows this for the cross-paradigm data. Specifically, panel (a) shows the average of median response times across observers, as a function of the response time predicted by the modelled priming signal of Experiment 1, binned by percentiles of 10%. Panel (c) displays the proportion of trials in which observers perceived rightward rotation, as a function of the modelled signal for search priming in Experiment 1, again binned in 10% percentiles. Panel (b) displays the proportion of bistable trials in which observers perceived rightward rotation of the spheres during bistable trials, as a function of the modelled sensory memory signal from Experiment 2, binned by 10% percentiles. Panel (d) displays response times to search trials, as a function of the modelled sensory memory signal of Experiment 2, binned by 10% percentiles. For panel (a) and (d), the *x* axis represents the modelled priming signal toward perceived leftward rotation for search trials in which the target rotated leftward, and the modelled priming signal toward rightward rotation for search trials in which the target rotated rightward. Panel (e) for Experiment 1 and (f) for Experiment 2 display fits of the modelled priming signal with cross-paradigm data, against within-paradigm data as reflected by Pearson correlation coefficients. Colors indicate significant correlations of the modelled priming signal and actual data: red for within-paradigm, blue for cross-paradigm, and magenta for both within and cross-paradigm *r* values. Gray reflects no significant correlation between the modelled priming signal and actual data.

cue as a function of dot position in depth whose purpose was to induce stronger disambiguation. We ensured that perceived rotation direction was fully unambiguous for the most strongly disambiguated spheres. We presented a total of seven different ambiguity levels, ranging from unambiguous leftward rotation, via ambiguous rotation, to unambiguous rightward rotation. For the various ambiguity levels, dot size was manipulated as follows. It was constant for ambiguous spheres, and for disambiguated spheres it increased linearly from far to near dots with a range of 99%–101%, 88% −112%, or 60%–140% relative to the dots positioned centrally on the depth axis (0.12° VA). Luminance was constant (35.3 cd/m^2) for ambiguous spheres and changed from 35.3 to 35.8, from 32.6 to 38.1, or from 25.9 to 47.5 cd/m^2 for the different ambiguity levels. To provide a perspective depth cue, the horizontal and vertical positions of dots were gradually compressed when moving away from, or inflated when moving toward the observer relative to the sphere's center. To do so, horizontal and vertical dot positions scaled linearly as a function of the depth-axis by factors ranging from 0.99 to 1.01, from 0.88 to 1.12, or from 0.60 to 1.40 for the different levels of disambiguation, or were not altered in the case of the fully ambiguous spheres.

The design was similar to Experiment 1. Series of one to three search trials were interleaved with trials that displayed a single sphere. Although the sphere on these trials had varying levels of ambiguity, we will still refer to these trials as "bistable trials" for convenience. On search trials, a display was presented with six disambiguated spheres. As in previous experiments, the target sphere and distractor spheres rotated in opposite directions. The task was identical to that of Experiment 1. Target and distractor rotation directions were reassigned randomly following each bistable trial. The different ambiguity levels were presented in random order, with each level occurring 24 times. This yielded a total of 168 series of search trials (504 trials for each observer).

Results and discussion

To assess within-paradigm search priming, we calculated median response times on search trials, as a function of the number of immediately preceding consecutive search trials that shared the current trial's target rotation direction. Figure 6a shows a negative slope for these median response times averaged across observers. Indeed, a repeated-measures ANOVA revealed that median response time changed significantly as a function of the number of preceding target rotation repetitions, $F(4) = 4.45$, $p < 0.01$. However, the Spearman's rank correlation coefficient between these

variables was not significantly different from zero across observers, $t(7) = -1.86$, $p = 0.11$; $BF = 1.10$. Although search priming was, therefore, not apparent when quantified in this manner, we did confirm search priming using our second measure, which focuses only on the first trial following a bistable trial. Specifically, Figure 6b shows that the median response time on trials where target rotation repeated with respect to the preceding search trial was lower compared to when target rotation direction did not repeat (two-tailed paired sample): $t(7) = 4.14$, $p < 0.01$; $BF = 12.67$.

To investigate if search priming biased bistable perception toward the preceding target rotation direction, the responses to bistable trials were split into two groups: all bistable trials that were preceded by a leftward rotating targets versus all bistable trials that were preceded by rightward rotating targets. For each we then investigated how the proportion of trials that resulted in perceived rightward rotation varied as a function of the value of the depth cue. Figure 6c shows this relation for the two groups of trials. A logistic curve was fitted to the proportions of reported rightward rotations over all observers as a function of the depth-cue value. To test whether the two groups were statistically different, we fit a logistic curve to the reported rightward rotations for each observer, to identify the degree of disambiguation for which observers were equally likely to report either rotation direction. If preceding search trials affect perception of these spheres, then this degree of disambiguation should differ between the two groups. There was, however, no such difference (two-tailed paired sample t test): $t(7) = 1.00$, $p = 0.35$; $BF = 0.50$.

Like our initial analyses of Experiments 1 and 2, this analysis did not incorporate any longer-term trial history. We also wished to include an analysis that would be sensitive to such longer-term trial history, in case it affected the level of priming. Therefore, we followed the same approach as in our Reanalysis of Experiments 1 and 2 (Figures 4 and 5) to calculate, for each individual search trial, the current internal level of the signal responsible for search priming. We found that this calculated level and search response times were correlated significantly for three out eight observers ($p < 0.05$), and marginally significantly for one remaining observer ($p = 0.08$). Across observers the correlation coefficient was significantly greater than zero (two-tailed one-sample t test): $t(7) = 2.66$, $p = 0.03$; $BF = 2.64$, thus confirming our ability to calculate a plausible estimate of the internal level of the search priming signal. To investigate whether this signal would also affect perception during bistable trials, we divided those trials into two groups, based on whether the calculated priming level favored rightward rotation or leftward rotation. For each of these two groups, we then again calculated the level of disambiguation at which observers were equally
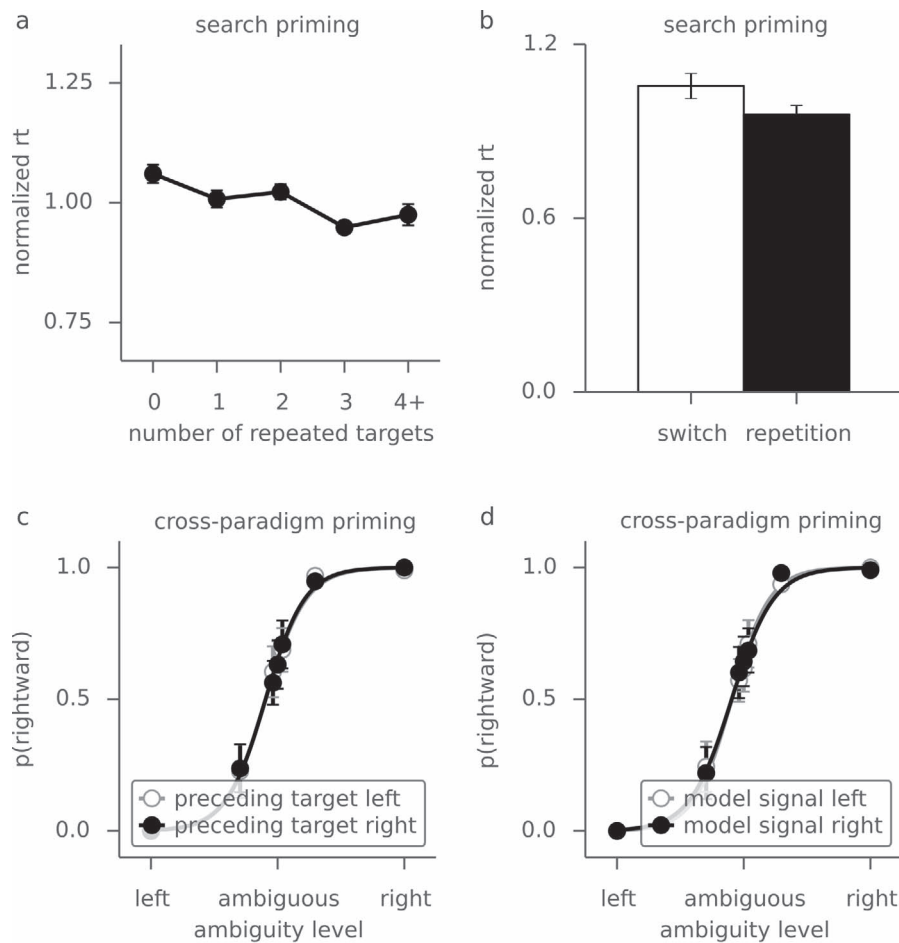
Figure 6. Results of Experiment 3. Panel (a) shows the average across observers of median response times as a function of the number of consecutive trials in which target rotation repeated. The 0-value on the *x* axis represents the first trial in a sequence of search trials in which target rotation did not change. Panel (b) displays response times to search trials that immediately followed a bistable trial when target rotation switched versus repeated with respect to the previous search trial. Panels (c) and (d) show the probability of perceived rightward rotation on bistable trials averaged across observers, as a function of the level of ambiguity either indicating leftward rotation, or rightward rotation in varying degrees. Logistic curves were fit to the average probabilities of all observers. In panel (c) the data was split by whether the immediately preceding search trial contained a leftward or rightward rotating target. In panel (d) the data was split by whether the modelled priming signal indicated a bias toward either leftward, or rightward.

likely to report either perceived rotation direction (Figure 6d), but we found no difference in this level between the two groups (two-tailed paired sample *t* test): $t(7) = -0.82$, $p = 0.44$; $BF = 0.44$. As a final check we repeated the same analysis including only the four aforementioned observers for whom the modelled level of search priming significantly predicted search reaction times, but still found no differences between the two groups of bistable trials (two-tailed paired sample *t* test): $t(3) = -0.83$, $p = 0.46$; $BF = 0.55$.

In sum, the aim of our final experiment was to minimize the build-up of within-paradigm sensory memory that could have affected Experiment 1, so that perceived rotation may be more sensitive to simultaneous search priming. Although we did establish the presence of search priming when investigating search

response times, we found no effect of search priming on perceived rotation during bistable trials. Note that the Bayes factors associated with the current experiment do not identify it as strong evidence against an interaction between paradigms, but these results do provide additional support in conjunction with our previous experiments.

General discussion

We set out to test for an interaction between priming by visual search and sensory memory for bistable perception. Specifically, in Experiments 1 and 3 we examined whether priming elicited by visual search could

affect the interpretation of an ambiguous stimulus, and in Experiment 2 we investigated whether sensory memory of an ambiguous image could affect search response times. Whereas we found within-paradigm repetition effects in all experiments, we did not find any evidence of across-paradigm history effects.

One of our motivations for hypothesizing an interaction between the two repetition effects was work showing a biasing effect of attentional cueing on subsequent bistable perception (Chong & Blake, 2006; Mitchell et al., 2004). One potential reason why we do not find a similar biasing effect of attention priming is that the locations of ambiguous and search stimuli in our experiments never overlapped, whereas the cueing work focused on a situation with full retinal overlap between attended stimuli and subsequent ambiguous stimuli. It is known that sensory memory for bistable perception is most effective if consecutive stimuli fall within the same area of the visual field (Chen & He, 2004; Knapen et al., 2009). On the other hand, retinal overlap is unlikely to be the sole explanation for our results, since priming in typical visual search paradigms does not depend strongly on spatial overlap (e.g., Ásgeirsson et al., 2014; Maljkovic & Nakayama, 1994).

A second factor to consider is the fact that our search displays consisted of unambiguous stimuli. In conventional paradigms sensory memory is less readily produced when an ambiguous stimulus is preceded by an unambiguous version of one of its interpretations than when using only ambiguous stimuli (Brascamp, 2007; De Jong, Knapen, & van Ee, 2012; Sterzer & Rees, 2008; but see also Kanai & Verstraten, 2005). In addition, positive biasing effects that do arise from unambiguous displays decay more rapidly (Brascamp et al., 2007; Pinkus & Pantle, 1997). Whereas our stimulus intervals were well below a second, they were not as short as, for instance, the intervals used in the afore-mentioned cueing experiments (Mitchell et al., 2004; Chong & Blake, 2006).

Apart from interstimulus intervals, the stimulus duration itself may be of importance here as well. We presented our search displays until the observer responded. Thus, considering response times, these displays were presented for more than a second per trial. Stimulus durations of over a few hundred milliseconds have been shown to induce adaptation to stimulus motion (Kanai & Verstraten, 2005; Pastukhov & Braun, 2013; Pavan, Campana, Guerreschi, Manassi, & Casco, 2009; Pavan, Campana, Maniglia, & Casco, 2010; Wolfe, 1984), which may counteract an initial bias toward that same motion direction. On the other hand, adaptation to the search displays may not play an important role in our particular case, considering the different retinal locations of search display elements and the ambiguous stimulus. Importantly, adaptation would also not explain why within-paradigm repetition

effects, themselves not overshadowed by adaptation, do not carry over across paradigms.

Finally, the target and distractors were presented simultaneously within each search display. If we assume that target processing and distractor processing both prime the perceived interpretation of a bistable sphere in the same way, then there may be no net effect. Note, however, that this is an unconventional view in light of common interpretations of, for example, distractor suppression in visual search, which has been interpreted as an inhibited sensitivity to distractor features (Kristjánsson & Driver, 2008; Tipper, 1985), whereas target features are thought to be enhanced.

To conclude, the rationale for the present study was that visual search priming and sensory memory for bistable perception show similarities that could reflect a shared underlying mechanism. Both tasks require a selective response by the observer, either between target and distractors during a search task, or between two possible interpretations of an ambiguous stimulus. Although attention allocation toward a stimulus or its features does affect perception of ambiguous stimuli (Chong & Blake, 2006; Fischer & Whitney, 2014; Kristjánsson, 2009; Mitchell et al., 2004), we find no evidence that priming elicited by target selection and sensory memory elicited by perceptual selection are directly related.

Keywords: visual search, bistable perception, priming, sensory memory

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