

Continuous flash suppression: Manual action affects eye movements but not the reported percept

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Diverse paradigms, including ambiguous stimuli and mental imagery, have suggested a shared representation between motor and perceptual domains. We examined the effects of manual action on ambiguous perception in a continuous flash suppression (CFS) experiment. Specifically, we asked participants to try to perceive a suppressed grating while rotating a manipulandum. In one condition, the grating's motion was fully controlled by the manipulandum movement; in another condition the coupling was weak; and in a third condition, no movement was executed. We found no effect of the movement condition on the subjectively reported visibility of the grating, which is in contrast to previous studies that allowed for more top-down influence. However, we *did* observe an effect on eye movements: the gain of the optokinetic nystagmus induced by the grating was modulated by its coupling to the manual movement. Our results (a) indicate that action-to-perception transfer can occur on different levels of perceptual organization, (b) demonstrate that CFS involves the shared representations between action and perception differently than paradigms used in earlier studies, and (c) highlight the importance of objective measures beyond subjective report when studying how action affects perception and awareness.

suggests that late stages of perception and early stages of action use shared representations, which then allow action planning to be promptly influenced by a connected percept. Furthermore, while an external influence of action on perception is trivial (by moving our eyes, changing location, or manipulating the world around us; e.g., see Wexler & van Boxtel, 2005), the common coding theory, as well as the theory of event coding (e.g., Müsseler, 1999), also implies an internal influence of action on perception. If the observation of an action creates motor resonance, the production of an action should lead to a similar, but perceptual, resonance (Schütz-Bosbach & Prinz, 2007). There is some experimental evidence to support this notion. Wohlschläger and Wohlschläger (1998) found that concurrent manual rotation led to faster performance in a mental rotation task when the directions of action and mental rotation were congruent as opposed to when they were incongruent. This, however, was only observed when the two rotations occurred about the same axis. Similarly, Wexler, Kosslyn, and Berthoz (1998) showed that speed as well as accuracy in an imagery mental rotation task can be enhanced by unseen motor rotation, in a direction that is congruent with the action. In line with Wohlschläger and Wohlschläger (1998), Wexler et al. (1998) also found that the facilitating effect of congruent action is dependent on the relative angle and velocity of the movements.

Further evidence for an internal effect of action on perception is provided by paradigms in which action leads to a bias in the percept of an external stimulus, instead of the outcome of imagery (for an overview of different methods, see Zwicker & Prinz, 2012). Multi-

Introduction

Perception obviously affects action, but there is also mounting evidence for the reverse direction, a direct effect of action on perception and perceptual representations. In an effort to determine the underlying mechanisms, the common coding theory (Prinz, 1997)

Citation: Veto, P., Schütz, I., & Einhäuser, W. (2018). Continuous flash suppression: Manual action affects eye movements but not the reported percept. *Journal of Vision*, 18(3):8, 1–10, <https://doi.org/10.1167/18.3.8>.

<https://doi.org/10.1167/18.3.8>

Received September 22, 2017; published March 23, 2018

ISSN 1534-7362 Copyright 2018 The Authors



stable stimuli are ideal tools for making internal biases measurable, while the external stimulation stays unchanged. This can be achieved through an inherent ambiguity, where the stimulus itself has two or more stable interpretations (ambiguous stimuli such as, for example, the Necker cube [Necker, 1832] or Boring's old/young figure [Boring, 1930]), or through the presentation of different stimuli in one eye as opposed to the other, leading to a conflict that is resolved by either one or the other eye gaining dominance at a time (binocular rivalry [BR]; Wheatstone, 1838).

Using an ambiguous rotating display, Wohlschläger (2000) primed the perceived direction of motion by both hand movements and planned actions, and found that either one can be sufficient for biasing the percept, if they share a common, cognitively specified dimension with the stimulus. In the case of planned actions, there is no kinesthetic information to bias the visual modality. He argues that this makes a direct, low-level, motor-to-visual information flow an implausible explanation for why the priming—or action capture—took place. Instead, he suggests that the phenomenon is more similar to attentional capture, where top-down control plays a crucial role, and where effects are object- and action-centered.

For an ambiguous structure-from-motion cylinder, Beets and colleagues (2010) demonstrated that rotating a manipulandum congruently with the current percept stabilizes its perceptual state, while an opposing rotation yields destabilization. In line with Wohlschläger's (2000) reasoning for the top-down nature of action capture, these effects were only observed when the manipulandum was used to report the percept, while no effect of action was found when concurrent rotation of the manipulandum was unrelated to the task.

Instead of ambiguous displays, Keetels and Stekelberg (2014) used an unambiguous stimulus with high perceptual uncertainty. With a flashing bar stimulus that was displaced only slightly (or remained stationary) at each trial, they found that concurrent, directional, button press actions shifted the point of subjective equality of perceptual displacement judgments in the direction of action.

While both Wohlschläger (2000) and Beets et al. (2010) used ambiguous displays, similar effects were also found in BR (Maruya, Yang, & Blake, 2007), where perception of the movement of one eye's stimulus was positively biased by manual control. Interestingly, the effect of action did not only occur when the coupled stimulus was dominant, but also when it was suppressed from awareness (i.e., when the stimulus of the other eye had exclusive dominance). This argues against an explanation that is solely based on top-down control.

Imitated hand action can also bias perception in BR. Di Pace and Saracini (2014) used a dynamic hand action presented in one eye and a checkerboard pattern in the other, and found that dominance durations for perceiving the hand action were longer when the same action was imitated by the observer.

In a stream-bounce display (Metzger, 1934), two identical objects move toward each other until reaching a common position, after which they move away from each other following a continuous path. The perceptual interpretation of this animation is ambiguous, as the objects may seem to either pass through or bounce off of one another. When the motion of the disks is controlled by the hand action of the observer, the visual interpretation that is congruent with the performed action is more likely to take place, as shown by Mitsumatsu (2009). Similarly to Beets and colleagues (2010), he also found that the mere presence of action is not sufficient for the effect to occur.

Perceptual resonance may happen simultaneously (online effects), or through motor learning on different time scales (offline effects; Schütz-Bosbach & Prinz, 2007). To our knowledge, only a few studies on the online effects of action on perception so far have used action as a way of controlling concurrent stimulus dynamics, and they only used action as either coupled or not coupled to the stimulus. To test whether the action–perception transfer is influenced by the degree of coupling between task-relevant hand movement and stimulus velocity dynamics, we used a continuous flash suppression (CFS; Tsuchiya & Koch, 2005) paradigm, where a faint, moving grating stimulus, presented to one eye, was set against a colorful Mondrian suppressor that was displayed to the other. This paradigm constitutes a highly biased variant of interocular conflict, where the strength of one stimulus (the suppressor) is maximal and the other stimulus can only be perceived when endogenous attention is deployed. We varied the degree of coupling between participants' rotational hand action and grating stimulus dynamics (fully coupled action, partially coupled action, no action). Observers were asked to report on their subjective percept by pressing and holding a button whenever they perceived the grating. In addition to this subjective measure, which is prone to subjective criterion and response bias and might only reveal percepts that are clearly suprathreshold, we used an additional measure, which might reveal effects on the suppressed stimulus: Throughout the experiment we measured eye position. When the grating becomes dominant, we expect the drifting grating to induce an optokinetic nystagmus (OKN). Unlike the button press, which is an all-or-none report, the gain of the OKN slow phase should be related to the degree of dominance (cf. Naber, Frässle, & Einhäuser, 2011, for the case of BR). Hence, we expect that measuring the

gain may reveal subtle changes in the visual representation of the grating, even if it is still subjectively suppressed from perception. Consequently, we use the OKN gain as a measure of whether concurrent action influences the perceptual representation of the grating, both above and below perceptual threshold.

This paradigm is particularly applicable for studying the effects of action on perception, as only one stimulus needs to be coupled with the action, while the other remains constant at all times. Since in our case, constant action is required, linear hand movements would not be suitable. For eliciting OKN, however, linear translation of the stimulus is most applicable. The coupling between rotational input and linear output is always arbitrary: As with a rack and pinion mechanism, the direction of coupling depends on the relative spatial configuration of the machine. This renders a traditional BR paradigm with two gratings of opposing directions unfeasible for our purposes, as coupling the manipulandum rotation to one stimulus would also result in an equal coupling to the other.

As a form of interocular conflict, CFS has close resemblance to BR, although it shows dissimilarities beyond the greater exerted strength of suppression (Tsuchiya & Koch, 2005; Tsuchiya, Koch, Gilroy, & Blake, 2006). As detailed above, several cases of dynamic multistable stimuli have been reported where action influences perception. Based on these results, we hypothesized an increase in perceived strength of the grating when action is coupled to the stimulus' dynamics, as compared to when the same visual stimuli are presented without action. In BR, there are two ways to operationalize the degree to which a certain stimulus is dominant over the competitor: first, the relative dominance of the stimulus (i.e., the time of dominance as proportion of total time), often referred to as predominance; and second, the distribution of dominance durations of either stimulus. Levelt's propositions (Levelt, 1965) relate the notion of stimulus strength to the two measures. Increasing the physical strength of a stimulus (e.g., its contrast) increases that particular stimulus' predominance. In principle, this can be achieved in two different ways: either by increasing the dominance durations of this particular stimulus, or by decreasing the dominance durations of the competing stimulus. In BR, increasing the strength of the weaker stimulus primarily decreases the dominance durations of the competitor (Brascamp, Klink, & Levelt, 2015; Levelt, 1965). The hypothesis that action–perception coupling increases stimulus strength therefore yields two predictions. First, irrespective of initial stimulus strength, coupling between manipulandum rotation and grating motion should increase the predominance of the grating. Second, if the grating is the initially weaker stimulus, we expect a decrease of the suppressor's dominance duration. If viewers per-

ceive the two stimuli as relatively balanced in strength, an increase in the dominance duration for the grating stimulus would also be expected. Consequently, we analyzed predominance as well as dominance durations for suppressor and grating. Aside from and in parallel with these changes in subjective reports of participants, we also expect to see an increased OKN response to the grating stimulus when it is coupled to manual action as opposed to when no action is performed.

Results from the partially coupled action condition of the experiment will show whether the action-to-perception transfer depends on the type of coupling. When action is coupled directly to the grating's movement, the change in stimulus position is predictable from action. When action is only partially coupled, the action remains task-relevant and still has an effect on stimulus dynamics; however, exact stimulus parameters cannot be estimated. If such perceptual estimates are not necessary for the action-to-perception transfer to take place, we would see similar results with partially coupled action as with full coupling. If, on the other hand, matching dynamics between action and perception do play a role in the expected facilitation, results will be either identical to when no action is required, or somewhere between the no action and fully coupled action conditions.

Methods

Participants

Twenty-four students (15 women, 9 men; four left-handed, mean age = 24.4, $SD = 5.8$) took part in the experiment. All of them were naïve to the purpose of the experiment, had normal or corrected-to-normal vision and normal stereo vision, and gave written informed consent to their participation. All procedures conformed to the Declaration of Helsinki and were approved by the applicable board (Ethikkommission FB04, Philipps-University Marburg).

Setup and stimuli

Manual action was tracked by a custom-built manipulandum device (Figure 1). The manipulandum consisted of a horizontal disk of 9-cm radius, which had an 11.5-cm long handle mounted perpendicular to the disk at 5 cm distance from the center. To track the angular position of the handle, the axis of the disk operated a Kübler Sendix 5020 incremental rotary encoder (Kübler Group, Villingen-Schwenningen, Germany). The angular position was recorded only relative to the arbitrary starting position; therefore, the



Figure 1. Experimental setup. The cold mirrors of the stereoscope allowed eye tracking from a table-mounted camera position as seen in the image. The manipulandum device (bottom right) was not visible to participants during the experiment. The experiment was carried out in a dark room.

data provide no information about the absolute angular position. Stimuli were generated using MATLAB (MathWorks, Natick, MA) and the Psychophysics Toolbox (Brainard, 1997; Pelli, 1997). Presentation took place at a viewing distance of 30 cm on two 21-in. Syncmaster CRT screens (Samsung, Seoul, South Korea), at $1,280 \times 1,024$ pixels spatial and 85 Hz temporal resolution. A mirror stereoscope with cold (infrared-transparent) mirrors (Naber et al., 2011) allowed for simultaneous dichoptic stimulus presentation and noninvasive infrared eye-tracking of one eye at 1,000 Hz (EyeLink 2000, SR Research, Ottawa, ON, Canada) with the EyeLink Toolbox (Cornelissen, Peters, & Palmer, 2002). Since the eye-movement characteristics that we needed to analyze for the purpose of this study are equitably carried by both eyes (Naber et al., 2011), binocular tracking was not necessary.

Each eye's stimulus was centrally presented within a red annulus (inner diameter: 34°), to ensure fusional vergence. The suppressor stimulus completely filled this

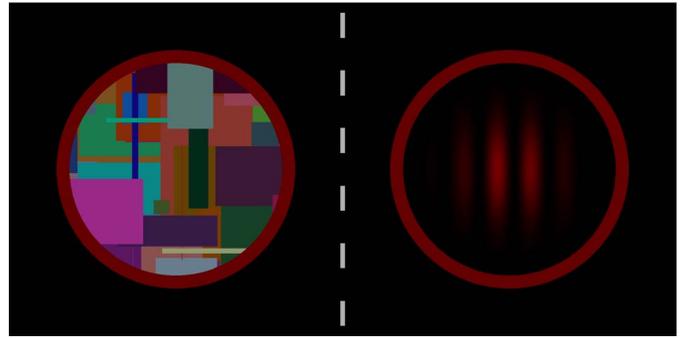


Figure 2. Stimulus. Stimulus display. The dashed line was added to indicate the separation of stimuli between the two eyes.

ring and consisted of overlapping rectangles of random size and color, presented with a refresh rate of 10 Hz. The target stimulus was a horizontally drifting, red, sine-wave grating on a black background. The grating's spatial frequency was 0.18 cyc/deg and its total diameter subtended 28° . A Gaussian mask, centered within the red annulus, decreased the grating's luminance smoothly towards the boundary of the spatially fixed circular aperture (Figure 2).

Procedure

The experiment consisted of three conditions, presented in separate blocks in an alternating fashion. In all conditions, the task of participants was to try to perceive the moving grating stimulus as dominant. They were also instructed to indicate their percepts by keeping a button pressed all the time when *full dominance* of the target was achieved, and released when the suppressor was dominant. Full dominance was defined to the participants as clearly visible and not only in parts. Note that this does not imply exclusive dominance, as the Mondrian was virtually never suppressed completely. For all participants, button presses were executed with the left hand, while the manipulandum was operated with the right.

In the coupled action (CA) condition, participants were instructed to continually rotate the manipulandum in the predefined direction at the velocity of their choosing. Grating velocity was directly coupled to this action at a fixed rate.

In the decoupled action (DA) condition, participants executed the same task as in the CA condition, but their action was largely decoupled from the grating's dynamics. The dynamics of the last completed CA block in the experiment was replayed and averaged with the participant's concurrent action with a weight of 4:5. By the concurrent action having only a weight of 1:5, no moment-by-moment prediction could be made regarding the velocity of the grating, while the

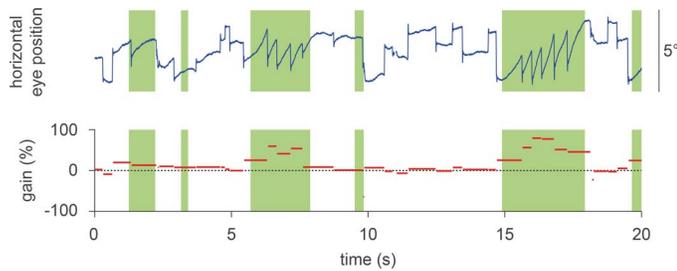


Figure 3. Example excerpt of Participant 6. Button press (green areas across both graphs indicate subjective perceptual dominance of the grating), raw data of horizontal eye movements (blue line), and gain (red line showing least-squares mean velocity of slow-phase eye movements as portion of stimulus velocity).

participant still had some effect on the overall dynamics of the stimulus.

In action blocks (conditions CA and DA), continuous rotation in the correct direction was invoked. If the participant stopped rotating or rotated in the wrong direction, a red rectangle in the centers of the stimuli on both screens warned them. Block 2 (first DA block) of Participant 12 was removed from analysis due to a failure of following the rotation instructions for 92.04% of the total duration of the block. In all other blocks and participants, the ratio of erroneous rotation remained negligible (mean = 0.55%, $SD = 0.76\%$).

In the no action (NA) condition, participants were instructed to perform no rotation, while keeping their hands on the manipulandum lever. Stimulus dynamics were entirely determined by the replay of the last completed CA block.

Experimenter and participant only knew whether action was required or a NA block was conducted, but both were blinded to whether a block, in which manual action was required, was CA or DA. Participants in addition were naïve to the fact that two different blocks with movement existed; in informal debriefing, most observers did not report that they had noticed the existence of two distinct conditions involving manipulandum movement.

The grating's direction was counterbalanced between blocks, while the directional pairing between grating translation and manual action was locked: Clockwise action was coupled with leftwards and counter-clockwise action with rightwards motion of the grating stimulus, such that the grating corresponded to the movement when the lever was in front.

Each participant started the experiment with a training block, where the grating stimulus was shown to both eyes for 200 s. This ensured that all participants knew the grating stimulus, regardless of its visibility in the subsequent CFS blocks, ensuring that they knew the nature of the stimulus they were supposed to report (most participants had little or no experience in visual

psychophysics prior to the experiment). Following the training, they completed 12 blocks, with block order following a counterbalanced design between the three conditions (four blocks each). Each block was preceded by an eye tracker calibration and lasted 200 s. In those cases when the experiment started with DA or NA blocks (thus, no action of the given participant was recorded yet), stimulus dynamics of the last CA block of the previous participant were replayed. For all other DA and NA blocks, recordings of the last CA block of the given participant were used. This allowed us to have a counterbalanced design while maximizing the similarity in stimulus dynamics between conditions.

Analyses

Button press responses were analyzed by comparing conditions in the following measures: predominance of the grating (overall dominance rate throughout the whole experiment), dominance durations (average length of individual dominance periods) for the grating stimulus and for the suppressor, and switching frequency between the two stimuli. Eye data were analyzed by similarly comparing the mean gain of the OKN slow phase (eye velocity as a portion of stimulus velocity). This measure was achieved by first removing OKN fast phases and blinks, using the built-in EyeLink saccade detection software with the parameters of $30^\circ/s$ velocity threshold and $8,000^\circ/s^2$ acceleration threshold. The average horizontal velocity of OKN slow phases was then calculated by least-squares fitting a linear function to each of the remaining sections. Giving this value the appropriate sign (positive if the slow phase was in the direction of the stimulus in the given block) and dividing it by stimulus velocity yielded the gain of eye movements, at each time point of the experiment when no saccade or blink occurred (Figure 3). Note that the gain is negative if the slow phase of the OKN is directed opposite to the grating's drift direction, and positive if both are in the same direction. Perfect OKN would imply a gain of 100%.

Measures were averaged across blocks for each condition and participant, and compared in a within-subject repeated measures ANOVA. In cases where Mauchly's test indicated a violation of the sphericity assumption, Greenhouse-Geisser corrected values were used. Post hoc t tests were carried out between all condition pairs if the variance analysis showed a main effect at a 0.05 alpha level. For post hoc tests, significance was asserted only when the p value fell below a Bonferroni-adjusted alpha-level of $0.05/3 = 0.0167$. For analyses on button press measures, blocks with no button press (12 blocks altogether across all participants) were treated as missing values.

Variable	Unit	Condition			<i>df</i>	<i>F</i>	η_p^2	<i>p</i>
		CA	DA	NA				
Predominance (grating)	%	38.47 (25.93)	38.82 (28.80)	38.05 (28.56)	2, 46	0.17	0.007	0.844
Dominance duration (grating)	s	7.74 (11.81)	8.64 (14.05)	8.73 (14.61)	1.32, 30.25	0.39	0.017	0.595
Dominance duration (suppressor)	s	8.61 (6.45)	8.49 (8.28)	10.04 (9.97)	2, 46	0.73	0.031	0.486
Switching frequency	1/s	0.21 (0.15)	0.20 (0.15)	0.21 (0.17)	1.40, 32.24	0.69	0.029	0.459
Gain (overall)	%	10.40 (7.89)	9.78 (7.51)	9.13 (7.52)	2, 46	4.40	0.161	0.018*
Gain (grating dominant)	%	16.95 (11.46)	16.48 (10.91)	15.17 (9.86)	1.54, 35.49	2.84	0.110	0.084
Gain (suppressor dominant)	%	7.52 (5.55)	7.34 (6.05)	6.99 (6.85)	2, 46	0.86	0.036	0.432

Table 1. Statistical measures of results from perceptual reports and eye movements (gain). Means and standard deviations are shown for all variables and conditions. Predominance of grating: portion of the experiment's total duration when perceptual dominance of the grating was indicated by button press. Dominance duration: average time of dominance between reported perceptual switches. Switching frequency: number of switches per second. Gain: slow phase optokinetic nystagmus velocity as portion of stimulus velocity. Notes: CA = coupled action; DA = decoupled action; NA = no action; * denotes $p < 0.05$.

Time-normalized analysis

For a more detailed view of temporal relationships between eye movements and the reported percept, we compared the gain for each condition on a scale of normalized time between button press and release. The absolute durations of individual segments from one perceptual switch to the other are variable between participants as well as between the two perceptual interpretations (dominance of grating or suppressor). In order to compare conditions and perceptual dominance without a bias by the absolute duration of the percept, gain data for individual intervals between perceptual switches were normalized to unit time (see also Einhäuser, Martin, & König, 2004). The gain trace between each button release and subsequent button press (and vice versa) was mapped by linear interpolation to 10,000 data points referred to as interval [0, 1], prior to averaging these segments. In this time frame, unit time corresponds to one-half cycle between two consecutive button presses.

To circumvent the multiple comparisons problem in studying a large number of points on the time scale, conditions were analyzed in a between-trials, cluster-based nonparametric test on the time-normalized data, separately for intervals in which the grating or the suppressor was dominant. Methods were based on Maris and Oostenveld (2007). In short, t values were obtained from a pairwise comparison of conditions at all data points of the time normalized scale. Clusters were formed where paired t tests resulted in statistics with $t > 2$. Gaps between clusters were ignored when they did not exceed 0.5% of the normalized time scale (corresponding to an average of 44.2 ms in the real-time data). Note that these thresholds do not affect the false alarm rate in the nonparametric test; instead, they only set the sensitivity for localizing the clusters. The sum of t values in the largest cluster was recorded as the observed test statistic. To form random partitions, trials (averages across blocks per participant) of the

different conditions were collected in a single data set, and new subsets of equal sizes were formed by random draws of trials. Test statistics were calculated on these random subsets similarly to those calculated on the actual conditions. By repeating the above method of random partitions 1,000 times, Monte Carlo p values were calculated by taking the proportion of random partitions that showed a larger test statistic than the observed test statistic.

Results

Subjective report and gain

Button press responses showed no significant difference between conditions in any of the examined variables (Table 1).¹ Gain evinced to be different between conditions when data were considered irrespective of button press data. Here, pairwise comparisons revealed a significant difference between CA and NA conditions, $t(23) = 2.79$, $p = 0.010$, but not between CA and DA conditions, $t(23) = 1.72$, $p = 0.099$, or DA and NA conditions, $t(23) = 1.41$, $p = 0.173$. In post hoc contrasts, a linear model showed the best fit to the pattern of results, $F(1, 23) = 7.78$, $\eta_p^2 = 0.25$, $p = 0.010$ (Figure 4).

Time-normalized analysis

For periods in which participants reported dominance of the grating, nonparametric test results revealed significant differences at a critical alpha-level of $p < 0.05$ between each condition pair ($p_{CA-DA} = 0.041$; $p_{DA-NA} = 0.034$; $p_{CA-NA} = 0.016$). In contrast, for periods in which participants reported the flash to be dominant, only the CA–NA comparison reached

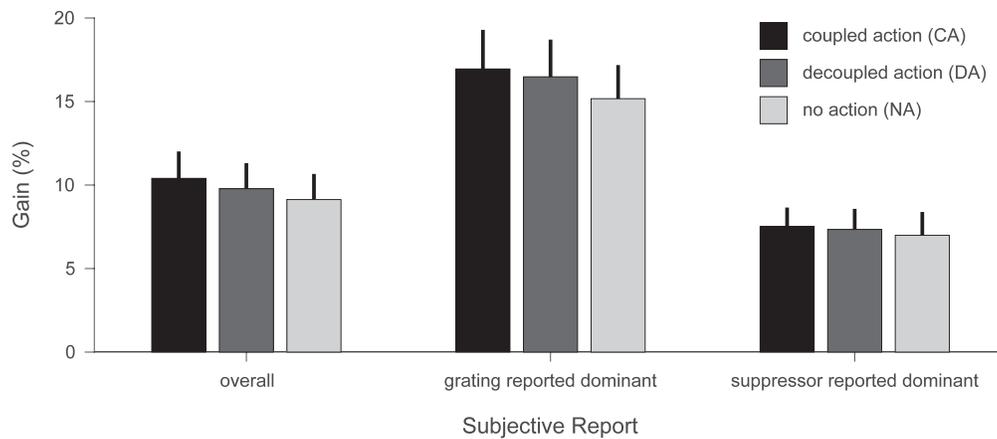


Figure 4. Means of gain. Groups from left to right: data across the whole experiment, portion of experiment when button press report indicated dominance of the grating, and portion of experiment when button press report indicated dominance of the suppressor. Error bars show standard errors of the mean.

significance ($p_{CA-DA} = 0.103$; $p_{DA-NA} = 0.120$; $p_{CA-NA} = 0.048$). More interestingly, the largest clusters of difference occurred at dissimilar temporal positions relative to the reported dominance switches (Figure 5). For comparisons between action conditions (CA and DA) and the NA conditions, clusters were found where the gain was highest (proximal to when the grating achieved dominance). However, CA and DA conditions differed the most during times when gain was low (near the end of the grating's dominance).

Discussion

Our results show that reported percept and eye-movement behavior are affected differently by action. Although earlier studies with ambiguous displays (Beets et al., 2010; Mitsumatsu, 2009; Wohlshläger, 2000) and BR (Di Pace & Saracini, 2014; Maruya et al., 2007) have shown a clear effect of concurrent, task-related action on perception, we did not find any sign of such an effect in a CFS paradigm.

Visually induced eye movements, on the other hand, were affected by action. One possible interpretation of this result is that the mechanisms underlying action-to-perception transfer for the conscious percept differ from those underlying action-to-perception transfer for eye-movements. Alternatively, both forms of action-to-perception transfer use the same mechanism, but at different sensitivities. While comparing the means of the gain during times of dominance of one or the other stimulus did not show clearly whether the effect stemmed from intervals of the experiment when dominance of the grating was indicated or from the portion when the suppressor was dominant, nonparametric test results showed that the effect was not distributed homogeneously across the time of domi-

nance of either stimulus. As opposed to binary button press responses, the gain of OKN eye movements showed a gradual transition of dominance between suppressor and target stimulus (cf. Fahle, Stemmler, & Spang, 2011; Naber et al., 2011). Relative to these transitions, the effect of action (both coupled and decoupled) as compared to no action was most expressed when eye movements elicited by the grating were highest. However, coupled and decoupled action conditions differed from one another mostly at times when the gain of OKN was at its lowest (Figure 5). This means that not only were eye movements affected by action independently of the reported percept of the stimulus, but also that most of the effect of coupling between action and stimulus dynamics took place when the coupled stimulus was least likely to be in awareness.

One possible explanation for why we did not find a similar action-to-perception transfer as shown in earlier studies, is that our paradigm could tackle an earlier stage of competition than all aforementioned experiments on the action-to-perception transfer. As such, the measures that we used would reflect a stronger influence of bottom-up processes, while selective attention could less readily bias the percept. This is feasible to be reflected in the lack of an online action-to-perception effect on the reported percept in our results. Eye movements, on the other hand, respond to a lower level of shared processing between action and perception, and display a gradual effect of action—the degree of coupling corresponds to the extent of OKN response to the grating's motion.

Although eye movements are a type of motor behavior, in our experiment they are inseparable from the visual information that originates from the target stimulus. To what extent the underlying perceptual processes also differ between the tested conditions remains an open question. Nevertheless, as the OKN response is reliably connected to the percept in BR

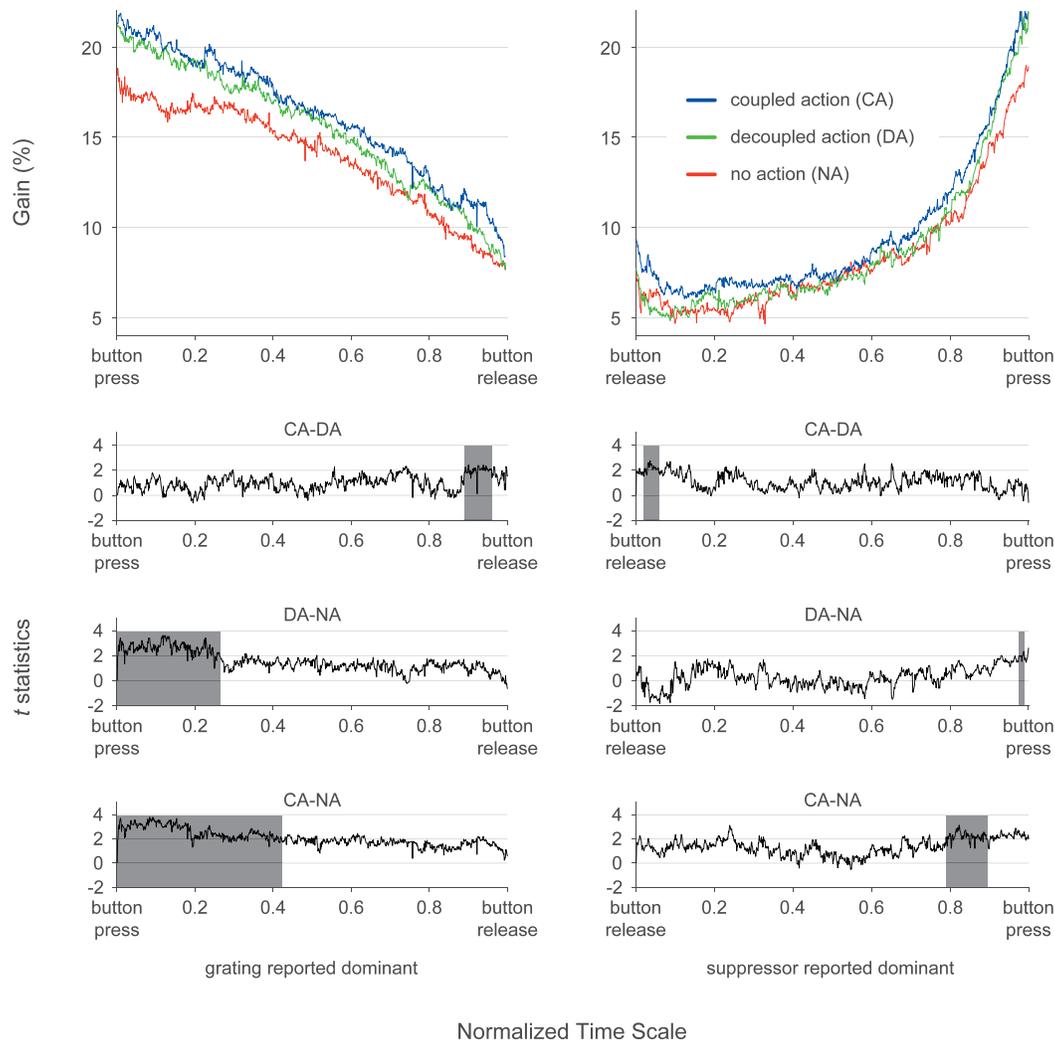


Figure 5. Means of gain, t values, and largest clusters on a normalized time scale. Left panels: intervals during which button presses indicated dominance of the grating, horizontal (time) axes are normalized such that this interval is mapped to unit time, with 0 being the time of press and 1 the time of release. Right panels: intervals during which button presses indicated dominance of the suppressor, time axes normalized to unit time from button release ($t=0$) to subsequent press ($t=1$). Means of gain are plotted based on individual segments of dominance normalized to this time scale. Conditions are compared in paired samples t tests across time. Test statistics are plotted for each condition pair, with the largest clusters of difference highlighted in gray (for details, see Analysis section).

(Naber et al., 2011), we can assume that lower level perceptual processes are affected by action, similarly to eye movements. The difference between our results and those of Maruya et al. (2007) and Di Pace and Saracini (2014), which, on the other hand, raise the possibility that BR and CFS are principally different in how they affect awareness.

One of the earliest and theoretically most important questions of the study of how action influences perception is whether any observed effect is a result of a direct, low-level information flow from the motor to the perceptual domain, or if higher-level representations or even endogenous attention serve as vehicle for the transfer. Taken together, the aforementioned previous research indicates that neither side can be clearly

excluded from an overarching explanation. If the action-to-perception transfer is a consequence of shared representations between perception and action, then results of all previous studies can only be accommodated in this model if we assume several such representations on different levels of processing. Our findings are in line with this notion, as they demonstrate a dissociation between these representations. On one hand, while earlier studies have demonstrated an effect of action on the reported percept in paradigms using ambiguous figures, our study using CFS did not find any such effect. This alludes to the same mechanism being differentially affected by distinct paradigms. On the other hand, the presence of an effect on eye movements reveals that a lower-level represen-

tation (operating in eye-movement control) can be influenced independently from the higher-level representations connected to conscious perception.

Keywords: event-coding, common coding theory, continuous flash suppression, action-perception coupling, action-to-perception transfer, eye movement, optokinetic nystagmus, ambiguous perception, bistable perception, rivalry, binocular rivalry

Acknowledgments

This project was supported by the German Research Foundation, International Research Training Group IRTG 1901, “The Brain in Action.” We also thank Adrien Pfeuffer, Alexander Platzner, and Matthias Born for their technical support with the manipulandum, and Monique Michl for running the experiment. We thank Marius ’t Hart, Denise Henriques, and Liad Mudrik for helpful discussion.

Commercial relationships: none.

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Footnote

¹ A post hoc sensitivity analysis (assuming $\alpha = 0.05$, $\beta = 0.95$), conducted using the G*Power software package (Faul, Erdfelder, Lang, & Buchner, 2007), indicated that the required effect size was $f = 0.34$ in our paradigm, leaving open the possibility that an effect smaller than this was not detected.

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