Uncertain reward cues show increased dominance in early phases of binocular rivalry

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Abstract

Binocular rivalry occurs when the eyes are presented with two dissimilar images and visual awareness fluctuates between them. Previous findings suggest that perceptual dominance of a rewarded stimulus may increase relative to an unrewarded stimulus, implying a direct effect of reward on visual representations. Here, we asked how uncertainty about reward occurrence and average reward expectancy affect dominance in binocular rivalry. In three experiments, participants learnt to associate drifting gratings of distinct colors with different levels of uncertainty and expectancy. Uncertainty was manipulated by rewarding each correct trial either with 100% probability (no uncertainty) or with 50% probability (high uncertainty). The amount of reward was either identical per rewarded trial, yielding a lower expectancy in uncertain trials (Experiments 1 and 2), or reward expectancy was matched across uncertainty levels by doubling the award per rewarded trial for uncertain trials (Experiment 3). In Experiment 2, an additional low-reward condition with no uncertainty was included. Using a no-report paradigm, we measured the perceptual dominance of these gratings relative to a grating that was unassociated with reward, before and after associations had been acquired. When the rewarded stimulus feature (color) was task relevant, dominance durations increased for all rewarded gratings after acquisition. In an early phase after rivalry onset we found increased perceptual dominance for cues associated with uncertain reward compared to cues associated with certain reward. This confirms an effect of reward on perceptual dominance, and suggests that reward uncertainty associated with a stimulus has a direct bearing on its visual representation.

Introduction

In our everyday lives, we frequently encounter stimuli that have consequences, such as reward or punishment. According to associative learning theories, these events – the stimulus and its consequence – become connected in memory upon co-occurrence. This connection grows stronger if the same combination of stimulus and consequence is experienced repeatedly, forming a cue-outcome-association (e.g., Pearce & Bouton, 2001; Rescorla, 1988). Many theories of associative learning assume that this association will in turn shape the way we perceive and allocate attention to the stimulus in the future (e.g., Kruschke, 2001; Mackintosh, 1975; Pearce & Hall, 1980). It is, however, highly unusual for a cue to be followed by the same outcome in every instance, constituting a 100% cue-outcome-contingency. In real-world scenarios, cue-outcome-contingencies vary, inducing uncertainty about whether a particular outcome will or will not ensue. Two opposite attentional processes have been theorized to take effect while attending to stimuli in a learning context. One body of research, pioneered by Mackintosh (1975), has been focused on the hypothesis that attention during learning will be preferentially allocated to *predictive* cues, i.e., cues that are consistently followed by the same outcome, as opposed to unpredictable cues that are followed by different outcomes. While originally drawn from animal conditioning studies, this hypothesis has gained substantial support from human perceptual-cognitive research. An attentional amplification of cues that reliably predict an outcome – albeit not necessarily reward or punishment – could be shown for variety of measures of visual attention, like overt visual attention (e.g. Beesley et al., 2015; Le Pelley et al., 2011; Le Pelley et al., 2013; Mitchell et al., 2012), a detection advantage during the attentional blink (Glautier & Shih, 2015; Livesey et al., 2009) and faster response times in a spatial cueing task (Haselgrove et al., 2016; Le Pelley, Vadillo, et al., 2013) (see Le Pelley et al., 2016, for a review).

Pearce and Hall (1980), on the other hand, proposed an opposite attentional mechanism that favors *uncertain* cues, which are not followed consistently by the same outcome. This approach has also gathered experimental evidence from animal conditioning studies (Haselgrove et al., 2010; Kaye & Pearce, 1984; Swan & Pearce, 1988). With respect to humans, an attentional effect of uncertainty has been reported in regard to total fixation dwell time (Beesley et al., 2015; Hogarth et al., 2008; Koenig et al., 2017a; Koenig et al., 2017b) and pupil dilation (Koenig et al., 2018) during associative learning. Although successful attempts have been made to integrate the two mechanisms (Beesley et al., 2015; Le Pelley et al., 2016; Luque et al., 2017; Pearce & Mackintosh, 2010), we will keep up the dichotomous distinction for simplicity.

It is important to note that during reinforcement learning, stimuli can be equally predictive but different in motivational outcome. Take, for example, an experimental setting in which one cue is rewarded with a contingency of 80% and another cue with the same reward with 20% contingency. Both cues predict the outcome 80% of the time, but the first cue has a higher motivational value than the second. One way that has been used to quantify the motivational value associated with an outcome is average reward expectancy. Also referred to as expected or learned value (Cho & Cho, 2020; De Tommaso et al., 2019; Le Pelley et al., 2016), reward expectancy linearly increases with the average amount of reward a stimulus is associated with. E.g., if you consider three stimuli, each one associated with the same reward (say a monetary reward of 10 Cent in a rewarded trial) but with different reward contingencies (reward in 10%, 50% or 90% of trials), the average reward expectancy of the stimuli will be 1, 5 and 9 Cent. In a situation where two stimuli predict high or low reward equally well, there is evidence suggesting that the cue associated with higher reward expectancy attracts more attention than the motivationally less salient cue (Anderson et al., 2011; Anderson & Yantis, 2013; Feldmann-Wüstefeld et al., 2016; Kiss et al., 2009; Theeuwes & Belopolsky, 2012). It has been suggested that even a reward-cue that is response-independent and task-irrelevant during learning has the ability to capture visual attention during learning (Le Pelley et al., 2015) and also after reward administration has ceased (Bucker & Theeuwes, 2017). In addition to motivational outcome, there is evidence suggesting an uncertainty-based type of attentional processing during learning and beyond (Cho & Cho, 2020; Koenig et al., 2018; Koenig et al., 2017a; Koenig et al., 2017b; Le Pelley et al., 2019). E.g., Koenig et al. (2017a) compared three reward-associated color cues' ability to capture overt attention when presented as distractors in a search task that was separate from a learning task. During the learning task, two colors were established as reliable predictors of high (10 Cent) and low (1 Cent) reward, while the third color was partially (50%) reinforced with high reward (10 Cent). This rendered possible a direct test of whether reward expectancy or uncertainty influences overt visual attention: The high and low reward cues induce low uncertainty about the outcome and the partially reinforced cue induces high uncertainty. Hence, if uncertainty is the key factor guiding overt attention, the partially reinforced cue should primarily capture and hold overt attention. But as the partially reinforced cue yields an intermediate reward expectancy ($10 \text{ Cent} \times 50\% \text{ reward contingency} = 5 \text{ Cent}$ reward expectancy), a gradual increase in attentional strength from low to partial to high reward should be observed. They found that the rate of attentional capture by the colors in the search task was dependent on reward expectancy, while fixation duration corresponded to uncertainty.

A suitable tool for exploring such differential effects of expectancy, uncertainty and predictiveness on stimulus processing during associative learning might be the study of perceptual awareness during binocular rivalry. Binocular rivalry is a phenomenon that is invoked when incompatible images are presented to the two eyes causing visual awareness to alternate between the left and right eye's percepts (Wheatstone, 1838). Because the input stimulus remains unchanged while perception fluctuates, the study of binocular-rivalry dynamics is an optimal paradigm to study determinants of perceptual competition and selection processes guiding visual awareness as well as neural correlates of visual perception (Blake & Logothetis, 2002). A wide range of factors has been demonstrated to influence dominance in binocular rivalry. When it comes to stimulus characteristics, simple features such as luminance (Kaplan & Metlay, 1964), contrast (Mueller & Blake, 1989), motion (Fox & Check, 1968), and spatial frequency (Fahle, 1982) as well as more high-level stimulus characteristics like meaningfulness (Yu & Blake, 1992) and scene coherence (Mudrik et al., 2011) affect dominance in binocular rivalry. Affective content has been shown to bias perception in binocular rivalry, pointing to an influence of motivational value. For example, emotional faces and scenes (Alpers & Gerdes, 2007; Alpers & Pauli, 2006; Coren & Russell, 1992) elicit dominance. Furthermore, linking up a stimulus to other domains can influence its dominance. This might happen through a pre-existing commonality, e.g. when a self-generated motor action corresponds to stimulus movement (Maruya et al., 2007), or through a newly formed association to another domain like another sensory modality (Einhäuser et al., 2017a; Kim & Kim, 2019) or reward (Marx & Einhäuser, 2015; Wilbertz et al., 2014). It seems that it is possible – at least to a certain degree – for observers to voluntarily influence perceptual durations and switches in binocular rivalry (van Ee et al., 2005), although it has been argued that this capability is more limited for binocular rivalry than for other bistable perceptual phenomena (Meng & Tong, 2004). Similarly, attending to one of the two presented images will increase its dominance durations compared to those of the unattended image (Marx & Einhäuser, 2015; Ooi & He, 1999). Attending to both will shorten dominance durations of both (Paffen et al., 2006) and taking attention away from them can abolish rivalry dynamics (Brascamp & Blake, 2012). Even without volitional or explicit attention to the stimulus, a stimulus' task relevance can lead to an increase in its dominance (Chopin & Mamassian, 2010).

Only few studies have addressed associative learning in the form of classical or instrumental conditioning in the context of binocular rivalry. Balcetis et al. (2012) briefly presented numbers and letters as incompatible stimuli to the eyes and participants reported their perceptual experience.

Report of numbers or letters was associated with the possibility of reward or loss of reward respectively. Across several experiments, participants more frequently reported experience of the rewarded percept than experience of the punished percept. Wilbertz et al.'s (2014) participants performed a target detection task where targets alternatingly appeared on the two rivalry stimuli of orthogonal rotating different-colored gratings. Unbeknownst to the observers who thought they were rewarded according to task performance, perception of one grating was rewarded throughout the experiment. During learning, i.e., while reward was administered, an increase in dominance durations for the percept associated with reward compared to the unrewarded percept was observed. In a second experiment that utilized the same design but a financial loss of 10 Cent instead of gain, an increase in dominance durations for the non-punished percept relative to the punished percept was found. Interestingly, in a subsequent study that combined a similar button press task with functional magnetic resonance imaging of neural rivalry correlates as an objective online measure of perception, Wilbertz et al. (2017) were unable to confirm this finding. Marx and Einhäuser (2015) found that rewarding a percept led to a similar increase in dominance as attending it, but at a constant level of attention reward still modulated dominance. Taken together, these results provide evidence for effects of reward on dominance in binocular rivalry. In this study we extend this line of work beyond the mere binary distinction between rewarded and unrewarded (or punished and unpunished) stimuli and link it to the questions asked in associative-learning research. Specifically, we ask how different levels of reward expectancy and reward uncertainty associated with a cue influence this cue's perceptual dominance in binocular rivalry.

Unlike most studies in binocular rivalry, we chose not to rely on the observers' subjective report of their perceptual experience as a measure of perceptual dominance: Besides being susceptible to response and experimenter biases, precise self-report via a button press or a similar mechanism can be impeded by concurrent task demands. Also, when studying motivational factors, veridical report can be disadvantageous for participants and therefore can be called into question. For these reasons, the use of no-report paradigms as an unobtrusive moment-by-moment account of perception has been encouraged (Tsuchiya et al., 2015). They also may better represent the gradual nature of multistable perception (Fahle et al., 2011; Naber et al., 2011), and are not prone to a subjective response criterion in case of mixed ("piecemeal") percepts, which frequently occur in binocular rivalry (Blake et al., 1992; Brascamp et al., 2006; Fechner, 1861). Moreover, no-report paradigms are unaffected by the impact reporting a percept can have on perception itself (Beets et al.,

2010; Veto et al., 2018; Wohlschläger, 2000). In our case, we used an eye-movement based measure that has been shown to faithfully mirror the subjective perceptual state (Naber et al., 2011). It capitalizes on the finding that if presented with a large moving field, the eyes show an optokinetic nystagmus (OKN), an eye movement whose slow phases follow the stimulus motion while intermittently being broken up by fast phases that reset the eyes in orbit. Consequentially, if two sufficiently large gratings that drift in opposite directions are presented to the two eyes in rivalry, the OKN slow phases will follow the perceptually dominant grating, acting as a proxy for perceptual experience.

We used two vertical gratings as binocular-rivalry stimuli, one presented to each eye. In three experiments, we associated gratings of different colors with different levels of uncertainty and expectancy regarding the reward that followed a button press in an associative learning task. As dependent measure, we assessed the gratings' dominance in direct binocular rivalry with a grating of a distractor color that was not associated with reward, before and after an association of grating color to reward had been acquired. In the interjacent acquisition phase, observers were required to learn through trial-and-error which of two button presses a drifting grating prompted in order to achieve reward at two levels of uncertainty (Experiment 1). Two combinations of color and button press were associated with certain reward of 5 Cent per correct response and for one color, each button was associated with uncertain reward (around 50% reward probability) of 5 Cent per response. This allowed for comparison of certain and uncertain reward.

In Experiment 2, we decoupled the intended button press in the acquisition phase from the grating color. The first intention behind this was to rule out alternative interpretations of results such as an association of button press to reward in the certain conditions as well as uncertainty regarding response selection in the uncertain condition. The second was to render the rewarded stimulus feature task-irrelevant and response-independent in order to replicate the aforementioned findings to that effect in the field of visual attentional capture. Instead, observers performed a trivial task reacting to a stimulus layered over the presented grating while being rewarded according to grating color. Two colors were associated with certain reward but high and low reward expectancy (10 vs. 1 Cent) while a third color was associated with uncertain reward and an intermediate reward expectancy (5 Cent). This design allowed to differentiate between three possible influential factors on dominance, just as in Koenig et al. (2017a). If uncertainty influences dominance in rivalry, the two colors that were consistently rewarded would decrease in dominance and the partially rewarded color would increase.

If predictiveness is critical, an opposite pattern of results would emerge. However, if visual awareness is determined by reward expectancy, a gradual increase of dominance between the three conditions (1 < 5 < 10 Cent) would occur.

In Experiment 3, we replicated Experiment 1 with critical changes. Among other things, the reward contingency in the uncertain condition was exactly 50% and we controlled for reward expectancy by lowering reward in the certain condition to 5 Cent so that reward expectancy was equal in the certain and uncertain conditions.

Given the aforementioned results of previous studies, we expected an increase in dominance for all gratings associated with reward relative to the grating not associated with reward, regardless of reward expectancy and uncertainty, and a relative additional increase for gratings associated with uncertain reward compared to gratings with certain reward, regardless of reward expectancy.

Methods

General Methods

We conducted three experiments to test the effect of reward, reward uncertainty and reward expectancy on dominance in binocular rivalry. A participant number of at least 16 per experiment was set a priori based on power estimates on the basis of similar studies. The lowest number above 16 that was compatible with appropriate counter-balancing constraints was chosen as number of observers needed for a particular experiment. If participants had to be excluded, further were invited until the pre-defined number of participants had been reached. In Experiments 1 and 3, it was realized after the experiment's conclusion that some observers (five and four; respectively, see Results section) had not effectively learnt the intended response in the condition with a fix color-response mapping. For these observers, hereafter referred to as "poor learners", a sufficient association between stimulus and reward could not be assumed with certainty. A second analysis excluding these poor learners was performed for Experiments 1 and 3. Results of these analyses are reported in the main text only if they differ from the first analysis' results, otherwise they are reported in Appendix A. All procedures were approved by the *Ethikkommission FB04, Philipps-University Marburg (case no.: 2011-04K)*. All observers gave written informed consent prior to participation and had normal or corrected-to-normal vision as well as normal stereo and color vision. They were either paid 6 € per hour or given course credit.

Setup

Stimuli were presented dichoptically at a viewing distance of 30 cm using a custom-built stereoscope with mirrors transparent to infrared light. Throughout each experiment, eye tracking was performed through the stereoscope's mirrors, using a table-mounted eye-tracking device (EyeLink 1000, SR Research, Ottawa, ON, Canada) sampling at 1000 Hz. As both eyes carry the information needed for the purpose of this study (Naber et al., 2011), only one eye was tracked. Participants responded by pressing the top or bottom face button on a game pad (hereafter referred to as up- and down-button) using their right thumb. The state of the game pad was recorded together with the EyeLink data. The experiments were conducted in a dark and sound-attenuated room. Stimuli were generated and presented using Matlab (MathWorks, Natick, MA) with the Psychophysics Toolbox (Brainard, 1997; Pelli, 1997) and the EyeLink Toolbox (Cornelissen et al., 2002).

Stimuli and Procedure

Visual stimuli were vertical square-wave gratings of alternating colored and gray phases of equal width. The color of the chromatic phases was either a pure red, green or blue or a yellow that was a mixture of two parts red and one part green – resulting in 4 different-colored gratings. Gratings were presented centrally, one to each of the observer's eyes, while drifting horizontally. In order to smooth the transitions between the chromatic and gray phases, the luminance of the chromatic phases was gradually reduced by 20% on each side following an inverse square function.

In all experiments, a three-phase paradigm was adopted, consisting of a calibration phase, an acquisition phase and a test phase. Observers were presented with written instructions before each phase and were able to take breaks between phases and experimental blocks if needed. The acquisition phase was intended to create associations between three informative grating colors and reward by coupling each grating color with a pre-determined reward schedule. Reward schedules varied reward expectancy and uncertainty by manipulating reward amount and contingency. The calibration phase and test phase served to determine the relative perceptual dominance of each of the gratings in the acquisition phase (three informative colors) over a fourth different-colored grating (one distractor color) in a binocular rivalry setting. For simplicity, we will refer to these gratings as the informative gratings and the distractor grating. Differences in perceptual dominance between the calibration phase and test phase could thus be attributed to an effect of the associations formed in the acquisition phase. Trial order was pseudo-randomized within experimental blocks. Participants were paid upon completion of the experiment.

Dependent Variables

To access perceptual dominance in the calibration and test phase, horizontal eye positions were analyzed with regard to direction and speed of the OKN slow phases as described in Einhäuser et al. (2017b) and Einhäuser et al. (2020): OKN fast phases' velocity and acceleration profiles resemble those of saccades (see, e.g., Garbutt et al., 2001), enabling fast phase detection by deployment of the Eyelink system's saccade detection software (Figure 1A). We used a velocity threshold of 35 deg/s and an acceleration threshold of 9500 deg/s². For further analysis, fast phases as well as periods of eye blinks were removed and treated as missing data. Only the horizontal eye positions of the slow phases of the OKN remained. The optimal linear function was fitted to each individual slow phase (Figure 1B). The slope of this fit determined the average horizontal eye velocity for this particular period. The sign of the slope indicated the slow phase's direction which in turn corresponded to the motion direction of the perceptually dominant grating during that time period.

As a measure of how well eye movement matched grating movement and consequentially vividness of perception, we defined the OKN gain which consisted of eye velocity divided by grating speed, resulting in one gain value, typically between -1 and 1 for each slow phase (Figure 1C). The sign of the gain was determined to be positive if slow phase direction matched the direction of the informative grating and negative if the eye moved in the same direction as the distractor grating.

Utilizing slow-phase gain and slow-phase direction, we initially analyzed three variables: relative dominance (1), gain (2) and dominant percept at onset (3). For each measure, we first aggregated data (slow phase gain and direction) over the relevant experimental conditions (individual to each experiment) and experimental phases (calibration and test phase). If a significant effect of any factor on relative dominance was found, we additionally considered the absolute dominance durations to assess where this effect originated (4).

Figure 1. Determining OKN gain from raw data. A) Excerpt of an example horizontal eye-position trace, detected slow phases in purple, fast phases in blue. B) Fast phases from the eyetrace in panel A are removed and the best linear fit in a least squared sense (green) is determined for each slow phase. C) The slope of each fit which can be likened to eye movement velocity of each slow phase is divided by grating speed to determine the OKN gain. Gain sign is defined as positive if the slow phase direction follows the direction of the informative grating and negative for the distractor grating.

Relative dominance

The sign of the OKN slow phase gain was defined such that positive gain corresponded to the informative grating's motion direction. We first separately summed the times in which the OKN slow phase gain was positive and those in which the OKN slow phase gain was negative, and then divided the difference of these two values by their sum. This provides a measure of relative dominance, which is +1 when only the informative grating is perceived, -1 when only the distractor grating is perceived, and 0 if both are perceived for the same aggregate time.

Gain

The measure of relative dominance only takes the gain's sign into account, not its value. But it seems plausible to assume that the (absolute) gain value carries information about the observer's perceptual state, associating higher gain values with clearer (more vivid) visual perception and lower

values with more mixed percepts. Hence, we also averaged the gain, weighing periods of large gains more strongly than periods of low gains. A measure near 1 implies exclusive perception of the informative grating, and of -1, exclusive perception of the distractor grating.

Onset

We analyzed which grating was perceived first in each trial. To achieve a measure that is more readily comparable with the other measures, we assigned a value of +1 to a trial if the first grating perceived was informative, and -1 if the first grating was the distractor grating. Averaging these numbers across trials, results in a positive measure if the informative grating is dominant at onset, and a negative measure if the distractor grating is dominant at onset, with +1 and -1 the theoretical extrema.

Dominance durations

We defined the dominance duration as the time between OKN sign changes; that is, the time that elapsed between the beginning of the first slow phase after a sign change and the end of the last slow phase before a sign change. The beginning and end of trial were treated analogously to sign changes. For analysis, we considered the median of all dominance durations (aggregated across trials) within each participant and grating. Since changes in relative dominance can occur as a consequence of increasing one grating's dominance duration or decreasing the other grating's dominance duration, dominance duration provides information beyond relative dominance. For our present analysis, we considered dominance durations only for cases where effects on relative dominance were found.

Statistical Analysis

We performed two-way repeated measures ANOVAs for each dependent variable with the within-subject factors experiment phase (calibration phase, test phase) and condition (individual to each experiment). In Experiment 1 and 3, we treated the two conditions that yielded the same reward expectancy and uncertainty as one condition. Pairwise follow-up *t* tests were conducted as appropriate. All reported *p*-values are uncorrected for multiple comparisons unless explicitly stated otherwise.

Methods – Experiment 1

Participants

Nineteen volunteers participated. Eighteen (age: 21–32, mean: 25.1, sd: 3.2; 6 women, 12 men; one participant did not disclose their age) were included in the analysis of experiment, one was excluded before data analysis due to a procedural error during testing.

Stimuli and setup

Presentation took place on two 21" CRT screens (Samsung, Seoul, South Korea). Monitors were set to a resolution of 1024 x 768 and a frame rate of 85 Hz. The monitors' CIE coordinates for each color channel were measured as: red: $x = 0.623$, $y = 0.344$; green: $x = 0.287$, $y = 0.609$; blue: $x = 0.151$, $y = 0.065$.

Gratings took up the entirety of the display, extending 67 degrees horizontally and 53 degrees vertically, with a spatial frequency of 0.2 cycles/degree and a motion speed of 25.7 degrees/s. All colors including gray were isoluminant (10 cd/m^2) except for red which was in retrospect determined to have had a luminance of 2.2 cd/m^2 . Since the assignment of reward schedule to color was balanced across observers, it is unlikely that this affects overall results. Blank screens were gray (10 cd/m^2). Visual text messages (color: white; font: Helvetica, size: 16) were presented centrally on both eyes on a blank screen.

Procedure

In the calibration phase, every trial started with a central black fixation cross on a blank screen. After fixation, the cross turned white for 0.5 s and the gratings were presented for 10 s. One of the informative gratings was presented to one eye, the distractor grating to the other eye, moving in the opposite direction. Participants were instructed to view the gratings freely and naturally without a response. Making use of the fact that the slow phase of the OKN follows the currently dominant grating (Naber et al., 2011), perceptual dominance could thus be determined continuously without querying the participant. The distractor color was yellow, and the informative colors were red, green and blue. The mapping of eye (left/right) to color condition (informative/distractor) and horizontal motion direction (temporonasal/nasotemporal) was balanced across trials, so that there were 12 trials.

In the acquisition phase, central fixation was ensured as in the calibration phase at the beginning of each trial. A grating with the same informative color and identical motion direction was then presented to each eye for 10 s, resulting in unambiguous presentation. After that, a visual

message called for response input. Participants had been instructed to maximize reward by pressing either the up- or down-button. They were not informed which button would produce reward, i.e., they had to learn which informative color indicated which button. Reward amount in all conditions was 5 Cent (0.05€) per rewarded trial. Two informative colors were assigned to two certain conditions: For one informative color, the up-button was continuously rewarded while the down-button was not (condition: certain up-rewarded). For another informative color, the down-button was rewarded, and the up-button was not (condition: certain down-rewarded). Both of these conditions were expected to produce low uncertainty about the reward outcome after completion of the acquisition phase and high outcome expectancy (5 Cent) relative to the third condition. For the third informative color, every trial had a 50% chance of reward, independent of response. This uncertain condition was theorized to lead to higher uncertainty and lower outcome expectancy (2.5 Cent) than the certain conditions.

Mapping of condition (certain up-rewarded, certain down-rewarded, uncertain) to informative color (red, green, blue) was balanced across observers. After participants had pressed a button, another message appeared on screen, informing them about whether their answer was correct as well as their rewarded amount: 'Correct. You win 5 Cent'. For an incorrect response, the message was 'Wrong. You win nothing.'. The message lingered for 1 s, followed by a blank screen for 20 s to avoid backward conditioning of the reward with the color of the previous trial. There were 36 trials: Three informative colors that drifted to the left in half of the trials and to the right in the other half, with 6 trial repetitions.

In the test phase, grating presentation – style and timing – matched the calibration phase, reintroducing binocular rivalry of informative and distractor grating. Observers continued the button press task they had been given in the acquisition phase with the same instruction and reward schedules in effect (Figure 2). With the same characteristics being balanced across trials as in the calibration phase (3 informative and distractor grating combinations, 2 eyes, 2 horizontal motion directions) and each trial being iterated six times, there were 72 trials. All earned rewards were added up and paid out.

Methods – Experiment 2

In Experiment 1, uncertainty in the uncertain condition arises not only regarding the occurrence of reward but also regarding response selection. In the certain conditions, an association may arise not only between color and reward but also between response and reward. To rule out influence of these factors on results, we rendered the rewarded stimulus feature task-irrelevant and response-independent in Experiment 2. Moreover, we devised three reward schedules that allowed for a direct comparison of effects of reward uncertainty and reward expectancy on results.

Participants

Sixteen observers (age: 20–33, mean: 26.4, sd: 3.5; 9 women, 7 men) were included in analysis. The data of the six further participants were lost or unusable due to technical failure.

Setup and Stimuli

The experiment was presented on the same displays as Experiment 1, set to a resolution of 800 x 600 and a frame rate of 60 Hz. Gratings were 34 degrees wide and 15 degrees high, with a spatial frequency of 0.3 cycles/degree, drifting at a speed of 23.2 degrees/s. Chromatic and gray phases were isoluminant (8 cd/m²). A vertical stream of squares (0.6 degrees length/width, interspace 1.2 degrees) was located centrally on the colored phases, drifting upwards or downwards at a speed of 1.9 degrees/s. The squares were of the same hue as the chromatic phase but darker (4 cd/m²) (Figure 3). In order to provide a plane with fixed depth, gratings and blank screens were surrounded by a high-contrast pattern of random black (< 0.1 cd/m²) and white (88 cd/m²) squares (1.2 degrees) that was identical in both eyes. Visual text messages (color: black; font: Courier New, size: 14) were presented centrally on both eyes on a blank screen.

Procedure

Experiment 2 matched Experiment 1 in procedure except for the following differences: At trial begin, the fixation cross turned white for 0.5 s before stimulus presentation. In the calibration phase, there were 24 trials needed to additionally balance vertical motion direction of the squares (up/down),

and there was an intertrial interval of 1 s. The assignment of color (red, green, blue, yellow) to color condition (3 informative colors with differing reward schedules and 1 distractor color) was balanced across observers, unlike in Experiment 1, where the distractor color was always yellow.

A trivial button press task was given in the acquisition and test phase. Gratings were presented for 5 s before participants were asked to respond – ‘Up or down?’. Observers had been instructed to indicate the motion direction of the vertical stream of squares that was drifting on top of the gratings’ chromatic phases by pressing the up-button if it was going up and the down-button if it was going down. Reward schedules only took effect when the task was solved correctly. The visual message for a correct button press was ‘Correct. Reward = [...] Cent’, for an incorrect button press ‘Wrong. No reward.’. The trial closed with a blank for a pseudo-random time interval between 5 and 9 s. One informative color was continuously rewarded with 10 Cent (condition: certain-high), another with 1 Cent (condition: certain-low), both leading to low uncertainty but high and low outcome expectancy respectively. The third informative color was rewarded with 10 Cent upon 50% of the correct button presses and with 0 Cent upon the other 50% of correct button presses (uncertain condition). This was expected to produce high reward uncertainty and an intermediate (5 Cent) outcome expectancy relative to the other conditions.

For the acquisition phase, 48 trials were performed to balance 3 colors, 2 horizontal motion directions and 2 vertical motion directions with 4 repetitions. Trials were presented in four blocks of 12. In the test phase, there were 96 trials (3 pairs of informative and distractor color x 2 eyes x 2 vertical motion directions x 2 horizontal motion directions x 4 repetitions) that were presented in four blocks of 24. In between blocks, participants were able to take breaks. The reward amounts for each block of the acquisition phase and test phase were summed up and the highest earning block of each phase was disbursed. To further motivate participants, we decided to brief them orally about the overall reward in the previously performed block in between blocks.

Methods – Experiment 3

In Experiment 3, we aimed at a replication of Experiment 1 with some refinements. We raised the reward in the uncertain condition from 5 to 10 Cent per rewarded trial so that reward expectancy was 5 Cent in all conditions and a prospective effect of condition could be attributed to uncertainty alone. Like in Experiment 2, we also counterbalanced the hue (red, green, blue, yellow) of the distractor color. Lastly, as the results of Wilbertz et al. (2017) suggest, awareness of the cue-outcome contingency might be necessary to reveal the effects of learned reward associations on binocular

rivalry. Thus, we decided to implement a follow-up interview to assess the participants' understanding of the cue-outcome relation.

Participants

Twenty-two volunteers participated. Sixteen (age: 19–29, mean: 21.8, sd: 2.6; 13 women, 3 men) were included in analysis, one was excluded because of technical failure; three were excluded because their contingency awareness, assessed by the follow-up interview (see Procedure), was poor, two further participants' data were excluded because of either excessive blinking or not exhibiting any OKN eye movements.

Setup and Stimuli

Stimuli presented on two 27" LED screens (LG Electronics, Seoul, South Korea), set to a resolution of 1920 x 1080 and a frame rate of 240 Hz, were used. According to manufacturer specification the color follows the NTSC 72% standard. Gratings (28 degrees width, 17 degrees height; spatial frequency 0.3 cycles/degree; drifting speed 14.3 degrees/s) had a luminance of 10 cd/m². Gratings and blank screens were gray, surrounded by a mask of randomly arranged black (< .1 cd/m²) and white (256 cd/m²) squares (1.3 degrees length/width). Blank screens and text messages were the same as in Experiment 2.

Procedure

The procedure of Experiment 3 equaled Experiment 2's with the following exceptions: In all three phases, Experiment 3 had the same balance of color, eye and horizontal motion direction across trials, implementing another trial repetition, so the overall number of trials remained the same as in Experiment 2 (where in addition the vertical motion direction had to be included in counterbalancing).

The instructions in all three phases, notably the button press task in the acquisition phase and test phase, were the same as in Experiment 1. The conditions also mostly matched Experiment 1: Two certain conditions were associated with certain administration of reward (0.05€) for the up- or down-button respectively. In one uncertain condition, partial reward was administered. But in contrast to Experiment 1, participants were rewarded 10 Cent instead of 5 in the uncertain condition to match reward expectancy between certain and uncertain conditions. In the uncertain condition, reward was administered in 50% of trials (while in Experiment 1, the probability per trial was 50%, such that the exact total number of rewarded uncertain trials could fluctuate between observers).

The experiment was followed up by a semi-structured interview to assess the participants' contingency awareness. Participants' data were only included if they could assign the two informative colors of the high and low conditions to the rewarded button press and expressed uncertainty about the indicated button press in the partial condition. Three participants were excluded from analysis on this account (note that these are not to be confused with the 'poor learners' who were excluded only in analysis). Upon completion of the interview, the acquired reward of two random blocks, one of the acquisition phase, one of the test phase, was paid. These blocks were selected by having participants twice pick one out of four concealed cards that revealed a block number (one to four).

Results

Experiment 1

Acquisition

During acquisition, observers were presented with gratings of the same color and direction in each eye. Two of the colors were always rewarded if the corresponding response (button up for one color, button down for the other color) was given ("certain conditions"). To verify that the correct association of button to color in these conditions had been learned, we analyzed the percentage of correct responses in the last six (of 24) trials of the certain conditions in the acquisition phase. On average, participants responded correctly in 77.8% of these trials (sd: 32.3%). We identified five poor learners who responded correctly at or around chance level (<60%). The main analysis includes all participants irrespective of learning performance; results that differ with respect to the set significance level when excluding the poor learners are mentioned in the main text. A complete analysis that excludes poor learners is provided as Appendix A.

The third informative color was rewarded with 50% probability in each trial, irrespective of the pressed button (uncertain condition). Since the reward is drawn independently in each trial of the uncertain condition, there is some variability in the reward actually achieved, ranging from 2 to 7 rewarded trials (out of 12) in the acquisition phase.

Perceptual dominance

Relative dominance was defined as the difference between the aggregated durations of slow phases following the informative (i.e., certain or uncertain) grating and slow phases following the distractor grating, divided by the sum of these durations. A positive sign indicates relative dominance

of the informative grating, a negative sign of the distractor grating. We conducted a 2×2 repeated-measures ANOVA with factors experiment phase (calibration, test) and condition (uncertain, certain). The relative dominance of informative gratings was larger in the test phase (after acquisition: $33.5\% \pm 6.7\%$, mean $\pm$ standard error of mean across observers) than in the calibration phase (before acquisition: $17.5\% \pm 3.6\%$), as quantified by a main effect of the factor experiment phase, $F(1, 17) = 6.80$, $p = .018$. This indicates an increase in perceptual dominance of the informative gratings relative to the distractor grating as a consequence of the acquisition. Note that the observation that these gratings are already more dominant than the distractor grating prior to acquisition (positive values of relative dominance) may result from the distractor color being constant (yellow) in all observers of Experiment 1. This, however, does not explain the significant increase in relative dominance between before and after acquisition.

We did not find a significant effect of condition, $F(1, 17) = 0.05$, $p = .823$, nor a significant interaction between the factors, $F(1, 17) = 3.12$, $p = .095$, Figure 4A. This suggests that there is no difference between uncertain and certain conditions, and informative stimuli increase in dominance irrespective of whether they give certain or uncertain information. However, with the interaction being not far from significance (note that the $p = .095$ refers to a two-sided test, although our hypothesis was directed), it is worth noting that numerically, the effect of experiment phase on relative dominance was stronger in the uncertain condition (difference in relative dominance between test and calibration phase: $23.6\% \pm 8.2\%$) than in the certain conditions ($8.5\% \pm 6.7\%$). Taken together with the issue that – as a consequence of using always the same distractor color – all informative colors being already more dominant than the distractor color prior to acquisition, it is possible that a subtle effect of uncertainty would go undetected. This was one rationale to counterbalance also the distractor colors across observers in the subsequent experiments. Moreover, the measure of relative dominance averages over the complete 10-s trial, potentially averaging out short-lived effects (see section ‘Analysis of gain over time’ below). We followed up on the main effect of experiment phase by analyzing the *dominance durations* of the informative gratings and the distractor grating before and after acquisition. Dominance durations were slightly shorter after acquisition ($1.41 \text{ s} \pm 0.10 \text{ s}$) than before ($1.62 \text{ s} \pm 0.10 \text{ s}$), $F(1, 17) = 5.58$, $p = .030$. The informative gratings’ dominance durations were longer ($1.82 \text{ s} \pm 0.13 \text{ s}$) than those of the distractor grating ($1.22 \text{ s} \pm 0.11 \text{ s}$), $F(1, 17) = 34.36$, $p < .001$. There was an interaction of both factors. $F(1, 17) = 6.59$, $p = .020$. Follow-up pairwise t tests revealed that the informative gratings’ dominance durations did not differ according to experiment

phase, $t(17) = -0.17$, $p = .893$, but the distractor grating's decreased from calibration to test phase (decrease of $0.45 \text{ s} \pm 0.06 \text{ s}$), $t(17) = 7.34$, $p < .001$ (Figure 4B).

For any given point in time, relative dominance is a binary measure, either one or the other grating being defined as dominant, ignoring its degree of perceptual vividness or exclusivity. As a continuous measure that presumably scales with perceptual vividness, we therefore used the *gain*, the ratio between eye-movement speed and grating speed, as an additional measure of perceptual dominance, and applied the same statistical analysis as for relative dominance. We found a trend to a main effect of experiment phase, $F(1, 17) = 4.24$, $p = .055$, with the gain in the direction of the informative gratings being larger after acquisition (0.18 ± 0.04) than before (0.09 ± 0.02), which is consistent with the increase in relative dominance of the informative gratings. There was no main effect of condition, $F(1, 17) = 0.002$, $p = .968$, and a non-significant interaction, $F(1, 17) = 3.27$, $p = .088$. Similar to the measure of relative dominance, the difference between calibration and test phase was numerically more pronounced in the uncertain condition (0.12 ± 0.05) than in the certain conditions (0.05 ± 0.04) (Figure 4C). Hence, the pattern of results is similar to the relative-dominance measure.

We analyzed which grating was dominant in the initial rivalry phase after trial onset, and defined an *onset* measure which analogously to our other measures is +1 for the informative grating being dominant and -1 for the distractor grating being dominant. There was a trend to a main effect of experiment phase, $F(1, 17) = 4.45$, $p = .05007$: the informative gratings were more likely to be dominant at trial onset after acquisition ($.28 \pm .06$) than before ($.14 \pm .07$). We did not find a main effect of condition, $F(1, 17) < .001$, $p = .989$, nor an interaction, $F(1, 17) = .002$, $p = .960$ (Figure 4D). When excluding poor learners (see Appendix A), the main effect of experiment phase is significant, $F(1, 12) = 5.30$, $p = .04$ (calibration phase: 0.15 ± 0.08 , test phase: 0.31 ± 0.06).

Experiment 2

Acquisition

In the acquisition phase of Experiment 2, participants had to indicate the vertical motion direction of drifting squares that were laid over the gratings, using a button press (see Figure 3, but both gratings had the same color and motion direction). Only correct responses were rewarded according to condition. Participants, depending on grating color, either received consistently high (10 Cent) or low (1 Cent) reward or they received partial reward (50% 10 Cent, 50% 0 Cent) for a correct response. Incorrect responses that failed to indicate the correct motion direction resulted in a message that said: 'Wrong. No reward.'. Thus, in order for the intended color-reward contingencies to take effect in each condition and not skew the contingencies towards more trials without reward than intended, a near 100% rate of correct responses would be needed. Therefore, we analyzed responses in all conditions throughout the acquisition phase. In the low condition, participants had perfect

performance, never giving an incorrect response. In the partial and high condition, mean correct responses were 99.6% (sd = 1.6%). We concluded that color-reward-contingency presentation was as intended.

Perceptual dominance

We tested whether the measures depended on condition (certain-high, certain-low, uncertain) and experiment phase (calibration phase, test phase) via a two-factor repeated-measures analysis of variance (rmANOVA) for each measure (Figure 5). According to Mauchly's test of sphericity, we found no evidence for a violation of sphericity at any of our tests with more than two levels (all $p > .15$). For *relative dominance*, we did not find an effect of experiment phase, $F(1, 15) = 0.04$, $p = .847$, or condition, $F(2, 30) = 0.24$, $p = .787$. The interaction of condition and experiment phase did not yield an effect either, $F(2, 30) = 0.56$, $p = .578$ (Figure 5A). There was no effect of experiment phase, $F(1, 15) = 0.33$, $p = .575$, or condition, $F(2, 30) = 0.41$, $p = .666$, on *gain*, or an interaction of the two factors, $F(2, 30) = 1.81$, $p = .180$ (Figure 5B). *Onset* direction did not change depending on experiment phase, $F(1, 15) = 0.25$, $p = .626$, or condition, $F(2, 30) = 0.46$, $p = .638$. The effects of experiment phase and condition did, however, interact, $F(2, 30) = 4.54$, $p = .019$. This effect most likely resulted from the low condition's onset being negative in the calibration phase ($-.08 \pm .13$), as opposed to the test phase and the other conditions where it was positive (Figure 5C). We followed up on this interaction with *t* tests comparing *before* and *after* for each level of condition. We found a difference for "certain low", which is significant ($t(15) = -2.21$, $p = .044$) at an uncorrected alpha-level of 5%, but does not survive a Bonferroni correction of the 3 comparisons (adjusted alpha-level = $0.05/3 = .167$). There were no differences for the other conditions (both $p > .508$).

Experiment 3

Acquisition

The button press task and conditions in the acquisition phase of Experiment 3 were similar to Experiment 1. There were two certain conditions that were always rewarded with 5 Cent for either the up or down button respectively and an uncertain condition that was partially rewarded: exactly 50% of trials were rewarded with 10 Cent, the other 50% were not rewarded, irrespective of which button was pressed (note that this is different from Experiment 1 where reward was random in every trial of the uncertain condition). This way, reward expectancy was 5 Cent in all conditions. Participants were instructed to maximize reward, initially naïve about the association of color to reward, and could learn about the contingencies during the acquisition phase. To ensure successful learning, we analyzed the percentage of correct responses in the last block of the acquisition phase. The average of correct responses in the certain conditions was 82.8% (sd = 27.0%). We identified four poor learners (correct response rate < 60%) and conducted a separate analysis without them. Results of this separate

analysis can be found in Appendix A. The main analysis including all participants as well as differences between the main analysis and the analysis excluding poor learners with respect to significance level are reported in the main text. There was no need to analyze the uncertain condition as contingency presentation was controlled: In 50% of trials, participants received reward, in 50%, they did not.

Perceptual dominance

Analogous to Experiment 1 and 2, we applied 2 x 2 repeated-measures ANOVAs to test whether the perceptual measures depended in Experiment phase (calibration, test) and condition (certain conditions, uncertain condition) (Figure 6). The informative gratings' *relative dominance* was larger after acquisition ($32.5\% \pm 9.4\%$; mean $\pm$ standard error of mean across observers) than before ($2.2\% \pm 7.9\%$), $F(1, 15) = 31.40$, $p < .001$. The main effect of condition was not significant, $F(1, 15) = 1.57$, $p = .230$. The factors did not interact, $F(1, 15) = 0.53$, $p = .477$. This pattern of results is similar to Experiment 1, indicating an effect of experiment phase, but not an effect of uncertainty, and, just like in Experiment 1, we followed up on the main effect of experiment phase by analyzing the *dominance durations* of the informative gratings and the distractor grating before and after acquisition. Dominance durations did not depend on experiment phase, $F(1, 15) = 1.50$, $p = .239$. Informative gratings were perceived longer ($1.79 \text{ s} \pm 0.07 \text{ s}$) than distractor gratings ($1.18 \text{ s} \pm 0.07 \text{ s}$), $F(1, 15) = 4.97$, $p = .042$. There was an interaction between the factors experiment phase and grating type (informative, distractor), $F(1, 15) = 10.76$, $p = 0.005$. The informative gratings' dominance durations were longer after acquisition ($2.11 \text{ s} \pm 0.35 \text{ s}$) than before ($1.47 \text{ s} \pm 0.14 \text{ s}$), $t(15) = -2.58$, $p = .021$. The distractor grating's dominance durations, on the other hand, were shorter after acquisition ($0.10 \text{ s} \pm 0.09 \text{ s}$) than before ($1.36 \text{ s} \pm 0.08 \text{ s}$), $t(15) = 3.50$, $p = 0.003$. After excluding poor learners, the results were the same, including the follow-up tests' results, but for the main effect of grating type which did not reach significance then. The *gain* presented itself in similar fashion to the relative dominance: Experiment phase did have an effect on gain, $F(1, 15) = 23.38$, $p < .001$. The informative gratings were perceived more clearly after acquisition (0.20 ± 0.06) than before (0.02 ± 0.04). The factor condition did not reach significance, $F(1, 15) = 3.15$, $p = .096$, and the two factors did not interact, $F(1, 15) = 0.90$, $p = .357$. For the *onset* measure, no effect of the factor experiment phase, $F(1, 15) = 2.17$, $p = .161$, or condition, $F(1, 15) = 0.38$, $p = .547$, could be found. They did not interact, either, $F(1, 15) = .02$, $p = .880$.

Figure 6. Measures of perceptual dominance in Experiment 3 as a function of experiment phase (before acquisition: calibration phase, after acquisition: test phase) and condition (certain conditions: certain up-rewarded and certain down-rewarded, uncertain condition: partial reward). Notation as in Figure 4.

Analysis of gain over time

To analyze how dominance develops over time, we averaged the gain for each time point over the course of the 10-s trial. For each time point (i.e., each millisecond), we conducted a 2×2 rmANOVA with the factors experiment phase and condition. Since this implies 10 000 tests, the alpha level was adjusted to an expected false discovery rate of 5% per effect.

In Experiment 1 before acquisition, we observed substantial fluctuations of the gain over the course of the trial (Figure 7A, top). After acquisition, the gains tended to be stable around a level of 0.2 (Figure 7A, bottom), and was larger for the uncertain than for the certain condition for most time points (Figure 7A, bottom). However, after applying a correction for multiple comparisons by estimating the expected false discovery rate (FDR) using Benjamini and Hochberg's (1995) procedure, we did not observe any significant effect of experiment phase, of condition, nor an interaction at an expected FDR of 5%. When considering uncorrected p-values, condition had no main effect at any time point (all $p > .096$). At the uncorrected level, there would have been some time windows with a main effect of experiment phase ($p < .05$ for 2 232/10 000 time points) and some time windows with an interaction ($p < .05$ for 1043 time points). The latter, however, is mainly carried by a spurious effect in the calibration phase. In sum, there is no statistically robust effect of either factor at any given time point or period in experiment 1.

Similarly, in Experiment 2 (Figure 7B) there were no significant main effects of either factor nor an interaction at the adjusted alpha level. The number of time points at which “significant” effects were observed for uncorrected p-values, were within the range expected by random fluctuations (condition: 424 / 10 000, experiment phase: 39/10 000, interaction: 568 / 10 000) and can be considered spurious. As for the average data reported above, fluctuations in both experiment phases were around 0 in Experiment 2, while in Experiment 1 (as a consequence of choosing the same distractor color for all observers) the gain fluctuated around a level above 0.

For Experiment 3, the factor experiment phase was significant at virtually every time point (9 978 out of 10 000 ms, corrected alpha level $p < .0497$), except some isolated points very early in the trial (Figure 7C). After alpha-level adjustment, there was no main effect of condition at any time point (at an uncorrected alpha level 1 743/10 000 points had $p < .05$). However, a significant interaction at an expected FDR of 5% (corrected alpha=.001) was first observed at $t = 470$ ms and last at $t = 723$ ms ($p < .001$). The largest continuing slot of time points with significant interactions stretched from $t = 577$ ms to $t = 711$ ms. This interaction largely reflected an effect of condition in the test phase (i.e., after acquisition; Figure 7C, bottom), as before acquisition the gain fluctuated largely around 0 (Figure 7, top). After acquisition, average gain in the uncertain condition showed a peak within the first two seconds of the trial with a maximum of 0.40 (sem = 0.10) at $t = 869$ ms. From the third second onward ($t > 2000$ ms), the range of the average gain remained between 0.29 and 0.15. Similar to the uncertain condition, there was a steep, but not as pronounced increase of the average gain at the beginning of the trial with a peak of 0.19 (sem = 0.07) at $t = 930$ ms. After the first second ($t > 1,000$ ms), the average gain remained relatively steady around the level it rose to in the first second (min = 0.12, max = 0.21). Notably, despite the absence of a significant interaction, the uncertain condition numerically exceeded the predictive condition after acquisition for all time points in the first 7 seconds of the trial. When comparing Experiment 3 to Experiment 1, the effects in Experiment 3 seem more pronounced and – unlike in Experiment 1 – significant effects are observed. However, when analysis in Experiment 1 is restricted to good learners, numerically the patterns after acquisition become remarkable similar (see Appendix A), indicating that potential effects in Experiment 1 are overshadowed by the abundance of poor learners.

In summary, the gain over time revealed an effect of uncertainty on perceptual dominance in binocular rivalry early after stimulus onset: The grating associated with uncertain reward exhibited a

significantly higher change in perceptual dominance as a consequence of the association acquisition than the grating associated with certain reward.

Discussion

In three experiments, we tested the effect of information and uncertainty associated with a visual stimulus about an upcoming reward on the stimulus' perceptual dominance. We found that in general stimuli that were informative about the outcome gained increased dominance when brought into rivalry with stimuli that were uninformative. However, this only held when the stimulus feature associated with the reward prediction was also relevant for the task. Uncertainty had a more subtle effect that was only significant early in the trial: stimuli with uncertain predictions about the reward initially achieved higher dominance than stimuli with certain predictions. This effect of uncertainty evened out over the 10-s course of a trial. To be robustly observable, the effect of uncertainty also required that the informative stimuli's dominance prior to acquisition was not yet systematically increased (as was incidentally the case in our Experiment 1, by using the same color as uninformative stimulus for all participants). This suggests that effects of uncertainty alone will not add arbitrarily to a stimulus' dominance, but rather level off (saturate) well below a level where one grating would become exclusively dominant. The effect of uncertainty peaks about 500 ms to 700 ms after stimulus onset. Together with the absence of an effect on our "onset" measure, this suggests that effects of

uncertainty manifest themselves early in the trial but are not related to a special role of the initial percept as such. In sum, we observe robust effects of informativeness on perceptual dominance throughout the trial, and a somewhat more subtle effect of uncertainty early in the trial.

An increase in relative dominance can in principle arise from a reduction in dominance duration of one stimulus or the increase of dominance duration of the other stimulus. In experiment 1, we found almost exclusively the former effect (reduction in dominance duration for distractors), while in experiment 3 both contributed. This is of theoretical interest, as the reduction has been considered a hallmark of an increased stimulus strength of the other stimulus according to Levelt's second proposition (Levelt, 1968). A recent refinement of the proposition (Brascamp et al., 2015) states that *"increasing the difference in stimulus strength between the two eyes will primarily act to increase the average perceptual dominance duration of the stronger stimulus"* (p. 215). As we find a reduction for the (weaker) distractor in Experiment 1 and both directions (increase for the informative stimuli and decrease for the distractor), it seems plausible that informativeness, at least in part, acts akin to stimulus strength in binocular rivalry.

Previous studies have shown an effect of outcome on dominance in binocular rivalry. Two studies paired one specific percept with reward and/or the other with punishment and found that the rewarded percept increased in dominance and the punished percept decreased in dominance relative to the other (Marx & Einhäuser, 2015; Wilbertz et al., 2014). While we also find an effect of reward in our Experiments 1 and 3 (the informative gratings increase in dominance relative to the distractor), there is an important conceptual distinction: in the aforementioned studies, reward was given depending on the duration the percept was dominant, in the present study, the color merely informs about the expected reward and the necessary action, but the size of reward does not depend on the duration the stimulus is perceived. That is, in the studies of Marx and Einhäuser and of Wilbertz and colleagues, a stimulus' dominance is affected directly through its (motivational) value, while here the informational (value) about the upcoming reward affects dominance. It should be noted that Wilbertz and colleagues (2017) could not replicate the effect of reward on dominance and found in a post-hoc analysis that it depended on observers being aware of the reward contingency and the subjective nature of percepts in rivalry. This provides an interesting parallel to our findings that also become more robust, when a. observers without contingency awareness are excluded (Experiment 3), and b. only observers that show good learning performance are considered (Appendix A). Importantly, as observers never report their perception, this modulation by contingency awareness cannot be

explained by good learners being better able to report their perception or even being biased towards an expected outcome. In turn, the no-report paradigm ensures that there is no necessity for monitoring or reporting the current perception that could potentially interfere with learning.

Besides the effect of outcome per se (informative vs. distractor gratings), we found effects of uncertainty – stimuli that provided uncertain information increased more in dominance during acquisition than stimuli that provided certain information, at least early in the trial. This effect of associative uncertainty on binocular rivalry is similar to a recently described effect of perceptual uncertainty (Einhäuser, Sandrock, & Schütz, 2021): stimuli that are harder to discern (more uncertain) increase in dominance over stimuli that are easier to discern (less uncertain). If the stimuli are task relevant, the dominance of the uncertain stimulus is stronger early in the trial, reminiscent of the time-course observed here. Interestingly, the effects of uncertainty persist after the stimulus has become task irrelevant, in a similar vein as task relevance itself keeps to have an effect on perceptual dominance even after the relevance has vanished (Chopin & Mamassian, 2010). This is in contrast to the effects of reward on perceptual dominance, which is extinct quickly (Wilbertz et al., 2014). In the present study, the contingencies remain throughout the test phase. Whether and how quickly such effects vanish remains an interesting issue.

The effect of outcome uncertainty on binocular rivalry bears similarities to attentional effects of uncertainty, which have been assessed with a variety of measures. Using eye-movement data, Hogarth et al. (2008) found that during learning, contingency-aware participants dwelled longer on cues that unreliably predicted an aversive noise than on reliable cues. At the outset of learning, pupil size, which relates to arousal levels, shows larger changes for cues that unreliably predict an outcome (financial reward, positive response feedback or an electric shock) than for their reliable counterparts (Koenig et al., 2018). For attentional capture, results are more mixed: Le Pelley et al. (2019) found in one experiment that the uncertain reward cue elicited an intermediate rate of attentional capture compared to a certain reward cue with high average reward expectancy and a certain reward cue with low average reward expectancy (the uncertain reward cue had an intermediate average reward expectancy, akin to our Experiment 2). In another experiment, when average reward expectancy was controlled, an uncertain reward cue captured attention more often than a certain reward cue. Effects of reward uncertainty on attentional measures are also found beyond the original learning context: Cho & Cho (2020) found higher interference on reaction times during a visual search task by distractors that previously were uncertain reward cues than distractors that reliably predicted reward in an earlier

experimental phase. In a similar fashion, the duration of oculomotor capture by a previously rewarded (Koenig et al., 2017a) or punished (Koenig et al., 2017b) distractor corresponded to uncertainty about the occurrence of punishment or reward. Although stimulus awareness during binocular stimulation is dissociable from attention (Koch & Tsuchiya, 2007), attention towards a stimulus also increases its dominance in binocular rivalry (Ooi & He, 1999; van Ee et al., 2005). The relation of uncertainty to attention on the one hand, and to binocular-rivalry perception on the other hand, makes the extent to which effects of uncertainty on perceptual dominance are mediated by attention an interesting issue for further investigation.

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Appendix A

Results after excluding poor learners

For Experiment 1 and Experiment 3, some participants performed below 60% correct in the last quarter of the acquisition phase. We repeated all analyses with these observers (“poor learners”) excluded, leaving $N = 13$ for Experiment 1 and $N = 12$ for Experiment 3.

Experiment 1

Relative dominance of the informative gratings was larger ($38.5\% \pm 7.8\%$; mean $\pm$ standard error of mean across observers) in the test phase than in the calibration phase ($19.9\% \pm 3.9\%$), $F(1, 12) = 6.08$, $p = .030$. There was no significant effect of condition, $F(1, 12) = 1.35$, $p = .268$. The interaction was not significant either, but showed a similar trend as in the main analysis, $F(1, 12) = 3.69$, $p = .079$, and the numerical differences between conditions were more pronounced than in the main analysis: the difference between calibration and test phase was $29.0\% \pm 10.5\%$ in the uncertain condition compared to $8.2\% \pm 7.9\%$ in the certain conditions. Again, we followed up on the main effect of experiment phase by analyzing the *dominance durations* of the informative gratings and the distractor grating. Dominance durations did not differ according to experiment phase, $F(1, 12) = 2.82$, $p = .118$. The dominance durations depended upon grating type, $F(1, 12) = 25.27$, $p < .001$. The informative gratings’ dominance durations were longer ($1.79 \text{ s} \pm 0.16 \text{ s}$) than those of the distractor grating ($1.44 \text{ s} \pm 0.12 \text{ s}$). There was no interaction of both factors. $F(1, 12) = 3.84$, $p = .074$.

For the *gain*, there was a trend for the informative gratings to have higher gain after acquisition (0.19 ± 0.05) than before (0.09 ± 0.02), $F(1, 12) = 3.57$, $p = .083$. The effect of condition on gain was not significant, $F(1, 12) = 1.69$, $p = .218$, nor was the interaction between the two factors, $F(1, 12) = 1.71$, $p = .216$. Similar to relative dominance as well as to the main analysis, the numerical difference between the gain in the calibration and test phase was more pronounced in the uncertain condition (0.13 ± 0.06) than in the certain conditions (0.08 ± 0.05). The *onset* indicated that the informative gratings were more likely to be dominant at trial onset after acquisition (0.31 ± 0.06) than before (0.15 ± 0.05), $F(1, 12) = 5.30$, $p = .040$. Condition did not have an effect on onset, $F(1, 12) = 0.36$, $p = .562$, and the two factors did not interact, $F(1, 12) = 2.07$, $p = .176$. In sum, compared to the main analysis including all participants, the numerical interaction between experiment phase and condition was more

accentuated for relative dominance and gain and the effect of experiment phase on onset reached significance (Figure 8).

Experiment 3

The informative gratings' *relative dominance* was higher after acquisition ($28.2\% \pm 10.8\%$) than before ($-2.2\% \pm 8.2\%$), $F(1, 11) = 25.13$, $p < .001$. The factor condition did not reach significance, $F(1, 11) = 1.14$, $p = .310$, nor did the interaction, $F(1, 11) = 3.01$, $p = .111$. *Dominance durations* did not depend on experiment phase, $F(1, 11) = 0.36$, $p = .562$. Informative gratings were not perceived longer than distractor gratings, $F(1, 11) = 2.19$, $p = .17$. There was an interaction between the factors experiment phase and grating type (informative, distractor), $F(1, 11) = 16.93$, $p = 0.002$. The informative gratings' dominance durations were longer after acquisition ($1.85 \text{ s} \pm 0.30 \text{ s}$) than before ($1.36 \text{ s} \pm 0.14 \text{ s}$), $t(11) = -2.71$, $p = .020$. The distractor grating's dominance durations, on the other

hand, were shorter after acquisition ($0.06 \text{ s} \pm 0.10 \text{ s}$) than before ($1.41 \text{ s} \pm 0.08 \text{ s}$), $t(11) = 3.19$, $p = 0.009$.

The *gain* was influenced by experiment phase, $F(1, 11) = 14.87$, $p = .003$. The informative grating was perceived more clearly after acquisition (0.16 ± 0.07) than before (0.0004 ± 0.04). Condition did not have an effect on gain, $F(1, 11) = 3.47$, $p = .090$, and the factors did not interact, $F(1, 11) = 1.13$, $p = .311$. There was no effect on the *onset* direction of the first rivalry phase after stimulus onset by experiment phase, $F(1, 11) = 0.20$, $p = .660$, or condition, $F(1, 11) = 0.49$, $p = .497$, and no interaction between the factors, $F(1, 11) = 0.017$, $p = .900$ (Figure 9).

Analysis of gain over time in Experiment 1 and Experiment 3

In Experiment 1, the gain over time was nominally higher after acquisition (median = 0.17) than before (median = 0.09). Additionally, a nominally elevated gain in the uncertain condition became apparent in the test phase (uncertain: median = 0.24; certain: median = 0.15). This effect presented

itself throughout the entirety of the trial. The gain of the uncertain condition took its highest values within the first two seconds of the trial, reminiscent of the peak in Experiment 3. There were no significant effects of condition or experiment phase.

In Experiment 3, a significant effect of experiment phase was observed at a false discovery rate–corrected alpha level of $p < .04$ almost continuously throughout the trial (8 776 out of 10 000 ms). Participants' gain was lower in the calibration phase (median = 0.0003) than in the test phase (median = 0.15). The largest period without an effect of experiment phase spanned between $t = 1\,657$ ms and $t = 2\,059$ ms. Condition did not have an effect on gain over time. A significant interaction between the factors was first observed at $t = 483$ ms and last at $t = 705$ ms (corrected alpha level $p < .001$). The largest continuing interval with significant interaction within that timeframe was from $t = 525$ ms to $t = 615$ ms. The underlying peak of the gain at trial begin in the uncertain condition during the test phase reached a maximum of 0.39 at $t = 869$ ms (sem = 0.11). After $t = 2,000$ ms, the gain covered values between 0.11 and 0.26. Numerically, the gain in the uncertain condition exceeded the gain in the certain condition in all but 42 observed timepoints that occurred around $t = 9\,500$ ms. The gain in the certain condition showed a small peak with a maximum of 0.15 (sem = 0.09) at $t = 972$ ms during the first second of the trial and spanned between 0.07 and 0.17 for the remainder of the trial. During the

calibration phase, the gain fluctuated between values of -0.09 and 0.13 in the uncertain condition and -0.15 and 0.06 in the certain condition (Figure 10).