Reward modulates perception in binocular rivalry

Svenja Marx
Neurophysics, Philipps-University, Marburg, Germany

Wolfgang Einhäuser
Neurophysics, Philipps-University, Marburg, Germany

Our perception does not provide us with an exact imprint of the outside world, but is continuously adapted to our internal expectations, task sets, and behavioral goals. Although effects of reward—or value in general—on perception therefore seem likely, how valuation modulates perception and how such modulation relates to attention is largely unknown. We probed effects of reward on perception by using a binocular-rivalry paradigm. Distinct gratings drifting in opposite directions were presented to each observer’s eyes. To objectify their subjective perceptual experience, the optokinetic nystagmus was used as measure of current perceptual dominance. In a first experiment, one of the percepts was either rewarded or attended. We found that reward and attention similarly biased perception. In a second experiment, observers performed an attentionally demanding task either on the rewarded stimulus, the other stimulus, or both. We found that—on top of an attentional effect on perception—at each level of attentional load, reward still modulated perception by increasing the dominance of the rewarded percept. Similarly, penalizing one percept increased dominance of the other at each level of attentional load. In turn, rewarding—and similarly nonpunishing—a percept yielded performance benefits that are typically associated with selective attention. In conclusion, our data show that value modulates perception in a similar way as the volitional deployment of attention, even though the relative effect of value is largely unaffected by an attention task.

Introduction

In decision making, the role of expected outcome (i.e., reward or punishment) and related variables has been studied intensely (Deco, Rolls, Albantakis, & Romo, 2013; Glimcher & Rustichini, 2004; Preuschoff, Bossaerts, & Quartz, 2006) and led to increasingly sophisticated theories of motivational learning (Rescorla & Wagner, 1972; Watkins & Dayan, 1992). Similarly, the interest in the (neuro-) physiological foundations of reward processing, which dates back to Pavlov (1927) and Skinner (1938), has flourished since dopamine’s role as signal for reward prediction error was unveiled (Schultz, Apicella, Scarnati, & Ljungberg, 1992), eventually leading to neuroeconomics (Glimcher & Rustichini, 2004) as a new field within the neurosciences. Especially in nonhuman primates, decision-making experiments frequently employ perceptual tasks, such as discovering coherent motion in random dot patterns (Newcombe & Pare, 1988). Despite the use of perceptual tasks, surprisingly little research has addressed direct effects of reward and punishment on perception per se. This is even more remarkable, given that contemporary models of perception under ambiguity and decision-making under uncertainty often use the same “Bayesian” formalism (Bülthoff & Yuille, 1996; Freeman, 1994; Kersten, Mamassian, & Yuille, 2004). At least in the context of perceptual rivalry, pupillometric data suggests shared neural mechanisms for decision making under uncertainty and the resolution of perceptual ambiguity (Einhäuser, Stout, Koch, & Carter, 2008). When viewing natural perception as inferring a unique perceptual interpretation from underconstrained sensory information (Von Helmholtz, 1867), it is tempting to think of perception as a decision process among the infinite number of possible interpretations. Under this hypothesis, valuation processes that modulate cognitive decision making should similarly exert a direct influence on the perceptual interpretation of constant stimuli.

Valuation processes can in principle exert an influence on perception in two ways: First, valuation may modify perception through selective attention, which directly alters perceptual appearance (Carrasco, Ling, & Read, 2004). Indeed, there is mounting evidence for effects of reward on attention: The processing of reward-associated features is facilitated in tasks requiring visual selective attention (Della Libera & Chelazzi, 2009; Hickey, Chelazzi, & Theeuws, 2010) and rewards affect attentional learning (Della Libera & Chelazzi, 2009). The effects of reward on attentional...
processing are present even several days later (Della Libera & Chelazzi, 2009), and differ between different forms of automatic orienting such as space- and object-based attention (J. Lee & Shomstein, 2013). Second, rewards may exert a direct influence on perception by modulating perceptual representations without or in addition to attentional mechanisms (Seitz, Kim, & Watanabe, 2009).

Binocular rivalry, a situation where the two eyes are presented with dissimilar stimuli, is an ideal paradigm to test direct effects on perception, since the stimulus remains unchanged while perception alternates between two alternatives (percepts). Effects of attention on rivalry are well established: Attention speeds up the alternations between percepts (Paffen, Alais, & Verstraten, 2006), and attention to one stimulus increases its perceptual dominance (Ooi & He, 1999; Van Ee, van Dam, & Brouwer, 2005). Whether reward exerts a similar effect on perceptual dominance and whether it uses attentional mechanisms or acts in addition to attention, is unknown.

In the present study we used binocular rivalry to test the hypothesis that reward has a direct effect on perception. In a first experiment (Experiment 1), we tested whether explicitly rewarding one percept has a similar effect as attending it. In separate parts we either asked observers to attend one of the percepts or explicitly associated a reward with seeing one of the percepts. To circumvent the issue of relying on observers’ report, we used the optokinetic nystagmus (OKN) to objectively measure at any point in time which percept observers were subjectively experiencing (cf. Fahle, Stemmle, & Spang, 2011; Naber, Frässle, & Einhäuser, 2011). In a second experiment (Experiment 2), we again explicitly rewarded one percept, but in addition asked observers to perform an attentionally demanding task either on the rewarded percept, the nonrewarded percept, or both, thus generating three attentional conditions. In a separate part of Experiment 2, reward was replaced by punishment, with otherwise unchanged instructions or stimuli. This allowed us to test the hypothesis that reward and punishment bias perception even when attention is engaged in a different task.

**Methods**

**Participants**

Eight participants (seven female, 27.0 ± 3.66 years) participated in Experiment 1. This number was decided upon prior to the experiment based on estimates derived from previous rivalry studies (e.g., Naber et al., 2011), which showed that—despite considerable interindividu-

al variability in absolute dominance durations—behavioral effects are typically robust, in that their qualitative direction (sign) can be expected to be consistent across individuals. Eight participants (six female 25.5 ± 2.98 years) participated in Experiment 2, with one participant (#6) participating in both experiments (15 participants in total). The number of participants in Experiment 2 was chosen to match Experiment 1, and was decided upon after the conclusion of Experiment 1, and prior to starting Experiment 2. Before the experiment, participants gave written informed consent. All procedures were in accordance with the Declaration of Helsinki and approved by the local ethics committee (Ethikkommission FB04).

**Setup and stimuli**

Stimuli were generated using Matlab (Mathworks, Natick, MA) and the Psychophysics Toolbox (Brainard, 1997; Pelli, 1997) and Eyelink toolbox (Cornelissen, Peters, & Palmer, 2002) extensions. They were displayed on two 21-inch Syncmaster CRT screens (Samsung, Seoul, South Korea), each set to 1280 × 1024 pixels spatial and 85 Hz temporal resolution, and presented dichoptically at a viewing distance of 30 cm by using a mirror stereoscope. Each observer’s left eye position was tracked by a noninvasive eye-tracking device (EyeLink 2000, SR Research, Osgoode, ON, Canada) at 500 Hz. The eye tracker’s infrared camera and illuminator were positioned behind the mirrors, which were transparent to infrared light (cold mirrors), such that the eye-tracking setup was not visible to the observer.

In both experiments, sine-wave gratings with a spatial frequency of 0.21 cycles per degree were presented to both eyes for 180 s in each trial. Gratings were of different color (red/green), differently oriented (± 20°) and drifted upward perpendicular to their orientation at a speed of 14.25°/s (Figure 1a). The gratings were presented in a circular aperture with a diameter of 30° in Experiment 1 and of 21° in Experiment 2. The aperture was surrounded in both eyes by the same blue annulus that could vary in width from 0° to 3.4° (60 pixels).

In reward trials, the annulus width grew proportionally to the amount of reward, in punishment trials proportionally to the monetary punishment. In trials without reward or punishment, the width remained constant at a value between 0° and 3.4° that was chosen randomly for each trial.

OKN slow phase as measure of perceptual dominance, assignment of reward

While most binocular-rivalry experiments in humans rely on the observers’ subjective reports regarding their
perceptual experience, this is suboptimal in the present context for at least two reasons: First, observers could strategically choose to report their percept nonveridically to maximize reward (i.e., they could “cheat”); second, the requirement to report one’s percept could interfere with attentional tasks. Since the direction of OKN’s slow phase closely replicates the observer’s perceptual experience when viewing drifting gratings (e.g., Naber et al., 2011), we used this objective measure throughout. For applying reward, eye velocity was calculated online by differentiation of the eye’s raw horizontal position collected at a frequency of 85 Hz. If three successive samples were in the required direction and velocity range (between 3.6°/s and 30°/s), reward (or punishment) was increased by one point.

For calculating dominance durations and alternation rates, the eye traces were processed offline. First, horizontal eye velocity was obtained by differentiation of raw horizontal eye position. Then all OKN fast phases were removed by applying thresholds to convolution-filtered (square-smoothing window of 0.1-s width) eye-velocity traces (>15°/s) and acceleration (>100°/s²; Figure 1b). All removed parts of the velocity trace were then interpolated using a piecewise cubic Hermite interpolation. An objectively measured switch from one percept to the other was then defined as a zero crossing of the resulting horizontal OKN slow phase. Dominance durations were defined as the time between successive switches; alternation rate was defined as the number of switches per time. For the active-report conditions of Experiment 1, we also verified the correspondence between button presses and OKN-defined dominance phases and found them to be well matched, with the exception of short dominance durations being missed by the observers’ subjective reports (Figure 1b; see also Naber et al., 2011).

Figure 1. Stimuli and objective measure of perceptual state. (a) Binocular rivalry stimulus: Using a mirror stereoscope, each eye was presented a different drifting grating; the gratings differed in color, orientation, and motion direction to robustly induce binocular rivalry; the blue annulus signaling reward (in some conditions of Experiment 2: punishment) was presented identically to both eyes. (b) Example excerpt eye-trace of one observer (Observer #4); gray trace: raw velocity; black trace: interpolated OKN slow phases; black vertical lines: time of zero-crossings of OKN slow phase that define a perceptual switch; red/green bars inside of graph: perceptual state as defined by OKN; red/green bars on top of graph: button corresponding to red/green grating pressed (gaps imply no button pressed at the respective time point). In general button presses, which are only available in the active-report condition, aligned well with the switch times inferred from the OKN slow phase, which were available in all conditions and on which all analysis was based.

Procedure

Assignment of reward and punishment

In reward/punishment trials, the online OKN analysis resulted in a reward/punishment point for each sample in which the rewarded/punished percept was dominant (provided the velocity criterion was met for at least three successive samples; see above). Each aggregated 180 points resulted in a one pixel increase of the blue annulus. This increase was sufficiently smooth to look continuous to the observers. We allowed a maximum annulus of 60 pixels, which corresponded to 10,800 points or 127 s (10,800/85 Hz) of dominance (70.5% of the trial) of the respective percept. In Experiment 1, the maximum reward (60 pixels) corresponded to 1 € of actual money with linear mapping of points to Euros. In the reward blocks of Experiment 2, 60 pixels corresponded 0.5 €; in the punishment blocks of Experiment 2, 0 pixels corresponded to 0.5 € and 60 pixels to 0 €.

Experiment 1

Experiment 1 consisted of three different conditions. In the reward condition, participants were instructed before trial onset that they were going to be rewarded for seeing one of both colors. Reward was then indicated by the width of the blue annulus surrounding the drifting gratings. In the attention condition, before trial onset participants were instructed to attend to one of both colors. In the no-instruction condition, stimuli were presented without specific instructions regarding reward or attention. In half of the trials of each condition, participants were in addition instructed to report the grating’s drifting direction by pressing and holding one of two buttons (active-report condition); in
the other half they were just passively viewing (passive-viewing condition). Including the active-report condition in Experiment 1 allowed us to probe possible interactions of the requirement to report with reward and to verify the OKN analysis (see above). For comparability between conditions, however, all analysis in both conditions was based on dominance durations as inferred from the OKN data.

The experiment was split in four sessions of three blocks each. Each block consisted of four trials. The instruction condition (reward, attention, none) was constant in each block, but the assignment of reward/attention to color and the report condition changed between trials within blocks.

**Experiment 2**

To test whether the effect of rivalry on reward prevailed when attention was engaged either on the rewarded stimulus or elsewhere, in Experiment 2 we aimed at increasing the attentional load on the observers. Unlike typical dual-task situations, the eyes in our paradigm were in constant motion, following the perceived grating. The equivalent to performing a task at fixation is therefore to perform a task that is spatially locked to the grating. Consequently, we asked observers to perform a task with the drifting grating. Specifically, participants were instructed to detect a change in duty cycle of the grating, which lasted for three frames (35 ms) and occurred 30 times per trial and grating in random intervals of 1 to 6 s. Participants were instructed for which grating they had to report changes; they reported their detection by a button press. Observers could either be instructed to report changes only in one grating (full attention) and ignore the other (attention away) or to report changes in both gratings (split attention). Reward and punishment instructions were given in addition to the attentional instructions. This yielded a 2 × 3 design: Besides being rewarded or not, a stimulus could receive full attention (duty cycle change only to be monitored for this stimulus), split attention (both stimuli monitored), or attention away (other stimulus monitored). For the time a grating was dominant, we calculated performance as the fraction of duty-cycle changes that an observer reported within 1 s, divided by the total number of duty-cycle changes that occurred in the respective grating during its dominance. For the correctly reported duty-cycle changes in each grating, we in addition computed the average reaction time from the onset of a duty-cycle change to its report. To ensure task compliance, participants were also told that they were only given the money if performance in the detection task “was sufficiently good.”

To avoid interference with the attention task, observers were not required to report their percept; that is, all conditions of Experiment 2 in this respect corresponded to the passive viewing condition of Experiment 1. Other than the duty-cycle changes, which themselves did not induce changes in dominance, and a slight reduction in size (see above), to ease monitoring the reward-signaling annulus during the attentional task, stimuli were identical to Experiment 1.

Experiment 2 consisted of two types of blocks. In the reward blocks, participants were rewarded for seeing one of the two possible percepts, indicated by the blue annulus. In the punishment blocks, participants were penalized for seeing one of the two percepts. The penalty was also indicated by the blue annulus with a thicker ring, meaning less money. Before every trial, participants were informed about which was the rewarded/penalized stimulus and in which grating they had to execute the detection task. This resulted in three conditions per block: The rewarded/penalized percept could equal the percept in which the detection task had to be executed, the rewarded/penalized percept could be the percept that should not be attended for the task, and the rewarded/penalized percept could be one of the two attended percepts.

The conditions were randomized in blocks consisting of six trials each and every condition appeared four times, resulting in 12 trials per reward and punishment condition. In one experimental session, one reward and one punishment block each consisting of six trials was measured and each participant took part in two experimental sessions.

**Statistical analysis**

For comparisons between two conditions paired *t* tests were used (within-subject design), and for comparisons involving more than one factor or more than two levels per factor, repeated measures ANOVAs were used, treating observers as repeated measures. As measures of effect size, Cohen’s *d* is reported for *t* tests and partial eta square (*η*<sup>p2</sup>) is reported for ANOVAs. All statistical analysis was conducted using Matlab.

**Results**

In Experiment 1, we tested the effect of reward on perceptual dominance in binocular rivalry, and separately the effect of attention. Using the OKN as an objective measure allowed us to include conditions in which observers actively monitored and reported their current percept and those in which they just passively viewed the stimulus.
Robust induction of rivalry

To induce OKN reliably, we deliberately used large gratings as stimuli. Large stimuli in rivalry frequently result in mixed percepts (piecemealing). Although we did not query piecemealing explicitly, we had instructed participants during active-report conditions in Experiment 1 to report exclusive dominance. Under this instruction, the times in which no percept was reported (or both percepts were reported simultaneously) gave an indication how frequently the percept was unclear; that is, times of possible piecemealing. These periods only accounted for 7.15% ± 3.58% (M ± SD over observers) of active-report trials, and we observed no difference between the attention and the reward condition [attention: 9.67% ± 11.5%, reward: 4.20% ± 3.42%, attention vs. reward: t(7) = 1.19, p = 0.27, d = 0.086]. Even though we cannot exclude piecemealing in full, more than 90% of time observers reported an exclusive, unambiguous percept.

Reward and attention similarly bias perception

When observers received no instructions regarding attention or reward, they had dominance durations between 0.578 and 1.50 s (M ± SD over observers: 0.978 ± 0.364 s), and there was no difference between active reporting and passive viewing, t(7) = 1.36, p = 0.22, d = 0.48, paired t test. There was no strong bias for either percept, neither in the active-report (56.2% ± 9.3% green percept dominant) nor in the passive-viewing (54.1% ± 11.0%) condition. Due to the high interobserver variability in absolute dominance durations, which is typical for rivalry, for the remainder we normalized dominance durations in each observer by dividing all data per observer by the median dominance duration over the whole experiment. The relative effects were, however, qualitatively consistent across observers (all individual data are shown in the Appendix). With the normalized dominance durations, we still observed no significant difference between active report and passive viewing, t(7) = 1.04, p = 0.33, d = 0.37 (Figure 2a).

When instructing observers to attend one of the stimuli, its dominance duration increased significantly as compared to the unattended stimulus irrespective of whether the dominance was actively reported or not [2 × 2 repeated-measures ANOVA; main effect attended vs. unattended: F(1, 7) = 8.62, p = 0.022, η² = 0.55; main effect active report vs. passive viewing: F(1, 7) = 1.40, p = 0.28, η² = 0.17; interaction attention × report: F(1, 7) = 2.99, p = 0.127, η² = 0.30; Figure 2b]. When observers were instructed that one stimulus was rewarded, the respective stimulus similarly became significantly more dominant [main effect rewarded vs. unrewarded: F(1, 7) = 33.48, p = 0.0007, η² = 0.83] irrespective of passive or active viewing [main effect: F(1, 7) = 0.27, p = 0.62, η² = 0.037; interaction: F(1, 7) = 0.29, p = 0.61, η² = 0.040; Figure 2c]. To compare the attention and reward sessions directly, we in addition performed a three-way ANOVA on all data with factors VIEWING (active, passive), INSTRUCTION_TYPE (reward, attention), and AFFECTED_PERCEPT (rewarded/attended vs. other). As expected, there was a main effect of whether the percept was affected by instruction [i.e., the rewarded or attended percept as compared to the respective other percept: F(1, 7) = 13.65, p = 0.008, η² = 0.66], but no effect of INSTRUCTION_TYPE [F(1, 7) = 2.90, p = 0.13, η² = 0.29] or VIEWING [F(1, 7) = 0.63, p = 0.45, η² = 0.083] and no interactions (all Fs < 3.28, all ps > 0.11).

Hence, reward and attention to a percept both yielded a significant increase in its dominance duration, which—
when applied independently—was indistinguishable in magnitude. Hence Experiment 1 demonstrates an effect of reward on perception, but leaves open whether this effect is achieved merely by the observers allocating attention to the rewarded stimulus.

As alternative measure to dominance durations, we calculated alternation rates, the number of switches in perception per unit time (Figure 3). A $3 \times 2$ repeated measures ANOVA revealed a significant main effect of INSTRUCTION_TYPE [no instruction, attention, or reward; $F(2, 14) = 8.30, p = 0.0042, \eta^2_p = 0.54$], no main effect of VIEWING [active or passive; $F(1, 7) = 1.28, p = 0.29, \eta^2_p = 0.15$] and a significant interaction between INSTRUCTION_TYPE and VIEWING [$F(2, 14) = 5.70, p = 0.016, \eta^2_p = 1.0$]. Posthoc paired $t$ tests showed that the effect of instruction type resulted from a difference between no instruction and the other two conditions ($ts > 2.58, ps < 0.037$, exception: active: attention vs. no instruction; Table 1), which did not differ from each other ($ts < 0.43, ps > 0.68$). Hence, the results on alternation rates show the same pattern as the analysis of dominance durations: Reward modulates rivalry to a similar extent as attention.

## Reward modulates perception at constant attentional load

In Experiment 2, we tested the interaction between attention and reward. As an attentional task, observers had to respond to changes in the duty cycle of the attended grating or gratings (Figure 4a) while one of the two percepts was rewarded. Observers complied with this attentional instruction, and responded within 1 s to duty-cycle changes for full-attention stimuli in $77.7\% \pm 6.8\%$, for split-attention stimuli in $82.3\% \pm 3.1\%$, and (incorrectly) for attention-away stimuli only in $7.0 \pm 6.7\%$ of cases. We found a main effect of attention, $F(2, 14) = 73.89, p = 3.6 \times 10^{-8}, \eta^2_p = 0.91$ and of reward, $F(1, 7) = 35.06, p = 0.0006, \eta^2_p = 0.83$, on dominance durations. Although there was a significant interaction, $F(2, 14) = 5.63, p = 0.016, \eta^2_p = 0.45$, posthoc tests showed that for each level of attention (full, split, away), reward had a significant effect on dominance durations (Figure 4b). This pattern was consistent across individuals (see Appendix). Reward had an effect on dominance durations in every attentional condition [full: $t(7) = 3.85, p = 0.0063, d = 1.36$; away: $t(7) = 9.07, p = 4.0 \times 10^{-5}, d = 3.21$; split: $t(7) = 3.76, p = 0.0071, d = 1.33$]. Comparing the same reward condition between different attentional conditions revealed significant effects of attention on rewarded stimuli [full vs. away: $t(7) = 6.39, p = 0.0037, d = 2.26$; full vs. split: $t(7) = 4.29, p = 0.0036, d = 1.52$; away vs. split: $t(7) = 4.02, p = 0.0050, d = 1.42$], and on unrewarded stimuli [full vs. away: $t(7) = 9.83, p = 2.4 \times 10^{-5}, d = 3.47$; full vs. split: $t(7) = 7.20, p = 0.00018, d = 2.54$; away vs. split: $t(7) = 8.91, p = 4.6 \times 10^{-3}, d = 3.15$]. This demonstrates that even at the same instruction regarding attention, dominance durations are in addition modulated by reward.

![](image)

**Figure 3.** Alternation rates in Experiment 1. From left to right: Trials with no specific instruction, trials with attended stimulus, trials with rewarded stimulus. Dark gray: active-response condition; light gray: passive-viewing condition.

<table>
<thead>
<tr>
<th>Conditions</th>
<th>$t$ value</th>
<th>$p$ value</th>
<th>Cohen’s $d$</th>
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<td></td>
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<td>Active</td>
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<td>No instruction vs. reward</td>
<td>$t(7) = 1.73$</td>
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<td></td>
<td>Attention vs. reward</td>
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<tr>
<td><strong>Experiment 2</strong></td>
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<td></td>
<td></td>
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<tr>
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<tr>
<td></td>
<td>Unattended vs. split</td>
<td>$t(7) = 0.062$</td>
<td>0.95</td>
</tr>
</tbody>
</table>

Table 1. Statistical measures and effect sizes of posthoc comparisons of alternation rates.
Absence of punishment biases perception similarly to presence of reward

In a separate part of Experiment 2, we replaced the reward instruction by an instruction regarding monetary punishment. Stimuli were exactly identical to the reward part, and the instructions only differed in so far that the increasing blue annulus now signaled a reduction in monetary gain. Again observers complied well with the attentional instruction and responded faithfully to duty-cycle changes in attended stimuli only (full: 75.3% ± 3.4%; split: 78.8% ± 6.9%; away: 2.1% ± 2.5%). Qualitatively, the nonpunished percept behaved similarly to the rewarded percept in the other experimental part, and vice versa (Figure 4c; all individual data are shown in the Appendix). Indeed, there was a significant main effect of attention, \( F(2, 14) = 20.80, p = 6.4 \times 10^{-5}, \eta_p^2 = 0.75 \), and a significant main effect of punishment, \( F(1, 7) = 20.12, p = 0.003, \eta_p^2 = 0.74 \). Although we found an interaction, \( F(2, 14) = 5.94, p = 0.014, \eta_p^2 = 0.46 \), posthoc tests revealed significant differences for punishment versus no punishment at each attentional level [Figure 4c; full: \( t(7) = 3.30, p = 0.013, d = 1.17 \); away: \( t(7) = 3.34, p = 0.012, d = 1.18 \); split: \( t(7) = 7.45, p = 0.00014, d = 2.63 \)]. Comparing the same punishment conditions between attentional conditions revealed effects of attention on the punished stimulus [full vs. away: \( t(7) = 3.81, p = 0.0066, d = 1.35 \); full vs. split: \( t(7) = 2.67, p = 0.032, d = 0.94 \); away vs. split: \( t(7) = 6.63, p = 0.00030, d = 2.34 \)] and the unpunished stimulus [full vs. away: \( t(7) = 4.66, p = 0.0023, d = 1.65 \); full vs. split: \( t(7) = 3.28, p = 0.014, d = 1.16 \); away vs. split: \( t(7) = 4.69, p = 0.0022, d = 1.66 \)]. In sum, punishing a percept had a similar effect to rewarding the competing percept: The more valuable percept increased in dominance for each attentional condition.

Direct comparison of reward and punishment

To compare the effects of reward and punishment directly, the difference between dominance durations of rewarded and unrewarded stimuli at the same attentional level was calculated (Figure 4d). A 3 × 2 ANOVA revealed a main effect of attentional level, \( F(2, 14) = 9.69, p = 0.0023, \eta_p^2 = 0.58 \), but no effect of instruction (reward/punishment), \( F(1, 7) = 2.57, p = 0.15, \eta_p^2 = 0.27 \), and no interaction, \( F(2, 14) = 1.79, p = 0.20, \eta_p^2 = 0.20 \). For the reward condition, posthoc paired \( t \) tests revealed significant differences between the full and split, \( t(7) = 2.57, p = 0.037, d = 0.91 \), as well as for the away and split, \( t(7) = 3.19, p = 0.015, d = 1.13 \), conditions while the difference between full and away only tended to be significant, \( t(7) = 1.98, p = 0.088, d = 0.70 \). In the punished condition, only the difference between the full and away condition was significant, \( t(7) = 2.98, p = 0.021, d = 1.05 \), while the other differences only tended to be significant [full vs. split: \( t(7) = 1.93, p = 0.096, d = 0.68 \); away vs. split: \( t(7) = 2.31, p = 0.054, d = 0.82 \)]. The missing effects of instruction type and interaction indicate that the effect of reward and punishment are symmetric (rewarding one percept is equivalent to punishing) and both are similarly modulated by the attention task.
stimulus. Note that in contrast to Figure 4, data are here sorted
trials with split attention between punished and unpunished
stimulus unattended (i.e., the punished stimulus is attended),
unpunished stimulus attended, trials with the unpunished
between rewarded and unrewarded stimulus, trials with the
unrewarded stimulus attended, trials with split attention
trials with the rewarded stimulus attended, trials with the
Figure 5. Alternation rates in Experiment 2. Left: sessions with
reward, right: sessions with punishment. From left to right:
trials with the rewarded stimulus attended, trials with the
unrewarded stimulus attended, trials with split attention
between rewarded and unrewarded stimulus, trials with the
unpunished stimulus attended, trials with the unpunished
stimulus unattended (i.e., the punished stimulus is attended),
trials with split attention between punished and unpunished
stimulus. Note that in contrast to Figure 4, data are here sorted
by trial type, not by stimulus.

As for Experiment 1, we considered alternation rates
as an alternative measure to dominance durations also
for Experiment 2 (Figure 5). Since the alternation rate
provides one number per trial, we distinguished three
types of reward trials: The rewarded stimulus was
attended (rew/att), one stimulus was attended and the
other rewarded (rew/unatt), both stimuli were attended
and one was rewarded (rew/split). To treat punishment
analogous to the absence of reward, we sorted the three
types of punishment trials according to the “unpun-
ished” stimulus: Either the unpunished stimulus was
attended (unp/att), the punished stimulus was attended
and the unpunished was not (unp/unatt), or attention
was split (unp/split). If punishment is indeed equivalent
to the absence of reward, we expect no effect of
instruction (reward vs. punishment) and no interaction
between instruction and attention. If, however, the
presence of reward or punishment has an arousing
effect on the rewarded or punished stimulus, effects of
reward absence and punishment should differ and
modulate the attentional effect. Performing a $2 \times 3$
ANOVA with the factors of attention (att, unatt, split)
and instruction (rew/unp) showed a main effect of
attention, $F(2, 14) = 18.27$, $p = 0.00013$, $\eta^2 = 0.72$, but
no effect of instruction, $F(1, 7) = 2.17$, $p = 0.18$, $\eta^2 = 0.24$, and no interaction, $F(2, 14) = 0.83$, $p = 0.46$, $\eta^2 = 0.11$. Posthoc $t$ tests showed that for the rewarded
and the unpunished stimuli, this effect of attention was
entirely due to the difference between the attended
condition on the one hand and the other two
attentional conditions on the other hand (all $t$s > 3.56,
all $p$s < 0.0092; Table 1), while there was no difference
between the split and the unattended condition ($t$s <
2.25, $p$s > 0.059). This lack of effect for instruction
supports the notion that for our paradigm, reward and
absence of punishment have the equivalent effect,
rendering the possibility that reward and punishment
merely augment the rewarded/punished stimulus in an
unspecific way unlikely.

**Reward has similar effects on performance as
attention itself**

Value exerts an effect on perceptual dominance on
top of the effect induced by the instruction to
volitionally attend a percept to use it for a task. Since
Experiment 1 had already suggested that the qualitative
impact of reward and attention are similar, we here ask
whether reward and punishment can also modulate
performance for an attended percept akin to atten-
tional effects. In the split-attention condition of
Experiment 2, both the rewarded and the nonrewarded
percept were not only present at the same time, but also
received identical instructions regarding attention.
Hence this condition allowed us to test whether the
analogy between attention and reward at constant
attentional load extended to typical attentional mea-
sures like performance or reaction time. Of the duty-
cycle changes happening while the rewarded percept
was dominant, 84.9% ± 3.5% were detected. During its
dominance, the nonrewarded stimulus tended to be
detected less frequently, 78.2% ± 7.6%, $t(7) = 2.28$, $p =
0.056$, $d = 0.81$. Conversely, in the punishment part of
the experiment, the punished percept tended to be
detected less frequently than the nonpunished percept,
though this difference did not reach significance, 73.1% ±
16.3% vs. 80.0% ± 7.7%, $t(7) = 1.11$, $p = 0.30$, $d =
0.39$. A slight difference was also evident for reaction
times, with reactions trending to be faster for rewarded
stimuli, 429 ± 49 ms vs. 443 ± 61 ms, $t(7) = 2.12$, $p =
0.071$, $d = 0.75$, and being significantly faster for
nonpunished stimuli, 440 ± 63 ms vs. 422 ± 65 ms, $t(7) =
2.38$, $p = 0.049$, $d = 0.84$, respectively. Even though
the effects of reward and punishment on processing the
already attended stimulus are comparably weak, their
trend is in line with the notion that value has a similar
effect on perception as attention.

**Discussion**

We exploited an objective measure of perceptual
dominance in binocular rivalry to assess effects of
reward and punishment on perception. Effects of
reward were qualitatively similar to effects of attention.
Nonpunishing showed similar effects as reward, sug-
suggesting that the observed effects are specific to positive value and not a mere consequence of general stimulus relevance. Directing attention to one stimulus did not abolish effects of value (i.e., of reward or punishment). Irrespective of whether or not valuation and attention share the same mechanism, this suggests that volitional deployment of attention according to task demands leaves room for additional modulation of perception by value.

Our data show many commonalities between volitionally attending a stimulus and being rewarded for perceiving it. Both attention and positive value (i.e., reward or nonpunishment) up-modulate a stimulus’ dominance and show a trend to improve processing (performance and reaction times) for a stimulus that is already attended. The latter may have three different, not mutually exclusive, explanations: First, the positively valued percept might have better visibility; second, positive value may improve processing directly; and third, positive value allocates additional attentional resources to an already attended stimulus. Provided our findings that reward can act in addition to volitionally deployed attention, the notion that reward effects are attentional in nature would be in line with the observation that reward can guide—or even capture—attention irrespective of other attention-guiding factors (Failing & Theeuwes, 2014).

Using an objective measure of perceptual dominance is critical for two reasons: First, since OKN cannot be controlled volitionally, we rule out that observers’ report (rather than their perception) is biased by reward; that is, we avoid any possibility of “cheating.” Second, when imposing an attentional task, we avoid that this interferes with the necessity of attending the rivalry stimulus for report. While other objective measures could be employed to assess an observers’ perceptual state (e.g., fMRI decoding; Tong, Nakayama, Vaughan, & Kanwisher, 1998), the OKN has been established as robust measure of perceptual dominance in rivalry in humans (Fahle et al., 2011; Frässlé, Sommer, Jansen, Naber, & Einhäuser, 2014; Naber et al., 2011) and animals (Fries, Roelfsema, Engel, König, & Singer, 1997; Logothetis & Schall, 1990).

It has long been known that attention influences perception during binocular rivalry. Endogenously attending to one percept can stabilize it, although perception cannot be controlled entirely (Breese, 1899; Meng & Tong, 2004; Ooi & He, 1999; van Ee et al., 2005). This stabilizing effect of voluntary control is stronger for perceptual than for binocular rivalry (Meng & Tong, 2004; van Ee et al., 2005). Attention modulates perception in binocular rivalry in different ways; exogenously cueing attention to the rivaling stimuli can initiate switches in rivalry and thus speeds alternations (Ooi & He, 1999; Paffen et al., 2006; Paffen & van der Stigchel, 2010) and, accordingly, drawing attention away from the rivaling stimuli slows alternation rate (Paffen et al., 2006). While perceptual rivalry can occur even without allocating attention to the rivaling stimuli (Pastukhov & Braun, 2007), binocular rivalry requires visual attention (Brascamp & Blake, 2012; Zhang, Jamison, Engel, He, & He, 2011). Using fMRI, S.-H. Lee, Blake, and Heeger (2007) showed that drawing attention away from the rivaling stimulus left rivalry-related activity in primary visual cortex (V1) but not in extrastriate visual areas (V2, V3) where activity was rivalry-related when the stimuli were attended. Both our experiments confirm the basic effects of attention on rivalry. In turn, reward influenced dominance in rivalry as well as typical measures of attention, such as reaction times. This possibly points to a deeper conceptual link between visual selective attention and rivalry, which both are competitive processes, for which one stimulus is selected at the expense of others (Leopold & Logothetis, 1999).

Viewed in isolation, the finding that reward decreases overall alternation rates and increases dominance of the rewarded stimulus could be interpreted as perception being biased by stimulus relevance (Alpers, Ruhleder, Walz, Mühlberger, & Pauli, 2005) in a rather unspecific manner akin to arousal. Such a generic relevance effect would predict some up-modulation for the punished stimulus, making the effect on the unpunished stimulus in punishment trials at least smaller (if not reversed) than on the rewarded stimulus in reward trials. The fact that we instead find symmetry between presence of reward and absence of punishment suggests that the effect of reward is specific and not explained by stimulus relevance per se. Hence, the effect of valuation on perception is selective. In this selectivity, value is similar to attention (rather than to arousal).

Since reward and attention in our Experiment 1 had similar effects on perceptual dominance, and attention modulates perceptual appearance (Carrasco et al., 2004), it is tempting to assume that reward and punishment act through attentional processes. By engaging attention either elsewhere or on the rewarded stimulus, Experiment 2 tested whether rewards can modulate perception irrespective of other attentional demands. While this attentional task follows the logic of dual-task paradigms (e.g., D. K. Lee, Koch, & Braun, 1999; Pastukhov, Fischer, & Braun, 2009), there are several conceptual differences. First, there is no actual primary task, since rivalry in Experiment 2 is restricted to passive viewing; second, the secondary task is not conducted at fixation, but aligned with the movement of the stimulus. The former can be considered uncritical, provided that Experiment 1 showed no difference between active and passive conditions with respect to attentional and reward effects. The latter is necessary to keep the task fixed in...
retinal coordinates, since the OKN stabilizes the dominant percept relative to the retina; thus the situation is similar to dual tasks at fixation for static stimuli. As with typical dual-task paradigms, however, there is no guarantee that residual attentional resources are made fully unavailable. Indeed, the trend to worse performance for unrewarded percepts may even be interpreted as evidence for value acting through attentional mechanisms: Value interferes with the attentional task and therefore the mechanisms mediating valuation and attention are not fully independent. In sum, dominance durations in Experiment 2 demonstrate that value modulates perception at any level of attention, implying that this volitional deployment of attention required for task performance leaves room for modulation of perception by value. In turn, the performance data suggest that attention and valuation share common mechanisms to bias perception. Besides plenty of behavioral links between reward and attention (Della Libera & Chelazzi, 2009; Hickey et al., 2010; J. Lee & Shomstein, 2013), the interaction of attention and reward has been widely studied in the neurosciences. In nonhuman primates, even in V1, neurons’ activities were predicted by reward value of the respective stimulus and neurons that exhibited strong value effects also showed strong attentional effects implying overlapping neuronal selection mechanisms for value and top-down attention (Stänisler, van der Togt, Pennartz, & Roelfsema, 2013). In humans, reward-associated distractors in a saccade tasks had large influence on saccade curvature even when they should be ignored, resembling behavior in tasks where distractors were made more salient (Hickey & van Zoest, 2012). This analogy to an increase in salience was also found in an electroencephalography (EEG) study employing a visual selective attention task where participants shifted attention to objects characterized by previously rewarded features even if they knew this was counterproductive (Hickey et al., 2010). In line with our results, reward affected vision independent of the pure allocation of endogenous attention but also changed visual saliency directly. Thus, even though reward often leads to attentional allocation to the rewarded stimulus, reward can also act independently of attention (Baldassi & Simoncini, 2011). A recent fMRI study varied attentional demand and reward independently and found that—at least for some subcortical reward-related structures, the ventral temporal area and ventral striatum—reward anticipation modulated the blood-oxygen-level dependent (BOLD) responses irrespective of attentional load (Rothkirch, Schmack, Deserno, Darmohray, & Sterzer, 2013). This provides one potential mechanism for attention-independent modulation by reward. In sum, there is converging evidence from behavior, animal neurophysiology, and human imaging that rewards can modulate perception akin to visual selective attention without necessarily employing attentional mechanisms.

With the present psychophysical data alone, we cannot distinguish whether the mechanisms underlying the attention-like effects of value are identical to attention mechanisms or act through partially distinct circuitry. If attention and reward influence perception similarly and if they indeed act through the same mechanisms, is there any distinction at all? Specifically, is there any conceptual difference between asking observers to attend a percept, to keep it dominant as long as possible (van Ee et al., 2005), or to provide reward for succeeding in doing so? In general, a conceptual distinction can be drawn if attention is understood as selective attention in a Jamesian sense, that is as the “withdrawal from some things in order to deal effectively with others” (James, 1890). In contrast to this selectivity, rewards can act through unspecific signals, and reward-based learning then requires relating outcome to stimulus features or to one’s own actions. In the present paradigm, and to our knowledge in all rivalry/attention paradigms to date, reward effects cannot easily be distinguished from attention, as the assignment between percept and reward is trivial: There are only two percepts and the mapping between percept and reward is unambiguous. In combination with our findings and with our proposal to objectify the apparently subjective perception in rivalry, this observation may point to a future research direction: To dissociate selective attention from valuation signals, one could—in addition to the perceptual ambiguity in rivalry—add associative uncertainty to the mapping between perceptual dominance and value.

Keywords: attention, reward, binocular rivalry, perception, decision making

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Corresponding author: Svenja Marx.
Email: svenja.marx@physik.uni-marburg.de.
Address: Neurophysics, Philipps-University, Marburg, Germany.

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**Appendix**

Dominance durations showed substantial interindividual variability between observers, prompting the use of normalized durations for analysis. However, the direction of the effects was consistent across all observers: For all eight individuals of Experiment 1,
active and passive conditions yielded similar results (Figure 6), the attended stimulus showed longer dominance than the unattended one (Figure 6b), and the rewarded stimulus dominated longer than the unrewarded one (Figure 6c). Similarly, for Experiment 2, for all levels of attentional load and each individual, the rewarded percept had longer dominance durations than the unrewarded one (Figure 7a). The same held—with the exception of two observers in the away condition where dominance durations were close to floor—for unpunished relative to punished stimuli (Figure 7b). Hence, despite the large interindividual variability in the dominance durations that is typical for rivalry, the effects of attention, reward, and punishment are remarkable robust across observers.