

The influence of action-effect anticipation on bistable perception: differences between onset rivalry and ambiguous motion

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Abstract

Perception is strongly shaped by the actions we perform. According to the theory of event coding, and forward models of motor control, goal-directed action preparation activates representations of desired effects. These expectations about the precise stimulus identity of one's action-outcomes (i.e. identity predictions) are thought to selectively influence perceptual processing of action-contingent effects. However, the existing evidence for such identity-prediction effects is scarce and mixed. Here, we developed a new paradigm to capture such effects and examined whether action-outcome predictions can bias the perception of binocular onset rivalry (Experiments 1a and 1b) and bistable motion (Experiment 2). Participants performed learning tasks in which they were exposed to action-outcome associations. On test trials, actions were followed by bistable stimuli that could be perceived as being either congruent or incongruent with the aforementioned associations (i.e. rivalrous oriented gratings in Experiments 1a and 1b and spheres with ambiguous rotation directions in Experiment 2). Across three experiments, we show that, whilst exposure to action-effect associations can bias the apparent motion direction of ambiguous spheres, it fails to influence perceptual selection of grating orientations in binocular onset rivalry. This pattern of results extends previous work on ambiguous motion by demonstrating that action-induced modulations do not generalize to all types of bistable percepts.

Introduction

Humans are active agents that can intentionally bring about desired effects in the world. This capacity inherently relies on predictions we make about the consequences of our actions. Indeed, it has been proposed that we can only behave in a goal-direct manner because we represent our actions in terms of their specific sensory effects (Aarts and Dijksterhuis 2000; Hommel et al. 2001), and, accordingly, automatically pre-activate the “identity” of these effects whenever we prepare to

act (Miall and Wolpert 1996). These specific expectations about the identity of one's action-outcomes (i.e. identity predictions) may help us to select the appropriate actions to reach our goals (Prinz 1997; Elsner and Hommel 2001) but are also thought to color the subjective perception of our action outcomes (Waszak et al. 2012). That is, if specific action-outcomes are pre-activated, actual, prediction-consistent effects, should be selectively affected (e.g. prediction-consistent, but not inconsistent, effects should have facilitated access to conscious awareness).

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However, as of yet, the existing evidence for such identity-prediction effects is scarce and mixed. In the present studies, we tap into this issue and examine whether anticipating a specific action-outcome can affect the very content of what is consciously perceived.

The view that predicted action-outcomes elicit pre-activation of sensory representations is typically substantiated by two perceptual phenomena: compared to sensory outcomes with an external origin (e.g. tones, haptic feedback), self-produced sensory input is perceived as occurring earlier (intentional binding; Haggard et al. 2002) and as suppressed in perceptual intensity and neurophysiological activity (sensory attenuation; Schafer and Marcus 1973). For instance, neural responses during self-produced speech are smaller compared to when listening to a recording of yourself speaking (Curio et al. 2000).

Importantly, however, these observations typically involve the comparison between self-produced and externally produced outcomes, which differ in more ways than the mere availability of action-outcome predictions. For instance, when preparing to speak, you do not only have information about what is going to be said, but also about when you will start speaking. This type of temporal control and temporal predictability is not present when listening to a tape or to someone else speaking. As such, typical intentional binding and sensory attenuation effects cannot be unequivocally attributed to anticipations about the “content (or identity)” of action-effects (see Hughes et al. 2013a for a review). A few studies have attempted to circumvent the aforementioned issue by manipulating the prediction congruency of self-produced outcomes (e.g. by comparing the perceived intensity of tones that were congruent or incongruent with previously learned action-tone associations); hence isolating identity predictions. The results of these studies were, however, mixed and inconclusive. Specifically, some studies have reported increased sensory attenuation for prediction congruent versus incongruent effects (Cardoso-Leite et al. 2010; Desantis et al. 2014; Hughes et al. 2013b), while other studies did not find (clear) evidence for these effects (Bednark et al. 2015; Hsu et al. 2013; Dogge et al. in preparation). In contrast, intentional binding seems unaffected by identity predictions (Bednark et al. 2015; Desantis et al. 2012; Haering and Kiesel 2014). Taken together, direct evidence for the influence of action-based identity predictions on the perception of action-outcomes is scarce.

Arguably, a more potent approach for capturing the hypothesized influence of identity-predictions on conscious perception, is to capitalize on the phenomenon of perceptual bistability. Bistable images are single stimuli that yield two conflicting perceptual interpretations (identities), one of which can match the expected perceptual outcome (Leopold and Logothetis 1999; Blake and Logothetis 2002). Considering that the perceptual conflict in such paradigms can be a conflict of stimulus identity, bistable phenomena are likely to be more susceptible to modulation by action-based predictions compared to intentional binding and sensory attenuation. A handful of studies has provided results compatible with this idea (Wohlschläger 2000; Maruya et al. 2007; Mitsumatsu 2009; Beets et al. 2010; Di Pace and Saracini 2014; Wallis and Backus 2016). In these studies, self-movement of participants biased the perceived motion of ambiguous stimuli in the direction of the action. Although these results are promising, and generally explained in terms of the pre-activation of action-effects, their reliance on these mechanisms is not unequivocal. In the aforementioned studies participants viewed the bistable stimuli while moving at the same time. This is problematic considering that the execution of an action is not only accompanied by a prediction of upcoming effects, but also

by tactile and proprioceptive feedback. Both these types of information are known to bias predominant percepts in favor of the congruent visual interpretation (Lunghi et al. 2010; Lunghi and Alais 2013; Salomon et al. 2013). Accordingly, the aforementioned studies cannot clearly distinguish the effects of outcome-anticipation from other action-related sources of information (see Wohlschläger 2000, Experiment 4 for an important exception). The role of identity prediction processes in conscious perception in general—and in bistable perception specifically—thus remains to be elucidated.

Across three experiments, we investigated whether action-outcome anticipation can bias the content of conscious perception. We did so, by utilizing different forms of bistable perception. Experiment 1a and 1b examined the influence of outcome prediction on binocular rivalry; a particular type of bistable perception in which each eye is presented with a conflicting image (e.g. house versus face, or vertical versus horizontal gratings), causing conscious perception to alternate between the two eyes’ images in periods of exclusive dominance (Blake 2001). The percept that initially becomes dominant during exposure to binocular rivalry stimuli (i.e. onset rivalry; Carter and Cavanagh 2007; Stanley et al. 2011) is of particular interest, as action-outcome predictions already emerge as early as the late stages of motor preparation (Desantis et al. 2014). A focus on onset rivalry thus provides a direct test of the proposed mechanisms underlying identity-prediction effects: If action-preparation results in early pre-activation of specific action-outcome representations, this specific outcome-identity should reach the threshold of conscious awareness faster (Waszak et al. 2012), and win the battle for initial dominance.

In Experiment 2, we built upon the few previously mentioned bistable perception studies involving actions (Wohlschläger 2000; Maruya et al. 2007; Mitsumatsu 2009; Beets et al. 2010; Di Pace et al. 2014; Wallis and Backus 2016), and employed bistable motion. Relative to stationary ambiguous stimuli, perception of motion direction is known to be more susceptible to factors like voluntary control (Hugrass and Crewther 2012). In addition, bistable motion can be modulated by identity predictions, such as expectations based on learned cue-movement associations (Haijiang et al. 2006; Schmack et al. 2016), and hence seems suitable to pick up action prediction effects.

To address our research question, we devised a novel learning task consisting of two types of trials. On induction trials, participants were exposed to associations between a manual rotary movement and a subsequent unambiguous percept (i.e. one of two grating orientations in Experiment 1a and 1b, and one of two motion directions in Experiment 2). On test trials, this same rotary movement was followed by ambiguous percepts (i.e. different gratings in each eye in Experiment 1a and 1b, and an ambiguously rotating sphere in Experiment 2). Importantly, the rotary movements were temporally separated from the bistable percepts allowing us to examine the role of outcome-anticipation while minimizing influences of other action-related sources of information. We hypothesized that participants would be more likely to report percepts that were consistent with action-outcome anticipations, both when presented with rivalrous stimuli and ambiguous motion.

Experiment 1a

Methods and materials

The current line of studies was conducted in line with the recommendations of the ethics board of Social and Behavioral

Sciences at Utrecht University and all participants provided informed consent prior to participating in the study. Participants received money and/or course credit in exchange for their participation.

In all experiments, Bayesian analyses were used to allow for both the assessment of the evidence in favor of the alternative hypothesis that action predictions affect conscious perception, as well as for the null hypothesis that action predictions do not affect conscious perception (Wagenmakers *et al.* 2017). Bayesian analyses were performed in JASP version 0.8.2.0 (JASP Team 2017), using the default Cauchy prior width of 0.707. Sample size was determined by a pre-specified optional Bayesian stopping rule: Data collection was terminated as soon as a Bayes factor of 6, favoring either the null or the alternative hypothesis, was obtained (i.e. reflecting substantial evidence; Jeffreys 1961; Lee and Wagenmakers 2013). However, we decided to collect a minimum of 20 participants (after exclusions based on strong color or eye-dominance, or failure to adhere to task instructions - see data exclusion). Note that, unlike in Frequentist statistics, Bayesian posterior probabilities and Bayes factors can be recomputed and re-evaluated at any point during the data collection process without error inflation (see Rouder *et al.*, 2014 for a more detailed explanation). Frequentist statistics are also reported to promote comparison with other studies, but should be treated with caution due the usage of an optional Bayesian stopping rule.

Participants

Thirty-two participants (28 females, 1 left-handed, $M_{age} = 21.84$, $SD_{age} = 2.53$) took part in the experiment.

Stimuli and apparatus

Participants viewed the stimuli through a mirror stereoscope consisting of two mirrors at a 45° angle, each reflecting one of two linearized 23-inch LCD monitors (Dell UZ2315H; resolution: 1920 × 1080; refresh rate: 60 Hz) that were facing each other (see Brascamp and Naber 2016 for a more detailed description). Despite matching the calibration of both displays with the Spyder3Elite (Datacolor, Lawrenceville, NJ), there were slight luminance discrepancies between the screens (mean discrepancy was approximately 9%). All reported luminance values are as measured on the left screen. A chin rest and forehead rest were used to ensure a stabilized head position at a viewing distance of approximately 82 cm.

The rivalrous stimuli comprised of circular square-wave gratings [diameter of 1.48° of visual angle (dva)] that were surrounded by a gray annulus (2.5 Cd/m², 1.67 dva; thickness: 0.11 dva) with four diagonal rectangular junctures (see Fig. 1). In addition, a vertical rectangle, which had to be aligned with two of these junctures (see procedure), was superimposed on the grating. Both the rectangle as well as the grating were colored gray on induction trials and red-gray or blue-gray on rivalrous test trials. To promote stereoscopic fusion of the complementary images presented to each eye, the stimuli were presented within identical circular frames of 2.59 dva in diameter (1.1 Cd/m²), which were in turn encapsulated by a Brownian noise rectangle (2.96 dva by 3.33 dva) on a black background (<1 Cd/m²). All gratings had a spatial frequency of 6.75 cycles per degree, and a Michelson contrast of 0.2 between minimum (1.6 Cd/m²) and maximum (2.5 Cd/m²) luminance values.

Procedure and design

The experimental task was framed as a “bridge building game” in which participants turned vertical gratings into oblique

(tilted) “bridges” by rotating a custom-made cylindrical knob with their dominant hand. The required rotation direction was indicated by a visual cue presented to the left or right side of the grating. Specifically, participants were instructed to rotate the vertical grating in such a way that an imaginary ball would be able to roll towards the cue following the line-orientation of the grating (i.e. a cue on the right side required a leftward rotation); see Fig. 1.

The task consisted of two types of trials: induction trials and test trials. In induction trials, rotary movements were immediately followed by presentation of the corresponding (unambiguous) grating to both eyes. These trials served as exposure to action-effect associations between rotary movements and oblique grating orientations. In test trials the perceptual outcome following the rotary movement was made ambiguous by presenting each eye with a different -45 or +45° grating orientation; one of which was consistent with the preceding movement. Accordingly, test trials allowed us to examine whether the action-effect associations that were learned in induction trials biased perceptual selection between rivalrous orthogonal gratings. Note that no changes in grating orientation occurred while the rotary movement was being executed. Once the movement was completed the vertical gratings immediately changed to the oblique outcome gratings.

Each trial started with the presentation of a fixation point for a randomly chosen duration of 1000, 1250, 1500, 1750 or 2000 ms. Subsequently, participants viewed a vertical grating with a movement cue on the left or right side, presented at an eccentricity of 1.05° of visual angle. In response to this cue, participants were required to execute a clockwise or counterclockwise manual rotation in order to rotate the grating by 45° towards the required ending position. In order to help participants to execute the proper movement (i.e. rotate the grating to the proper ending position), four diagonal junctures were shown on the annulus surrounding the grating. The vertical superimposed rectangle presented in the center of the grating had to be aligned with two of these diagonal junctures. In addition, the rotary button produced a soft but audible click when reaching a rotation angle of 45°. In induction trials, this movement resulted in the presentation of an action-coherent outcome (500 ms), as well as textual feedback on the accuracy of the movement (i.e. the Dutch words for “correct” or “incorrect”; 1000 ms). To motivate participants to pay attention to the cue position, participants could earn money with correct rotations and lose money with incorrect rotations on induction trials. In the test trials a different grating was presented to each eye, at corresponding retinal locations and participants were instructed to verbally report the color of the first dominant percept and of all subsequent percepts during 5 s. The verbal responses were recorded by a microphone. Note that by asking participants to report a feature of the grating that was orthogonal to the feature of interest (i.e. color instead of orientation), we reduced the likelihood that prediction consistent responses are caused by demand characteristics; see Attarha and Moore (2015) for a similar approach.

Before the experiment participants completed pre-screening tests to check for color vision (Ishihara 1917), visual acuity (customized, digital Landolt-C test) and stereoscopic vision. Participants did not take part in the experimental phase if they displayed abnormal color vision, failed to distinguish a gap of 0.07° of visual angle in the Landolt-C task (corresponding to one line in the gratings) or experienced diplopia. In addition, participants were screened for eye dominance (i.e. a bias for perceiving percepts in a particular eye), and color dominance (i.e. a bias for seeing one of the two grating colors) as both of these biases

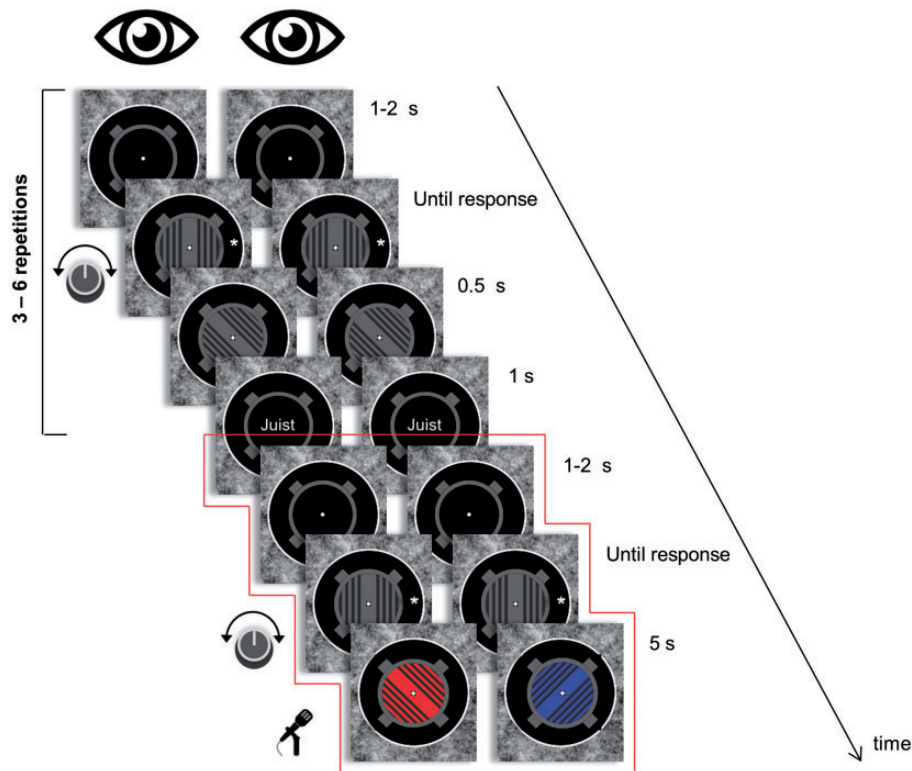


Figure 1. Schematic representation of trial events in induction and rivalry trials of Experiment 1a. Contrasts and colors deviate from those used in the experiment for illustrative purposes. Participants were instructed to rotate a vertical grating in such a way that the lines of the grating were pointing towards the side of a cue (*). In a sequence of three to six induction trials, rotary movements were followed by the presentation of the same (action-coherent) oblique grating in both eyes, and by feedback on the accuracy of the action [i.e. the Dutch word for correct (“juist”) or incorrect (“onjuist”)]. In the rivalry trials (outlined in red), each eye was presented with a different grating whose orientation was either consistent or inconsistent with the preceding movement. Participants were asked to verbally report the initially dominant percept and all subsequent switches. Cue position could vary within a sub-block.

reduce the amount of variance that can be explained by prediction consistency effects. As part of this screening participants completed 16 trials in which they passively viewed a vertical grey grating that changed into a colored rivalrous grating (i.e. the same gratings that were used in the actual experiment). This rivalrous grating was presented for five seconds while participants indicated their dominant percept by means of the “q” and “p” key on the keyboard (representing red and blue respectively). Orientation placement (left-eye -45 and right-eye $+45$ vs. left-eye -45 and right-eye $+45$), and color placement (left-eye red and right-eye blue vs. left-eye blue and right-eye red) was randomized over trials. For six of the inclusions, the prevalence of different factor levels was not perfectly equated due to a programming error. As this pre-screening procedure was only used to assess whether participants were allowed to participate in the experiment in the first place (with the aim to minimize post-experiment exclusion), and color and eye dominance were also assessed during the main experiment, this is unlikely to have affected the reported results. Participants who showed either eye or color onset-dominance on more than 85% of the trials did not participate in the experiment (the first four trials were not included in this calculation). After successfully completing the pre-screening participants completed several practice rounds to become familiar with the rotary button and task-setup.

Induction and test trials were presented in sub-blocks consisting of a sequence of three to six induction trials and one final test trial. Length of sub-blocks was varied to prevent anticipation

of test trials. The experiment was divided into four blocks that each contained sixteen sub-blocks. The four possible sub-block lengths were each presented four times in a randomized order within each block. This resulted in a total of 288 induction trials and 64 rivalrous test trials per participant. Cue position (left vs. right), orientation placement (left-eye -45 and right-eye $+45$ vs. left-eye -45 and right-eye $+45$), and color placement (left-eye red and right-eye blue vs. left-eye blue and right-eye red) were manipulated within participants. Each combination was shown two times in each block in a randomized order.

Results

Data exclusion

Despite successfully completing the aforementioned pre-screening tests, data sets from ten participants had to be excluded because eye- or color dominance exceeded 85% during the task. For one participant the task was terminated after two experimental blocks in which only the red percept reached initial dominance. The remaining sample consisted of twenty-two participants (18 females, 1 left-handed, $M_{\text{age}} = 21.68$, $SD_{\text{age}} = 2.08$). In addition, trials were excluded from analysis when the button was incorrectly handled, such as when it was rotated too fast (before the presentation of the cue), too slow (not within the response limit of 2 s), not far enough, back and forth or more than once; $M = 0.92\%$, $SD = 1.33\%$). In addition, trials in which the button was rotated in the wrong direction

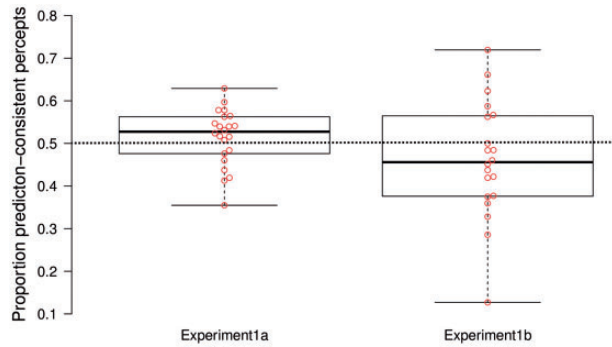


Figure 2. Proportion of prediction-consistent percepts for all participants in Experiment 1a and 1b. The boxes span the interquartile range. Red circles represent individual participants. Center lines represent medians and whiskers extend to data points that are <1.5 times the interquartile range. Dotted line represents chance.

(i.e. not in the direction that was indicated by the movement cue; $M = 0.14\%$, $SD = 0.46\%$) and trials in which the first spoken response after presentation of the rivalry stimulus was something other than “red” or “blue” were also excluded from analysis ($M = 0.79\%$, $SD = 1.06\%$).

Perceptual selection

Only the first verbal responses to the rivalry stimuli were considered in the analyses. The proportion of prediction-consistent percepts of all participants (see Fig. 2) were submitted to a directional one-sample *t*-test against chance (i.e. a proportion of 0.5 prediction-consistent responses). This analysis revealed that perceptual selection of prediction-consistent percepts ($M = 0.51$, $SD = .07$) was not likely to be greater than what is expected by chance ($BF_{+0} = 0.59$; $t(21) = 1.02$, $P = 0.16$, $d = 0.22$). Instead the data were 1.7 times more likely to reflect a null effect (no influence of prediction) than to reflect greater prevalence of prediction-consistent responses.

Discussion

Experiment 1a did not show convincing evidence for the influence of action-based predictions on perceptual selection during onset rivalry. These results have to be interpreted with caution, considering that the outcome of the Bayesian analysis was inconclusive and therefore also failed to provide support for the null hypothesis. We opted to end the experiment preliminary (i.e. prior to reaching all of the stopping rule requirements) as sequential analysis of the Bayes factor failed to consistently diverge to either of the pre-specified, stopping-rule thresholds. Participant debriefings suggested that a potential reason for the absence of the prediction effects might be related to suboptimal task design. Specifically, participants indicated that they used the position of the cue to determine the correct rotation direction, rather than the required position of the grating. In other words, rather than envisioning which oblique orientation would allow the ball to roll towards the cue, they used an easier stimulus-response strategy (e.g. “if the cue is presented on the left, I have to rotate to the right”). This strategy clearly reduces the task relevance of the grating orientation, which might have prevented participants from picking up on the associations between these stimulus features and preceding actions. Indeed, it has been shown that the acquisition (and/or retrieval) of action-effect associations is hampered for non-salient, task-irrelevant outcomes (Dutzi and Hommel 2009). As expectations about

upcoming action-outcomes cannot be formed in the absence of these associations, the reduced relevance of grating orientations might explain the absence of the prediction effects in this study.

In Experiment 1b, we tackled this issue by discouraging participants from using aforementioned stimulus-response strategies. Instead of always starting in a vertical position, the grating could now also be presented in a horizontal position. Accordingly, the position of the cue itself was no longer sufficient to determine the required rotation direction (i.e. a cue presented on the left required a rotation to the right for a vertical grating and a rotation to the left for a horizontal grating). In comparison to Experiment 1a, this approach promotes visualization of the action outcome. In addition, we would like to point out that, in contrast to experiment 1a, each oblique grating could now result from both a clockwise and a counterclockwise rotation, which precludes the possibility that potential prediction effects are caused by mere action execution rather than anticipated action-outcomes.

Another design element that might have accounted for the absence of the predicted effect is the difference between gratings presented in the induction trials and test trials. While participants are presented with chromatic gratings in the test trials, they learn to produce (and presumably predict) gray oblique gratings in the induction trials. These predicted perceptual outcomes in grayscale might not (fully) transfer to chromatic gratings. There is some evidence that is compatible with this notion from sensory attenuation research. Specifically, neurophysiological suppression has shown to be largest for the action-outcomes that most closely match predicted outcome features (Bäñ et al. 2008; Heinks-Maldonado et al. 2005). The partial mismatch in the predicted and actual features of the gratings in the present study might therefore have reduced modulation of onset rivalry by predictions of action outcome. In Experiment 1b, we reduced this mismatch by utilizing identical grayscale gratings in the induction and test trials.

On top of the aforementioned adjustments, several other changes were implemented to further increase the likelihood of observing prediction effects. Firstly, participants used keys instead of verbal reporting in Experiment 1b. Verbal reports are significantly slower, which means that participants sometimes found themselves in the process of verbalizing a percept, while a switch to another percept already occurred. This possibly noise-inducing factor is less likely when using key responses. Secondly, participants reported significant fatigue and loss of concentration while doing the task. We therefore shortened the length of the task by showing the rivalrous stimuli for one second instead of five seconds (see Carter and Cavanagh 2007 for a similar approach to measure onset rivalry).

Experiment 1b

Methods and materials

Participants

Thirty participants (23 females, 3 left-handed, $M_{\text{age}} = 23.17$, $SD_{\text{age}} = 2.88$) completed the experiment. None of the participants participated in Experiment 1a.

Stimuli and apparatus

Stimuli were the same as in Experiment 1a, with a few exceptions. Only gray gratings were used. Moreover, feedback text was replaced by a red or green fixation point (i.e. incorrect versus correct responses, respectively) to facilitate a focus on the fixation point throughout the trial. We also sought to reduce

eye dominance effects by adjusting the contrast of the grating presented to the non-dominant eye for each participant, so as to equate perceptual dominance of the two eyes. To do so, two adaptive, accelerated stochastic approximation staircases (Kesten 1958) of 40 trials were used in which the contrast of the dominant eye was held constant (Michelson contrast of 0.2 between background (9.5 Cd/m²) and minimum/maximum luminance), while the contrast of the non-dominant eye (determined by means of a hole-in-the-card task) was adjusted based on the initially dominant percept (starting at a Michelson contrast of 0.2 or 0.8). The mean contrast value of the last ten trials of both staircases was the contrast used for the non-dominant eye in the main experiment ($M = 0.27$, $SD = 0.14$).

Procedure and design

The procedure was the same as Experiment 1a with a few exceptions. In order to emphasize the association between the rotation of the knob and the rotation of the gratings, the instructions were slightly altered. Participants were told the gratings were visual representations of the knob that had to be set in the correct position. Specifically, the gratings had to be rotated in such a way that all the lines would point towards a cue (*) presented slightly above the left or right bottom juncture on the annulus surrounding the grating (see Fig. 3). In addition, the starting position of the grating could now be either vertical or horizontal, the duration of rivalry stimuli was shortened to one second, and participants reported their dominant percept by means of a button press. Specifically, participants used the upward or downward arrow key to select one of two vertically stacked images depicting either a -45° or a $+45^\circ$ grating. Vertical rather than horizontal response options were chosen such as to minimize response bias elicited by the preceding leftward or rightward rotary action. In addition, these responses were executed with the non-dominant hand, whereas the dominant hand was used for rotating the knob.

The aforementioned changes resulted in a design comprising starting position (vertical vs. horizontal), cue position (left vs. right) and orientation placement (left-eye -45 and right-eye $+45$ vs. left-eye -45 and right-eye $+45$) as within subject factors, and response mapping (top -45 and bottom $+45$ versus top $+45$ and bottom -45) as a between subject factor. Due to participant exclusion, response mapping was not equally divided between groups (13 participants received the first response mapping and 7 participants received the second response mapping). A Bayesian ANOVA with mapping as a between-subject factor did not provide conclusive evidence for (nor against) a difference in prediction consistency between these two groups ($BF_{10} = 1.16$). However, we would like to stress that there is no reason to assume that one of the response options would lead to more prediction consistent responses. Each combination of within subject factors was shown two times in each block in a randomized order.

Before the experiment participants completed pre-screening tests to check for stereoscopic vision and eye dominance. Since a staircase was used to diminish eye dominance effects, participants were only excluded if they displayed diplopia.

Results

Data exclusion

For eight participants eye dominance exceeded 85% during the task. The datasets of these participants were excluded from further analyses, as motivated in Experiment 1a. The fact that we had to exclude participants for excessive eye dominance,

despite the use of the staircases, concurs with previous work demonstrating that equating stimulus strength of rivalry stimuli does not necessarily prevent dominance biases in onset rivalry (Stanley et al. 2011). In addition, the datasets of two participants were excluded for failing to keep the head rested in the chinrest and for consistently executing multiple instead of one knob rotation, respectively. The remaining sample consisted of twenty participants (15 females, 1 left-handed, $M_{age} = 23.65$, $SD_{age} = 3.18$). Trials in which the button was incorrectly handled (i.e. rotated too fast, too slow, not far enough, back and forth or more than once; $M = 1.88\%$, $SD = 2.61\%$) or rotated in the wrong direction (i.e. not in the direction that was indicated by the movement cue; $M = 0.39\%$, $SD = 0.69\%$) were also excluded from analysis.

Perceptual selection

The proportion of initially dominant prediction-consistent percepts was submitted to a directional one-sample t-test against chance (i.e. a proportion of .50). In contrast to our hypothesis, this analysis provided substantial evidence “against” the hypothesis that participants are more likely than chance to perceive prediction-consistent percepts ($M = 0.46$, $SD = 0.14$; $BF_{+0} = 0.12$; $t(19) = -1.25$, $P = 0.89$, $d = -0.28$). That is, the observed results were roughly eight times as likely to be observed under the null hypothesis compared to the alternative hypothesis (see Fig. 2).

Discussion

Onset rivalry was not influenced by exposure to action-effect associations. Unlike the previous experiment, the Bayesian analysis now yielded substantial evidence in favor of the null hypothesis. Even a complete match between gratings on induction and rivalry trials, as well as more relevance of the grating orientation was not sufficient to bias perceptual selection. Together, the combined findings of Experiment 1a and 1b suggest that, at least under the current experimental conditions, onset rivalry is insensitive to action-based predictions.

Experiment 2

One possible reason for the absence of prediction effects in Experiment 1 might be that onset rivalry involves competition that is not, or only weakly, influenced by top-down factors. Indeed, onset rivalry is very sensitive to bottom-up stimulus features (e.g. contrast, luminance), and early trait-like influences such as eye dominance, while the role of top-down processes has not yet been extensively examined (Stanley et al. 2011).

In Experiment 2 we attended to this issue by examining whether action-outcome anticipation can influence perception of a structure from motion sphere; a bistable percept comprised of moving dots that can be perceived as a globe rotating in a leftward or a rightward direction (Andersen and Bradley 1998). Perception of ambiguous spheres has been shown to be sensitive for modulation from a variety of top-down factors including beliefs (Schmack et al. 2013; Sterzer et al. 2010), working memory (Scocchia et al. 2013), associative learning (Schmack et al. 2016) and voluntary control (Brouwer and Van Ee 2006). By keeping all other aspects of the task as similar as possible to the previous experiments, Experiment 2 therefore allows us to examine whether the influence of action-based predictions can be observed when using a type of bistable perception that is known to be susceptible to modulation by top-down factors.

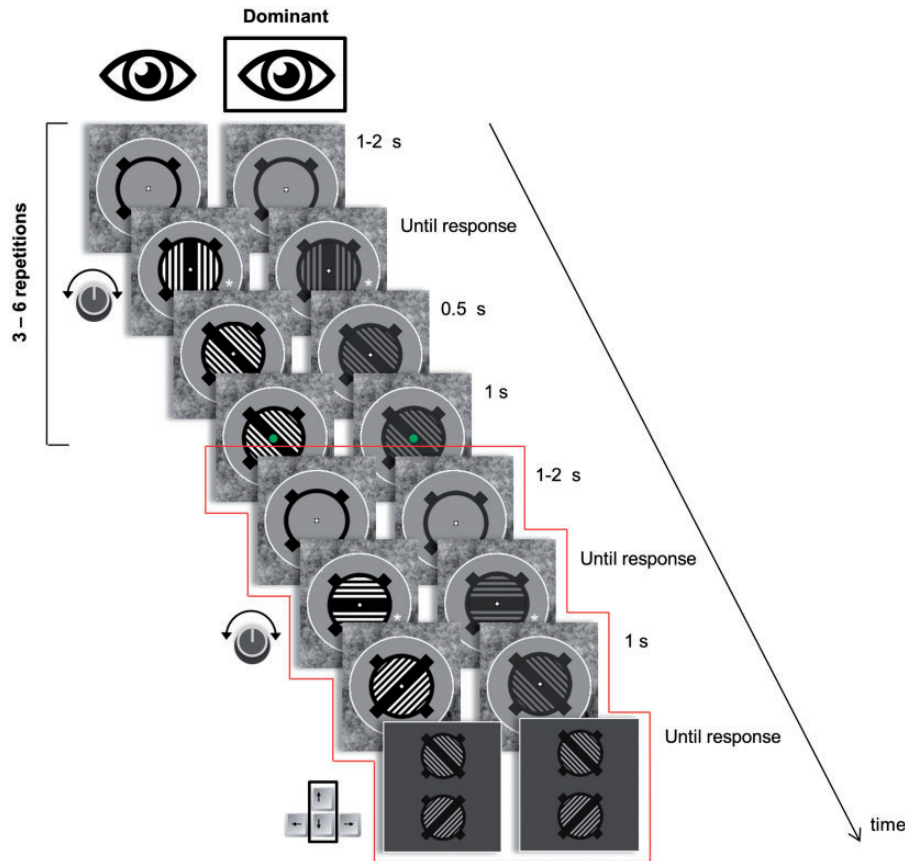


Figure 3. Schematic representation of trial events in induction and rivalry trials of Experiment 1b. Contrasts and colors deviate from those used in the experiment for illustrative purposes. Participants completed sub-blocks consisting of three to six induction trials and one rivalry trial (outlined in red). Cue position could vary within a sub-block.

Methods and materials

Participants

Twenty participants (15 females, 2 left-handed, $M_{age} = 23$, $SD_{age} = 2.99$) participated in the experiment.

Stimuli and apparatus

Visual stimuli were structure-from-motion spheres (diameter = 2.22 dva) consisting of 240 white squared “dots” (0.06 dva; 113 Cd/m^2), which each had a fifty percent chance of moving in a rightward or a leftward direction. In the center, the dots moved with a speed of 45 degrees/s, which decreased to a speed of zero near the edges of a circular aperture following a sinusoidal profile, thereby eliciting the percept of a sphere. Dot lifetime was one second (to avoid that all dots would be replaced simultaneously, the initial dot “age” was randomly chosen between zero and one seconds). The rotation direction of the sphere was either unambiguous (induction trials) or ambiguous (test trials). Ambiguous spheres consisted of two identical 2D sphere projections that were presented to both eyes. Due to the sinusoidal speed profile, observers tend to see the dots moving in one direction as being in a different depth plane than the dots moving in the other direction, causing the percept of a leftward or rightward rotating globe (depending on whether the leftward or rightward dots are perceived in the front plane respectively). Unambiguous spheres were created by adding binocular disparity to the dots (i.e. adding a horizontal offset between the two eyes; maximum offset from fixation = 0.04 dva), inducing a stable depth percept (e.g. by

presenting the leftward moving dots on the near depth plane, and the rightward moving dots on the far depth plane). Importantly, the monocular stimulation induced by presentation of the unambiguous and ambiguous spheres were virtually identical, while the percept elicited by the unambiguous spheres could still be reliably manipulated experimentally. All stimuli were presented on a black background ($<1 \text{ Cd/m}^2$) and viewed through the same stereoscope as described for the first two experiments.

Procedure and design

The experiment consisted of two types of trials: (i) unambiguous induction trials in which only the prediction-consistent rotation was presented and (ii) ambiguous test trials in which perception could be of either the prediction-consistent or prediction-inconsistent rotation direction. Each trial started with a gray fixation point (56.2 Cd/m^2 ; 0.13 dva) that was presented for a randomly chosen duration of 1000, 1250, 1500, 1750 or 2000 ms. Subsequently, participants observed a stationary 2D sphere with a fixation point in the center and a red movement cue (23.3 Cd/m^2 ; 0.13 dva) presented left or right of the sphere at an eccentricity of 1.48° of visual angle. Participants were instructed to keep their gaze fixated on the fixation point and to use a rotary button to rotate the front of the sphere towards the cue (i.e. a cue on the right side required a leftward rotation). To motivate participants to pay attention to the cue position, they were told that correct rotations would be rewarded with a monetary compensation. Similar to the previous onset rivalry experiments, participants could only earn

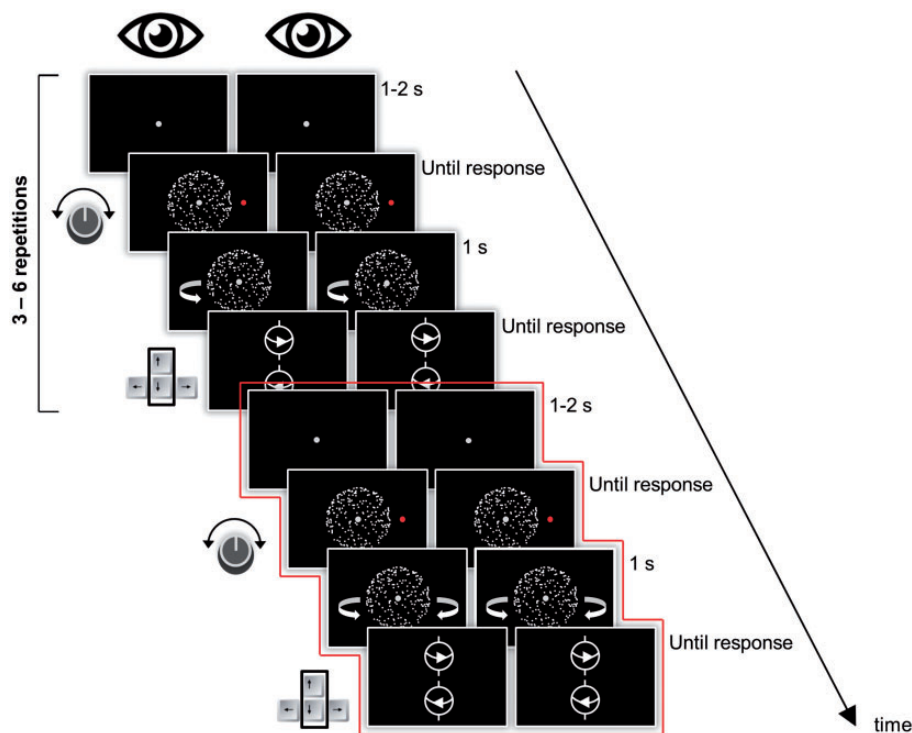


Figure 4. Schematic representation of trial events in induction and test trials of Experiment 2. Participants were instructed to rotate the front of a sphere towards a red dot presented on its left or right side. In induction trials, movements resulted in an unambiguous, action-coherent, rotation. In test trials, participants were presented with ambiguous bistable spheres that could be perceived as rotating in either a leftward or rightward direction. Participants indicated the perceived rotation direction by selecting the corresponding image with the arrow keys. Cue position could vary within a sub-block.

money on the induction trials. This rule was not explicitly mentioned in the present experiment to not draw attention to differences between induction and test trials. After correctly executing the rotary movement within response time limit (2 s), a rotating ambiguous or unambiguous sphere was shown for one second. Participants reported the perceived rotation direction by selecting one of two vertically stacked images depicting either a leftward or rightward rotation. Images were selected by means of the upward or downward arrow key (rather than the leftward or rightward keys) to minimize bias by the preceding leftward or rightward rotary action (see Fig. 4).

Induction and test trials were presented in the same sub-blocks as described in experiment 1. Cue position (left vs. right) was manipulated within participants. On half of the induction trials (36 trials) and half of the test trials (8 trials) in each block a target was presented on the left side of the sphere and on the other half of the trials a target was presented on the right side of the sphere. The order of the targets was randomized within each block. Response mapping (upward arrow = leftward rotation and downward arrow = rightward rotation vs. upward arrow = rightward rotation and downward arrow = leftward rotation) was counterbalanced between participants.

Before the experimental phase participants were pre-screened for stereoscopic vision by inducing varying retinal disparity. Participants who experienced diplopia did not take part in the experiment.

Results

Data exclusion

One participant showed a remarkably low accuracy level in the unambiguous induction trials (accuracy = 0.62; z -score = -3.68).

Considering that this resulted in significantly reduced exposure to correct action-effect associations, this participant was excluded from further analyses. The remaining sample consisted of nineteen participants (14 females, 2 left-handed, $M_{\text{age}} = 22.68$, $SD_{\text{age}} = 2.71$). Trials in which participants incorrectly handled the button (i.e. rotated the button too fast, too slow, not far enough, back and forth or performed more than one rotation; $M = 0.58\%$, $SD = 1.07\%$), as well as trials in which participants rotated the button in the wrong direction (i.e. not in the direction that was required by the movement cue; $M = 0.82\%$, $SD = 1.59\%$), were excluded from further analyses.

Perceived motion

The proportion of test trials in which the perceived rotation corresponded with learned action-effect associations was calculated for all participants for both induction and rivalrous trials. Mean accuracy on induction trials was high ($M = 96.50\%$, $SD = 4.54\%$) indicating that the rotation directions of unambiguous spheres were clear and easily distinguishable. Mean proportion of prediction-consistent percepts on rivalrous trials were submitted to a directional one-sample t -test. This test indicated that the observed data was more than a million times more likely under the alternative hypothesis (prediction-consistency > chance), compared to the null hypothesis (prediction-consistency = chance; $M = 0.59$, $SD = 0.04$; $BF_{+0} = 1.16 \times 10^6$; $t(18) = 9.41$, $P < 0.001$, $d = 2.16$). Including the data set of the excluded participant in the analysis (see “Data exclusion”) did not change this pattern of results: $BF_{+0} = 1.54 \times 10^5$. Numerically, every single participant had a higher proportion of prediction-consistent than prediction-inconsistent responses (see Fig. 5).

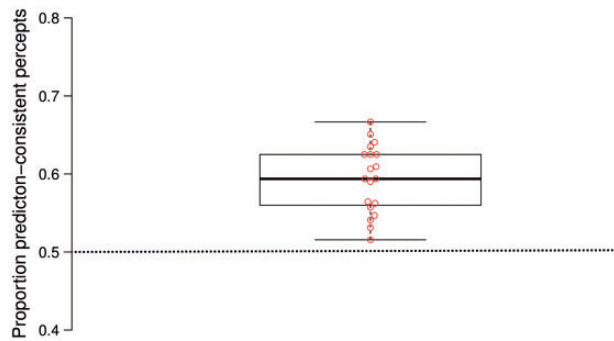


Figure 5. Proportion of prediction-consistent percepts for all participants in Experiment 2. The box spans the interquartile range. Red circles represent individual participants. The center line represents the median and whiskers extend to data points that are <1.5 times the interquartile range. Dotted line represents chance.

General discussion

Across three studies we demonstrate that while action-outcome anticipation does not affect perceptual selection during onset rivalry, it does modulate the perceived rotation direction of ambiguous spheres. These latter results are in line with previous demonstrations of identity prediction effects in sensory attenuation (Cardoso-Leite et al. 2010; Desantis et al. 2014; Hughes et al. 2013b). Here, we move beyond this work by showing that action-outcome anticipation cannot only modulate perceptual processing (i.e. the perceived “intensity” of stimuli), but can also affect perceptual content (i.e. the perceived “identity” of stimuli). Moreover, the observed prediction effect on bistable motion corroborates previous work showing that actions tend to bias perceived motion in the direction of movement (Beets et al. 2010; Di Pace and Saracini 2014; Maruya et al. 2007; Mitsumatsu 2009; Wallis and Backus 2016; Wohlschläger 2000). However, in contrast to these previous studies, we separated expectations about action-outcomes from other action-related information sources (e.g. proprioception), and, as such, provide more direct evidence for the proposed role of outcome-anticipation in perceptual processing (Waszak et al. 2012).

Interestingly, action-identity prediction effects do not appear to generalize to all types of bistable perception, as no effects were observed for onset rivalry. These diverging results raise the question of whether predictive processes might have been weaker or absent in Experiment 1a and 1b compared to Experiment 2. We deem this unlikely considering that the exposure to action-effect associations, in terms of number of trials, was identical across experiments. There are, however, several other important differences between the experiments that might explain the divergent effects; the most apparent being the variation in the type of bistability that was employed. One possible, albeit speculative, explanation of the results is that these different levels of bistable perception might reflect different levels of visual processing, with varying susceptibility for top down modulation. Specifically, we propose that (onset) rivalry might be resolved at a lower stage of visual processing than structure-from-motion, which might be less permeable to top-down influences (see Meng and Tong 2004 for a similar argument). There are several arguments that can be put forward in support of this line of reasoning.

With respect to permeability by top-down influences, binocular rivalry has been shown to be less susceptible to top-down modulation compared to other forms of bistable competition or

perceptual suppression. For instance, Meng and Tong (2004) showed a reduced ability of participants to selectively switch between rivalrous stimuli as opposed to the two possible orientations of a Necker cube. In addition, perception of ambiguous structure-from-motion spheres is biased towards the concurrent content of visual working memory (Scocchia et al. 2013), whereas perception during binocular onset rivalry is not (Gayet et al. 2015). Also, only basic visual processing can be applied to an image that is binocularly suppressed (for reviews, see Lin and He 2009; Gayet et al. 2014), compared to other forms of perceptual suppression that allow for more elaborate processing of the suppressed image (Breitmeyer 2014).

In addition, there are at least two ways that rivalry seems different from structure-from-motion spheres in terms of the level of visual processing. First, the “perceptual manifestation” of binocular rivalry differs from that of other forms of bistable perception, such as structure-from-motion (Brascamp et al. 2018). Specifically, in an ambiguous structure-from-motion sphere, one of the two percepts is effectively perceptually suppressed (e.g. the leftwards moving percept), but the visual elements that constitute this percept are nonetheless consciously accessible (i.e. the dots that make up the sphere). In binocular rivalry suppression, however, the observer not only fails to see the suppressed percept of interest (i.e. the grating orientation), but also lacks conscious access to image-parts that constitute the suppressed percept, suggesting more complete suppression. This “deeper” suppression might render rivalry stimuli less accessible to top-down influences, potentially explaining the lack of observed prediction effects in Experiment 1a and 1b. In contrast, structure-from-motion spheres are more similar to other forms of bistable perception, like Necker cubes, whose visual elements remain accessible and, are therefore modifiable by factors such as voluntary attention (e.g. voluntarily attending to certain ribs of the cube can be used to induce switches; Kawabata 1986).

Second, there are some indications that rivalry can be resolved at very early stages of visual processing, such as V1 (Lee and Blake 2002) and even at the level of the lateral geniculate nucleus (Haynes et al. 2005). Whilst rivalry has also been associated with activity of higher fronto-parietal areas (Sterzer et al. 2009), the extent to which these areas play a role in modulating interocular competition, or are involved in cognitive processes that arise after the interocular competition is resolved (e.g. task demands, or perceptual reports), remains a topic of vehement debate (Zaretskaya and Narinyan 2014; Giles et al. 2016; Brascamp et al. 2018). In addition, there is some recent evidence suggesting that, although frontal-parietal involvement might sometimes be observed during rivalry, it is not necessary for perceptual reversals to occur (Brascamp et al. 2015; Zou et al. 2016). These latter findings are in line with our proposal that rivalry reflects a relatively low stage of visual competition (although note studies showing modulations of perceptual switching as a function of parietal-TMS; Carmel et al. 2010; Zaretskaya et al. 2010).

At first glance, the idea that binocular rivalry occurs too early in the visual processing hierarchy for top-down modulation by action-outcome anticipation might seem to contradict recent findings showing that onset rivalry can be biased by motion predictions (Denison et al. 2011; Attarha and Moore 2015). In these studies, participants were more likely to select the rivalrous grating with an orientation that logically followed the preceding motion sequence than a grating with a motion-inconsistent orientation. Although these results might be interpreted as evidence for the influence of top-down predictions on

(early) visual competition, an alternative explanation has been offered. Specifically, Attarha and Moore (2015) posit that instead of reflecting high-level predictive influences, these results might also have resulted from more local, low-level, priming mechanisms, in which motion-consistent percepts are primed by synchronized activity between subcortical areas and the visual cortex. This interpretation is in line with the observation that both predictions based on semantic context and more complex pattern motion failed to bias onset rivalry (Attarha and Moore 2015), as well as with our failure to observe an influence of outcome-predictions on perceptual selection.

Taken together, there is some, although not unequivocal, evidence to support the idea that the difference in findings between the two present experiments might be the result of differences in the stages of visual competition that were involved. We like to stress that this notion is speculative, and point out that the current results and explanation might be restricted to the initial dominance percept of rivalry. Indeed, there is evidence to suggest that the underlying mechanisms of onset rivalry and ongoing rivalry might be at least partially independent (e.g. Stanley et al. 2011). Additional research comparing various forms of bistable perception (and binocular rivalry), with varying depths of suppression, could provide valuable insights into these issues.

There are several alternative explanations, relating to subtle procedural differences between the experiments that need to be considered. One of these procedural differences pertains to the extent of spatial correspondence between hand movements and grating rotations. In the rivalry studies, the rotation plane of the knob was perpendicular to the movement of the grating on the screen. In contrast, in Experiment 2, the sphere rotated on the same plane as the rotary button. Although previous work has suggested that spatial correspondence between action and motion displays facilitates action-based modulation of bistable perception (Wohlschläger 2000; Experiment 1), these effects have also been observed in the absence of such correspondence. Specifically, when action and motion display share a cognitive dimension, a congruent spatial relation has shown not to be a prerequisite for the effects (Wohlschläger 2000; Experiment 3). Considering that such cognitive coupling between hand movements and bistable stimuli was equally induced across studies, we are confident that action-identity prediction occurred in all experiments.

Another procedural factor that could be argued to account for the observed differences between Experiments 1 and 2 is demand characteristics. That is, the results of Experiment 2 might not be a reflection of outcome prediction effects, but instead reflect the propensity of participants to report their explicit expectations concerning what they should perceive instead of their actual percepts. We assume that such demand characteristics are especially probable in the absence of a clear sensory signal. In contrast, if participants are very certain about what they see, they will tend to rely on (and report) their percepts. If demand characteristics are fully responsible for the effect we observed in Experiment 2, the question remains why they would not have been present in Experiments 1a and 1b. We have reasons to believe that such demand characteristics were, in fact, more likely to play a part in Experiments 1a and 1b (in which no effect of action-prediction was observed). One indicator of perceptual uncertainty in bistable perception paradigms is the number of reported mixed percepts, referring to situations in which participants do not exclusively perceive one of the competing percepts, but rather a mixture of the two [i.e. parts of each eye's stimulus during binocular rivalry (Blake 2001), and two convex

or concave half spheres during ambiguous motion (Hol et al. 2003)]. While participants in our lab regularly report the former, the perception of mixed sphere percepts is rare. Considering the absence of prediction effects in the first two experiments, in which perceptual uncertainty was higher, it is unlikely that demand characteristics can exclusively account for the observed effects in Experiment 2.

Conclusion

We extend previous work by showing that action-outcome anticipation cannot merely modulate perceptual processing, but can also bias the actual content of our conscious perception. Importantly, prediction effects were only observed when actions were followed by bistable motion, but not by rivalrous gratings. The present results coincide with previous work suggesting that binocular rivalry in general, and onset rivalry in particular, might be less susceptible to top-down influences. This discrepancy might point towards differences in underlying mechanisms. Further examination of the commonalities and discrepancies between distinct forms of bistable perception, as well as the possible restrictions to the influence of top-down biases, will provide important insights in the role of predictive processing on awareness.

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