Online action-to-perception transfer: Only percept-dependent action affects perception

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ABSTRACT

Perception self-evidently affects action, but under which conditions does action in turn influence perception? To answer this question we ask observers to view an ambiguous stimulus that is alternately perceived as rotating clockwise or counterclockwise. When observers report the perceived direction by rotating a manipulandum, opposing directions between report and percept ('incongruent') destabilize the percept, whereas equal directions ('congruent') stabilize it. In contrast, when observers report their percept by key presses while performing a predefined movement, we find no effect of congruency. Consequently, our findings suggest that only percept-dependent action directly influences perceptual experience.

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1. Introduction

The integration between action and perception makes up one of the most important facets of everyday life. The common coding theory (Prinz, 1997) and the theory of event coding (Hommel, Müsseler, Aschersleben, & Prinz, 2001) posit that the final stages of perception and the initial stages of motor control share common representations, in which planned actions are represented in the same format as perceived events. Many studies support the idea that perception affects action (Hecht, Vogt, & Prinz, 2001; McCullagh, Weiss, & Ross, 1989). In addition, visual stimuli tend to dominate over perception in other modalities, even when the visual modality has no task-relevant information (e.g., Colavita, 1974; Posner, 1980; Posner, Nissen, & Klein, 1976; Sinnett, Spence, & Soto-Faraco, 2007). On the other hand, if perception and action share the same representation, changes due to action should lead to corresponding changes in perception (Hecht et al., 2001; Prinz, 1997; Schütz-Bosbach & Prinz, 2007 for review).

Some studies demonstrated an influence of action on perception. Previously learned movements improve visual discrimination of the same movement (Beets, Rösler, & Fiehler, 2010; Casile & Giese, 2006; Hecht et al., 2001) and lead to increased cortical activity of the motor-related brain areas when observing that movement

(Calvo-Merino, Glaser, Grèzes, Passingham, & Haggard, 2005; Engel, Burke, Fiehler, Bien, & Rösler, 2008; Reithler, van Mier, Peters, & Goebel, 2007). This is not restricted to motor learning, but also applies to online interactions between the motor system and visual perception (for review, Müsseler, 1999; Schütz-Bosbach & Prinz, 2007). For example, when reaching to grasp a bar with a certain orientation, the mere motor preparation suffices to facilitate responses to a congruent visual stimulus (Craighero, Fadiga, Rizzolatti, & Umiltà, 1999). Hence on various time scales – learning or online – an action can facilitate perception of a related visual stimulus.

Direct and online influence of action on the corresponding perceptual representations so far has mainly been investigated in the oculomotor system. For example, smooth pursuit eye movements can induce a distorted perception of image velocity (e.g., Freeman, Champion, & Warren, 2010; Souman, Hooge, & Wertheim, 2006). Moreover, eye movements necessarily change a visual stimulus in either retino- or craniocentric coordinates. Limb movements, in contrast, allow a visual stimulus to be stationary in both reference frames. It is less well understood how limb movements directly influence motion perception.

Here we use a dynamic ambiguous stimulus, so called "perceptual rivalry", to test action-to-motion perception transfer without changing the visual input. Rivalry refers to a situation in which a constant stimulus evokes multiple perceptual interpretations that alternate over time (e.g., Leopold & Logothetis, 1999). Frequently, rivalry is induced by presenting distinct stimuli to either eye ("binocular rivalry", Blake & Logothetis, 2002 for review). Alternatively, an ambiguous figure, such as the Necker Cube (Necker, 1832) or

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Rubin's vase-faces image (Rubin, 1915), can be applied ("perceptual rivalry"). Besides in vision, rivalry has been observed in other modalities such as touch (Carter, Konkle, Wang, Hayward, & Moore, 2008), audition (van Noorden, 1975), and olfaction (Zhou & Chen, 2009). Thus, rivalry seems to be a ubiquitous phenomenon covering many modalities. Rivalry is also subject to cross-modal interactions: for instance, the direction of tactile stimulation biases the perceived direction of an ambiguous visual stimulus (Blake, Sobel, & James, 2004). Yet, research on how the motor system affects the perception of visual ambiguity is sparse. Since in rivalry the stimulus remains unchanged, action planning and execution cannot operate on the stimulus itself but can affect its perceptual representation. Hence, such ambiguous stimuli are ideal to test the direct effects of action on perceptual representations of motion.

In binocular rivalry, movement has indeed been found to relate to perceptual changes, in particular in the realm of oculomotor effects. Reflexive eye movements, like optokinetic nystagmus (OKN), have been used to monitor dominance in binocular rivalry (Logothetis & Schall, 1990; Sun, Tong, Yang, Tian, & Hung, 2002) and are modulated by the perception of ambiguous motion (Laubrock, Engbert, & Kliegl, 2008). Whether or not eye movements in turn have an influence on perceptual dominance has been a subject of debate for over a century (Einhäuser, Martin, & König, 2004; Necker, 1832; Wheatstone, 1838). While the coupling between oculomotor behavior and rivalry has been studied extensively, little is known about the role of other effectors in rivalry. In one of the few studies on the effect of other effector movements on rivalry perception, Maruya, Yang, and Blake (2007) used a binocular rivalry paradigm. Observers were trained to make sinusoidal hand movements when the percept of either a rotating sphere or an unrelated stimulus was dominant. The self-produced movements (which determined the speed of the stimulus motion) led to prolonged durations in the perception of the same movement and shorter stimulus suppression rates. It is possible that this visuo-motor coupling as well as training may have affected these results. Furthermore, it is unknown how these findings generalize to perceptual rivalry, which shares most but not all the characteristics of binocular rivalry (van Ee, 2009).

Wohlschläger (2000) investigated the effect of manual action on perceptual rivalry presenting a circle of dots which could be perceived to be rotating clockwise or counterclockwise. In different task conditions, observers either rotated a knob by hand, or pressed a button, or planned to press a button. The frequency of the perceived movement direction was determined for each condition. Observers were more likely to perceive the stimulus move in the same direction as their planned or executed movement than in any other direction or plane. Importantly, observers' hand movements started and ended the presentation of the visual stimulus, causing a confounding effect of action on perception. This pioneering study leaves the question open as to how action needs to be coupled to perception in order to exert an effect on perception.

The present study addresses this question by asking whether concurrent action influences the visual perception of a constant (ambiguous) stimulus and to what degree the motor output needs to be related to the perception in order to trigger action-to-perception transfer. Specifically, we ask whether a mere generation of actions in a predefined direction will shape perception, or whether the action needs to be functionally coupled with the current percept. Therefore, a structure-from-motion cylinder which may be perceived as rotating either clockwise (CW) or counterclockwise (CCW), is presented. We carefully distinguish between conditions in which action, the rotation of a manipulandum, is used to report the current perceptual experience from conditions in which observers perform the same movements, but unrelated to their current perceptual state. In other words, in contrast to previous studies, we present observers with a visual stimulus whose motion is independent of the observers'

actions. That is, our findings are not confounded by a direct influence of action on the stimulus. While viewing this stimulus, the observers either perform predefined actions which are independent of the current percept, or actions which depend upon the current perceptual state. To investigate the effects of action, we determine the duration that one percept dominates, i.e., percept stability.

The main experimental conditions in the present experiment follow a 2 ∗ 2 design with the factors movement type (percept-dependent movements vs. percept-independent, predefined movements), and congruency (percept-congruent movements vs. percept-incongruent movements). We measure how long observers stay in one perceptual state ("dominance durations"). If movements per se affect the perceptual state, we hypothesize changes in dominance durations for predefined movements, perception-dependent movements and even for unrelated vertical movements. If, however, action must depend upon perception to trigger action-to-perception transfer, there should be no or little effect of congruency on dominance durations during predefined movements. Dominance durations during movements depending on the perceptual state should then be the only ones affected by congruency.

2. Materials and methods

2.1. Observers

Seventeen naïve observers participated in the study. Data from three observers was excluded due to technical reasons: one observer aborted the experiment; in another, the movement data was not usable due to a technical problem; and another failed to comply with task instructions. Before analyzing the data, we tested observers' ability to perform the task using congruent and incongruent tracking of an unambiguous stimulus in the 'catch blocks' (see Section 2.2). Out of the 14 observers that provided a usable dataset, three were excluded due to low performance in these catch blocks (see Section 3). Data from the remaining 11 observers between the ages of 20 and 27 years (mean age ± standard deviation: 23.5 ± 2.5 years; 4 males, 7 females) was used for analysis. These observers had normal or corrected-to-normal vision, were right-handed as assessed by a German translation of the Edinburgh Handedness Inventory (89.1 ± 12.5) (Oldfield, 1971), and had no history of psychiatric or neurological disorders. All observers were recruited from the Philipps-University Marburg, and were compensated with course-credits or money (€6 per hour) for their participation. Written informed consent was obtained, and the procedure was in accordance with the ethical standard laid down in the Declaration of Helsinki (2000) as well as with departmental guidelines.

2.2. Stimuli

Four-hundred white dots of ∼0.065° ∗ ∼0.065° were presented within an aperture of ∼2.86° ∗ ∼6.53° on a 1024 ∗ 768 pixel, 16" black screen (refresh rate 75 Hz) to perceptually induce the shape of a rotating cylinder (structure-from-motion) (Fig. 1A). The cylinder made one full revolution every 3.6s. Dot life-time was set at 0.3s. This ambiguous structure-from-motion stimulus produced a percept of a cylinder, switching between CW and CCW rotation.

For some conditions, we created an unambiguous version of the stimulus. A red bar of ∼0.16° ∗ ∼8.16° was drawn over and rotated along with the cylinder. When moving along the 'back' of the cylinder, the bar was partially occluded. To enhance disambiguation, the dots at the back were fully occluded.

2.3. Apparatus

Stimuli were viewed through a black cardboard tunnel with a length of 110 cm to prevent interference from other visual input
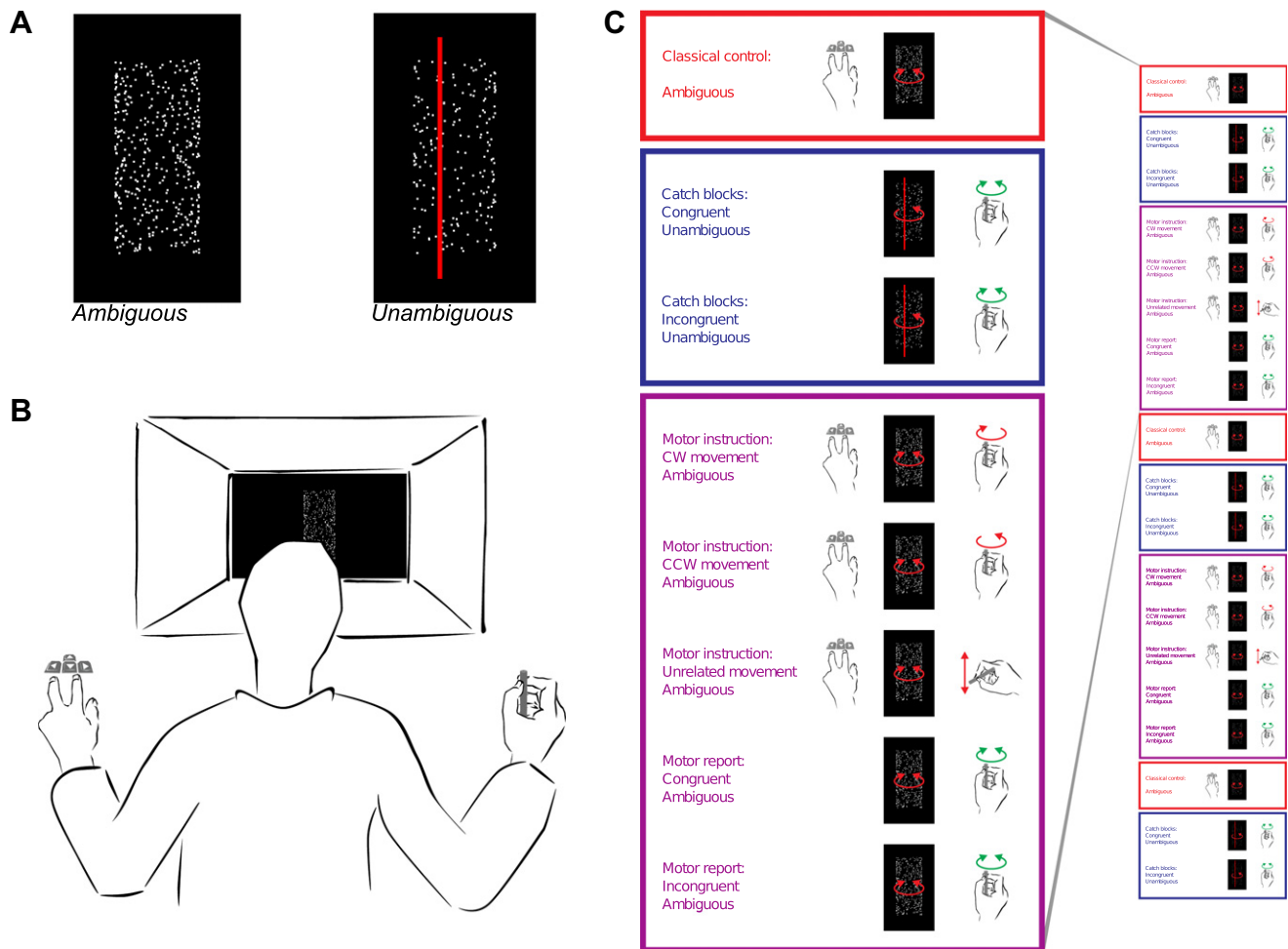
Fig. 1. Stimuli, setup and conditions. (A) Visual structure-from-motion stimuli which observers viewed through the tunnel. Left: The ambiguous stimulus could be interpreted as a cylinder rotating CCW or CW. Right: The unambiguous stimulus over which a red bar was drawn. (B) Setup. Observers sat in front of a tunnel through which the visual stimuli were presented by which the self-produced movements were occluded. Observers pressed one of the arrow keys with the index and ring finger of the left hand. The right hand was used for rotating the turntable, or to make movements along the vertical plane of the right side of the tunnel (not shown). (C) Conditions. Within each colored frame, the blocks were randomized. A green arrow above the right hand indicates that the manipulandum was used to indicate the perceived rotation direction of the cylinder. The block order is illustrated on the right.

(Fig. 1B). Observers' distance to the monitor was ~110 cm. A black cloth covered the back of the head and part of the tunnel to prevent observers from watching their own movements. Observers were instructed to direct their gaze toward the center of the stimulus and to try seeing the stimulus as a whole. A manipulandum with a turntable on the horizontal plane was used to perform actions during perception of the ambiguous cylinder (Fig. 1B). Observers rotated the turntable using the attached vertical handle with an effective radius of 5 cm. In the motor conditions (see Section 2.4), observers sat facing the screen and grasped the vertical handle of the manipulandum with a precision grip using their thumb, index and middle finger of the right hand (Fig. 1B). The perception of the direction of motion of the visual stimulus was indicated by either moving the manipulandum or by pressing one of two arrow keys (left arrow key for CW; right arrow key for CCW) with the left hand (see Section 2.4). For the unrelated movement condition (see Section 2.4), a freely movable stylus was used to execute straight vertical trajectories. The stylus was 78 mm long and had a diameter of 15 mm and was held between the thumb and fingers with the same precision grip as used for the manipulandum handle and was moved between an upper and a lower stopper mounted on the right side of the tunnel. A chinrest was used to keep a stable head position throughout the experiment. The chair and chinrest were adjusted individually to assure a comfortable position.

Movement trajectories were recorded with an ultrasound motion recording device (ZEBRIS CMS20, Zebris Medical GmbH, Isny im Allgäu, Germany). To measure hand movements, a sensor was attached to the top of the vertical handle of the turntable or to the top of the stylus. The movement data was sampled with 100 Hz and analyzed offline.

2.4. Procedure

The unambiguous stimulus (Fig. 1A, right) was used only for a control condition ('catch blocks', Fig. 1C, blue frame) to investigate motor behavior, whereas the ambiguous stimulus (Fig. 1A, left) served to investigate the durations of the dominating percept (CW or CCW rotation) in all other conditions. There were two kinds of report modes: a key press and the rotation of the manipulandum. In the case of key presses, observers held the key corresponding to the percept, until it switched. In all conditions that involved moving the manipulandum (Fig. 1C, blue and purple frames), observers were asked to match their velocity with that of the cylinder. When observers were not sure about the rotational direction of the ambiguous stimulus, they were asked to press no key in case of keyboard report, and not to move in case of manipulandum report.

The experiment consisted of eight conditions (Fig. 1C). The main experimental conditions of interest used the ambiguous stimulus (Fig. 1A) and were organized into a 2 * 2 design. In these conditions the effects of movement type (instructed vs. percept-dependent movements) and congruency (actions and perceived motion in equal vs. opposite direction) were investigated. The first two conditions of interest were the 'motor instruction' blocks in which observers rotated the manipulandum either CW or CCW throughout the block regardless of percept, resulting in 'motor instruction CW' and 'motor instruction CCW' blocks (Fig. 1C, purple frame, first two conditions). The action performed was thus independent of the perceptual interpretation of the visual stimulus. Concurrently, observers indicated using the keyboard with the left hand, which percept was currently dominating. The effect of congruency was later investigated by splitting dominance durations into percepts that were congruent with the instructed movement and percepts that were incongruent with the instructed movement (when active movements were CCW but cylinder perception was CW, or vice versa). The other two conditions of interest were the 'motor report' blocks in which the manipulandum was rotated either CW or CCW, depending upon the current perceptual interpretation of the visual stimulus (Fig. 1C, last two conditions in the purple frame). Instead of using the keys to report the percept, the percept was reported by rotating the manipulandum in the same direction as the visually perceived rotation in the 'congruent motor report' condition (Fig. 1C, purple frame, 4th condition), or in the opposite direction from the visually perceived rotation in the 'incongruent motor report' condition (Fig. 1C, purple frame, 5th condition). The performed action was thus dependent upon the perceptual interpretation of the visual stimulus. In a fifth experimental condition (Fig. 1C, purple frame, middle condition), the effect of movement per se was investigated by executing movements unrelated to the stimulus ('motor instruction unrelated'). Here, ongoing vertical movements (i.e., unrelated to the rotational axis of the visual stimulus) were made along the vertical axis of the tunnel using the stylus. Simultaneously, key presses were used to indicate rotation direction of the ambiguous stimulus.

The other conditions served as control conditions to obtain a baseline measurement of perceptual dominance durations ('classical control') and to test if observers were able to perform the task equally well when reporting a percept by using congruent or incongruent rotation of the manipulandum ('catch blocks'). In the classical control condition (Fig. 1C, red frame), the ambiguous cylinder stimulus was viewed while the observer indicated by key presses in which direction the ambiguous stimulus rotated. During the catch blocks (Fig. 1C, blue frame), observers viewed an unambiguous cylinder stimulus and were instructed to rotate the manipulandum; either along with the stimulus in the congruent catch blocks or to rotate in the opposite direction from the stimulus in the incongruent catch blocks. The rotational direction of the red bar and the cylinder changed repeatedly within each block. To make the task, and the experience of switches in the cylinder comparable to the 'motor report' blocks, the durations per rotation direction were determined by the observers' own shuffled dominance durations from the preceding 'classical control' block (with all dominance durations shorter than 500 ms removed). No key presses were made. Since the timing of 'switches' was known in these blocks, they were suitable as a baseline measure of the ability to report switches of percept equally well for congruent and incongruent blocks.

Before starting the experiment, observers were familiarized with the procedure and the stimulus by performing each of the eight different conditions for 1 min. The experiment consisted of 19 blocks lasting 5 min each. In between blocks, there was an opportunity to take a break. The order of the blocks was as follows (see Fig. 1C): the experiment started with the classical control after which the unambiguous catch blocks were performed. The order of congruent and incongruent catch blocks (Fig. 1C, blue frame) was counterbalanced over observers. Then, all five experimental conditions (Fig. 1C, purple frame) were performed in a randomized order. Finally, this sequence was repeated and a second repetition of classical control and unambiguous catch blocks was performed at the end of the experiment. Thus, the experiment consisted of two sets of experimental blocks surrounded by three sets of control blocks at the beginning, in the middle, and at the end of the procedure. The three sets of control blocks allowed the effect of time-on-task on dominance durations to be quantified. Within each colored frame in Fig. 1C, the order was randomized (the order in the figure serves as an example) but held constant for repetitions within observer.

2.5. Movement data pre-processing

Since observers' movement trajectories were constrained by the manipulandum to a circular movement with a constant radius, we had a one-dimensional movement given by the angle as a function of time. The direction of this movement (counterclockwise or clockwise) corresponded to the reported percept in the catch blocks and the two motor report conditions. In order to extract motion direction and velocity from the raw manipulandum position data, the data was pre-processed in Python (Version 2.6.5) using Numpy (Oliphant, 2007) and SciPy (Jones, Oliphant, Peterson, et al., 2001). Due to measurement noise, some samples fell out of the radius, which could be misinterpreted as a perceptual switch. Therefore, we discarded samples whose Euclidian distance deviated more than three standard deviations from the mean with respect to the previous sample. Cubic splines on the remaining data were used to interpolate the discarded samples. A circle was fitted to the samples which allowed converting the position data to angles. This signal was smoothed using a 5-sample median filter before conversion to an angular velocity signal and extracting the perceptual states indicated by the observers.

2.6. Data analyses

Dominance durations for CW and CCW percepts were extracted from the keyboard data in the classical control and motor instruction blocks. The dominance duration was the period of time that exactly one key was held down. Periods in which no key or two keys were simultaneously pressed were discarded. When one percept was interrupted by a short period in which both keys were pressed, the percept was separated and thus resulted in two dominance durations (plus the short period of discarded data). In 2.4% of the time across blocks in which the task was executed, either no key or two keys were pressed. These intervals were discarded from analysis as the dominant percept could not be determined. Dominance durations were extracted from the manipulandum movement data for the unambiguous catch blocks and the motor report blocks. Velocities below a threshold of 1°/s were counted as no movement. From the classical control condition, we defined for each observer a threshold as the first half percentile of dominance durations; we discarded values below this threshold to remove jitter in the motor report conditions. Due to these differences in extracting dominance durations from key press and manipulandum data, any direct comparisons between key-press report and manipulandum-report data should be interpreted with caution.

Besides dominance durations in the ambiguous stimulus blocks, movement characteristics were investigated in the catch blocks and the motor report blocks. In the catch blocks, we determined root mean-squared error (RMSE) from the required speed to check whether congruent and incongruent reports were comparable. In

the motor report blocks, the acceleration was compared at the moment of direction change between congruent and incongruent movements.

2.6.1. Statistical tests

Since dominance durations in rivalry typically follow leptokurtic (heavy-tailed) distributions (e.g., Logothetis, 1998), we use medians (rather than means) to characterize the distribution of dominance durations per observer and block. Across observers, however, the median dominance durations can safely be assumed to follow a Gaussian distribution such that statistics could be performed with standard parametric tests. First, we conduct a $2 * 2$ ANOVA to investigate the effect of movement type (motor instruction vs. motor report) and action–perception congruency (congruent vs. incongruent). For testing effects directly between conditions, pairwise t-tests and repeated measures ANOVA (for testing effects over multiple blocks in the classical control condition) were conducted. All statistics were computed using R (Version 2.10.1; R Development Core Team, 2009) maintaining a critical alpha level of 0.05.

3. Results

The question addressed in our study was to what extent action needs to be coupled to perception to cause perceptual changes. More specifically, we investigated how concurrent actions, congruent or incongruent with perception, influence processes underlying perceptual rivalry in ambiguous structure-from-motion stimuli.

3.1. Catch blocks

To test whether observers could veridically report their percepts by rotating the manipulandum, we used a disambiguated version of the rotating cylinder. To obtain an accuracy measure, we calculated the mean response time (RT) to a switch of rotation direction. This was done by dividing the total time observers rotate opposite from the required direction by the number of direction switches given by the stimulus. Most observers' average RT's were in the range 0.28 s–0.51 s for congruent catch blocks, although one subject had an average RT of 2.34 s. In the incongruent catch blocks most observers had an average RT in the range of 0.17 s–0.91 s, whereas two had an average RT of 2.99 s and 8.72 s. The three observers with very high RT's were excluded from all further analyses as the reliability of their reports in the motor report condition cannot be guaranteed (see Table 1 in Appendix A for their median dominance durations). For the remaining 11 observers the RTs were 0.40 s ± 0.15 s (mean ± SD over observers) for incongruent catch blocks and 0.36 s ± 0.05 s for congruent catch blocks. These did not differ significantly ($t(10) = 1.170$, $p = 0.269$) and represent a typical response time. Speed accuracy as measured by RMSE from the goal angular velocity was 62.4°/s ± 26.1°/s in the congruent and 64.7°/s ± 19.4°/s in the incongruent catch blocks, which did not differ significantly ($t(10) = 0.489$, $p = 0.636$). Both RT and RMSE show that the 11 remaining observers performed the task correctly and reported movement directions with the manipulandum equally well for congruent and incongruent movements in the catch blocks. This strongly suggests that observers also performed equally well in the congruent and incongruent motor report conditions.

3.2. Experimental conditions

To investigate the effect of movement type and congruency, a $2 * 2$ ANOVA was conducted. The main effects of movement type and congruency were not significant ($F(1, 10) = 0.161$, $p = 0.697$; $F(1, 10) = 4.247$, $p = 0.066$, respectively), suggesting that dominance
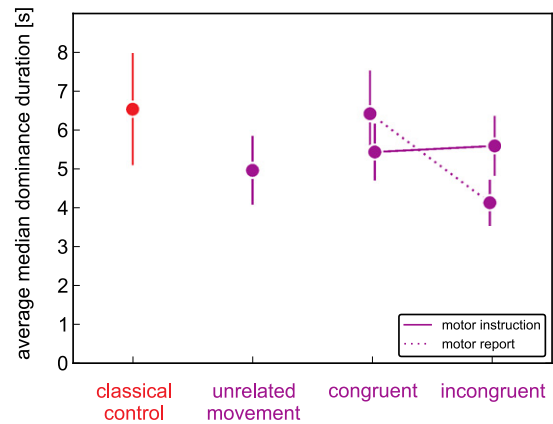

Fig. 2. Dominance durations per condition in seconds. Median dominance durations for classical control, motor instruction (CW and CCW are split into congruent/incongruent and are connected by a solid line) and motor report conditions (congruent and incongruent are connected by a dashed line). The error bars represent standard errors of the mean.

durations did not differ between motor instruction and motor report conditions nor between congruent and incongruent movements in general. The borderline significant main effect of congruency is probably due to the effect of congruency on motor report dominance durations. Indeed, the two factors interacted significantly ($F(1, 10) = 7.801$, $p = 0.019$), showing a differential effect of congruency between both movement types (Fig. 2, right). To explore this interaction more closely, we examined the results of both the motor instruction and motor report conditions in more detail.

In the motor report conditions, observers were asked to report their percept with the movement of the manipulandum. In one condition observers were instructed to move the manipulandum in the same direction as their percept ("congruent motor report"), and in the opposite direction in the other condition ("incongruent motor report"). In these conditions (Fig. 2, dashed line) percept durations were significantly shorter for incongruent movements than for congruent movements ($t(10) = -2.522$, $p = 0.030$). This shows that percept-related action affects the perceived direction of ambiguous stimuli.

When observers rotated the manipulandum irrespective of the perceived motion, they reported their percept by key presses. We separated the data according to times when manipulandum movement and perceived motion were in the same ("congruent motor instruction") or in the opposite ("incongruent motor instruction") direction (Fig 2, solid line). Dominance durations did not differ significantly between incongruent and congruent movements in these conditions ($t(10) = 0.509$, $p = 0.621$; Table 1 in Appendix A). These dominance durations also did not differ from a condition in which observers performed an unrelated movement perpendicular to the table (comparison to congruent movements: $t(10) = -1.023$, $p = 0.331$; comparison to incongruent movements: $t(10) = -1.189$, $p = 0.262$). Nor did the motor instruction conditions differ from a condition in which no manipulandum movement was required (congruent vs. classical control: $t(10) = 1.295$, $p = 0.224$; incongruent vs. classical control: $t(10) = 0.927$, $p = 0.376$; unrelated vs. classical control: $t(10) = -1.684$, $p = 0.123$). In summary, none of the movements that were conducted irrespective of the current perceptual state exerted an influence on the percept duration.

These results show that the dominance durations are not affected by congruency in the motor instruction condition, that is, when predefined movements are executed independent of the perceptual experience. In the motor report condition, however, dominance durations are affected by congruency suggesting that only actions which are dependent on the current percept can influence visual perception.

3.3. Classical control condition

The median dominance duration in the 'classical control' blocks (where no movements except for key presses are executed) was 6.49 s ± 4.99 s. In line with earlier findings (Blake et al., 2004; Nawrot & Blake, 1991), none of the observers showed a significant bias toward CW (48.5% ± 5.7%) or CCW (51.4% ± 5.7%) percepts. When the longer median dominance durations of all observers were taken and tested against all shorter median dominance durations, no significant difference was found ($t(10) = 1.476$, $p = 0.170$). Furthermore, dominance durations were stable across repetitions ($F(2, 10) = 2.271$, $p = 0.129$). This verifies that pooling dominance durations from both percepts and across repetitions for all other analyses is justified.

3.4. Direction transitions in motor report conditions

To verify whether transitions were similar for reporting percept by congruent and by incongruent movements using the manipulandum, we investigated the change in direction of the movement data in the motor report conditions. To this end, we aligned all movement traces to the time of transition between the two rotation directions (Fig. 3). Visual inspection of the velocity traces (Fig. 3A and B) suggest that the velocity profile is smooth and is comparable between conditions. To quantify this, we investigated the acceleration (i.e., the derivative of speed) on the moment of the transition, and compared this between conditions (Fig. 3C and d). We found that acceleration did not differ between congruent and incongruent motor report conditions ($F(1, 36) = 1.316$, $p = 0.259$), nor between transition types (i.e., from CW to CCW and from CCW to CW) ($F(1, 36) = 0.658$, $p = 0.422$), nor was there an interaction between transition type and condition ($F(1, 36) = 0.070$, $p = 0.792$). Hence, our findings that dominance durations were shorter in

the incongruent motor report condition than in the congruent one cannot be explained by a difference in motor performance in the two conditions.

4. Discussion

Our results show that action shapes perception, but only when the action is dependent on the current percept. When observers use rotational movements to indicate their percept of an ambiguous stimulus, percept durations change significantly. In contrast, rotating in a predefined direction does not lead to changes in percept durations in the same visual stimuli.

In previous studies (Maruya et al., 2007; Wohlschläger, 2000), it has been shown that predefined movements influence the visual interpretation of ambiguous stimuli. In these experiments, however, observers' movements initiated and terminated the movement of the stimulus. Furthermore, in Maruya et al. (2007), observers were trained to make movements in order to drive the speed of the visual stimulus. Thus, in these studies action had a direct effect on the perceptual form of the stimulus which may have led to a tight interplay of action and perception through stimulus manipulation, rather than a direct effect of action on perceptual representations. Here, in contrast, stimulus presentation was always independent of observers' actions, allowing us to compare task conditions in which the executed movements were independent of or dependent on percept. Our results clearly show that a direct effect of action on perception requires the action to be percept-related. The stability of percept is affected by congruency only in percept-related actions, in which congruent movements stabilize the percept and incongruent movements destabilize the percept.

Recent studies have demonstrated that rivalry elicited in one sensory modality can be altered by other sensory modalities. In these cases the perception of the ambiguous stimulus is biased
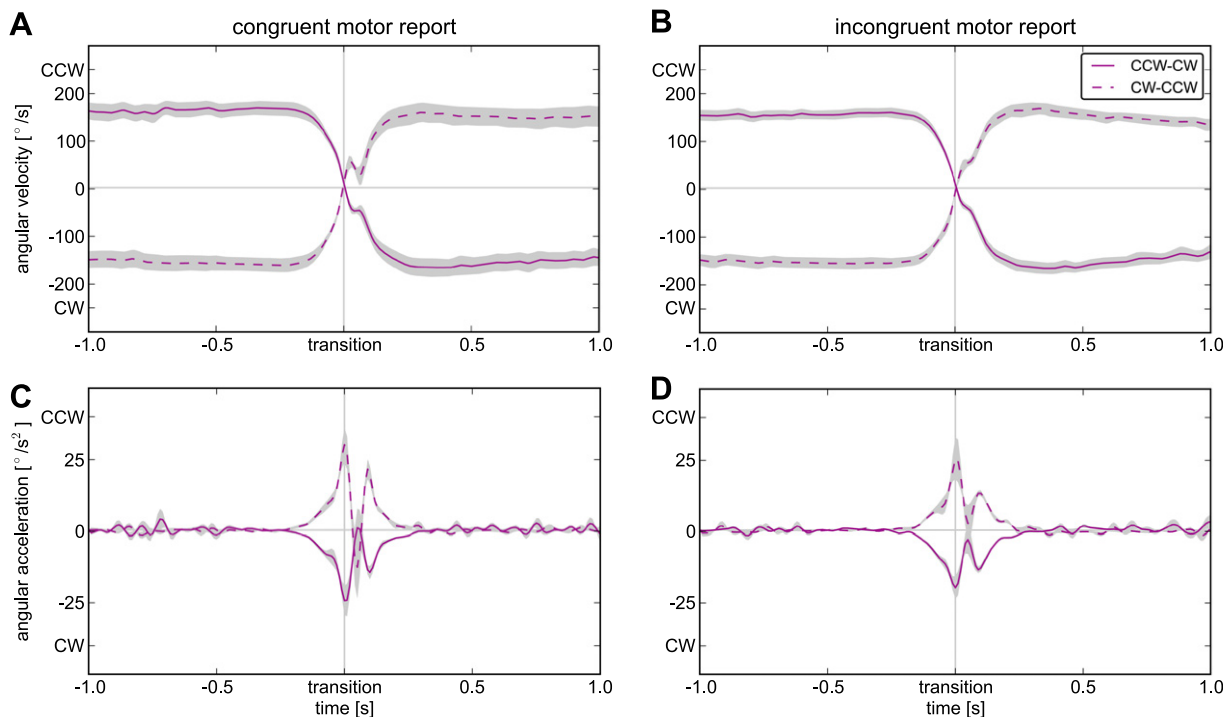

Fig. 3. Movement transitions. Movement trajectories were aligned to time of perceptual transitions (defined as zero-crossings of the angular velocity) in motor report conditions; positive values denote CCW movement, negative CW movement; solid lines denote mean velocities across observers for switches from CCW to CW, dashed lines from CW to CCW; shaded areas represent standard error of the mean. (A) Speed in the motor report condition in which percept was indicated by congruent movement. (B) Speed in the motor report condition in which percept was indicated by incongruent movement. (C) Acceleration in the motor report condition in which percept was indicated by congruent movement. (D) Acceleration in the motor report condition in which percept was indicated by incongruent movement.

towards the percept consistent with the non-ambiguous modality (Blake et al., 2004; van Ee, van Boxtel, Parker, & Alais, 2009). Here we confirm that not only other modalities but also action influences rivalry (Maruya et al., 2007; Wohlschläger, 2000). Beyond these earlier studies, our findings demonstrate that motor effects on rivalry are specific to movements that relate to the percept. The similarity between the effect of other modalities and action may provide a link between two seemingly distinct fields: common coding theory (Prinz, 1997) or the theory of event coding (Hommel et al., 2001) on the one hand and multisensory processing (e.g., Alais & Burr, 2004; Ichikawa & Masakura, 2006; Repp & Knoblich, 2007; Sekuler, Sekuler, & Lau, 1997; Shimojo & Shams, 2001; Witten & Knudsen, 2005) on the other hand. In cross-modal rivalry, it seems that if the unambiguous modality provides a signal converging with the ambiguous modality this stabilizes the interpretation of the visual input, whereas two diverging signals destabilize it. One of the signals accompanying movement execution is somatosensory (re)afferences, which may have the same function. For example, passive motor training, which in large part relies on reafferent information, can lead to the acquisition of new motor skills (Beets et al., 2010). The sensory information accompanying active movement execution could thus have contributed to the effects on visual perception. To what extent efferent vs. afferent information contributes to action-to-perception transfer remains an interesting topic for future research.

While there has been little research on the effect of hand movements on rivalry, many studies have addressed the relationship between *eye* movements and rivalry. Over 175 years after Necker's (Necker, 1832) original proposal that perceptual switches of his eponymous cube were a consequence of "the adjustment of the eye for obtaining distinct vision" (Necker, 1832, pp. 336–337), a wide consensus on a coupling between eye movements and perceptual dominance seems to exist (e.g., Brouwer & van Ee, 2006; Laubrock et al., 2008; Toppino, 2003; van Dam & van Ee, 2005), although the direction of causality is still in debate (Ellis & Stark, 1978; Eure, Hamilton, & Pheiffer, 1956; Kawabata, Yamagami, & Noaki, 1978; Zimmer, 1913) and is likely to be bi-directional (Einhäuser et al., 2004). In the context of (visual) rivalry, oculomotor behavior brings two additional challenges: first, any eye movement has a direct impact on the retinal stimulus; second, eye movements are coupled to shifts in focal attention, which itself influences switch rates (Paffen, Alais, & Verstraten, 2006). Despite all the advantages of the oculomotor system acting as the interface between input and output (i.e., between perception and action) to test how action influences perceptual representations while minimizing other factors (stimulus, focal attention), manual movements, as used here, circumvent these potential confounds.

Since attention speeds up rivalry (Paffen et al., 2006) and this increase in speed is not restricted to one modality (Alais, van Boxtel, Parker, & van Ee, 2010), we have to ask whether our results can be explained by attention alone. One may argue that reporting by incongruent tracking is more difficult and thus requires more attentional resources which would consequently speed up switching between percepts. We consider this explanation unlikely for several reasons. First, one can also argue for the opposite with equal justification: incongruent action requires more attention, thus less attention is available for perception and thus rivalry should slow down, contrary to our findings. Second, we failed to find any differences in dominance durations between classical control and unrelated movements on the one hand, and between dominance durations in predefined incongruent or congruent movements (i.e., percept unrelated) on the other hand. This implies that movement per se is not an attentionally challenging task. Third, for unambiguous stimuli, movement characteristics and errors between congruent and incongruent tracking were very similar, again arguing against a different attentional effect on both. However, it is undisputable

that attention plays a key role in rivalry. We argue, however, that there is no differential effect of attention on incongruent and congruent movements, and consequently, our main finding cannot be explained solely by differences in attentional demand. As binding diverse representations is a main function of attention in the sensory domain (Wolfe & Bennett, 1997), it seems conceivable that attention is a key ingredient to bind sensory and motor representations. This implies that in certain cases, the common coding framework only applies when additional attention is given to corresponding movements of an effector. Beyond a potential impact of attentional processes, our findings provide support for the common coding concept and refine this model by demonstrating that action-to-perception transfer requires the action to be directly coupled to motion perception.

The common coding theory (Prinz, 1997) and the theory of event coding (Hommel et al., 2001) state that action and perception share common representational domains. Therefore action and perception reciprocally influence each other. Although these theories have been supported by empirical data that demonstrate a bidirectional link between action and perception (Hecht et al., 2001) and direct effects of action on perception (e.g., Beets et al., 2010; Casile & Giese, 2006; Craighero et al., 1999; Wohlschläger, 2000), it is unknown to what extent action-to-perception transfer is dependent on percept-related action. Our results show that action can only influence perception when it acts on the perceptual representations, i.e., a mere generation of an action is insufficient to trigger a transfer from action to perception. Action planning in relation to the stimulus thus seems to be crucial to induce binding between action and perception (Hommel, 2004). When an action does not need to be integrated with a visual stimulus in order to perform the task, this effect is absent. In summary, common coding of a stimulus and an action seems to occur only when they are directly relevant to each other and the predicted effects of action on perception can only occur when this is the case. This fits with the prediction that perception and action planning can only interact when they refer to the same feature of the motor system (Hommel et al., 2001).

Future research will determine to what extent action-to-perception transfer can still occur when for example, the axes involving action and perception are at odds (e.g., diagonal vs. vertical). In summary, this study demonstrates for the first time that action and perception need to be functionally coupled in order to affect each other. Given that people make movements within a continuously changing and moving environment, the notion that only actions that are relevant for the perceived events can influence the perception of these events, is likely the most efficient strategy for human behavior.

Acknowledgments

Appendix A

To illustrate the large inter-observer differences in dominance duration and to provide a condensed version of the data to the interested reader, all median dominance durations and their standard deviations in the experimental conditions and the classical control conditon are listed in Table 1.

Table 1
Dominance durations per observer.

Observer	Classical control	Motor report		Motor instruction		
		Congruent	Incongruent	Congruent	Incongruent	Unrelated
1	4.92 ± 8.07	3.58 ± 6.03	6.26 ± 6.22	5.98 ± 8.07	6.09 ± 6.81	6.97 ± 5.41
2	4.22 ± 7.08	7.34 ± 13.97	3.00 ± 4.64	4.36 ± 7.64	5.08 ± 5.86	4.56 ± 5.53
3	14.31 ± 33.61	14.90 ± 16.16	7.23 ± 12.21	8.04 ± 26.63	6.12 ± 12.87	5.20 ± 11.99
4	7.46 ± 7.19	7.41 ± 8.06	4.79 ± 6.20	6.38 ± 8.63	6.93 ± 9.20	7.14 ± 3.76
5	0.92 ± 16.38	2.61 ± 10.84	1.53 ± 7.87	2.26 ± 18.22	3.85 ± 19.42	1.91 ± 15.72
6	10.08 ± 12.40	7.97 ± 18.81	6.27 ± 18.02	8.40 ± 15.07	10.28 ± 11.44	6.25 ± 7.10
7	4.22 ± 15.92	2.72 ± 3.67	2.83 ± 5.26	6.35 ± 9.55	5.15 ± 9.65	5.25 ± 21.20
8	2.01 ± 2.76	2.01 ± 5.68	2.04 ± 1.92	1.67 ± 4.54	1.55 ± 2.07	1.76 ± 2.71
9	16.93 ± 18.74	9.06 ± 10.36	2.54 ± 5.24	9.88 ± 16.36	9.91 ± 14.77	12.61 ± 16.52
10	7.85 ± 31.71	6.31 ± 10.25	2.82 ± 6.17	8.17 ± 35.23	21.74 ± 18.30	9.30 ± 20.40
11	4.01 ± 5.02	4.50 ± 5.39	2.92 ± 3.45	4.53 ± 4.31	4.50 ± 3.86	3.83 ± 3.73
12	3.97 ± 6.23	5.48 ± 5.78	3.49 ± 3.60	4.59 ± 4.26	4.03 ± 4.68	4.01 ± 4.67
13	5.18 ± 8.94	4.62 ± 4.91	4.70 ± 4.24	3.84 ± 4.43	3.31 ± 3.46	2.57 ± 2.59
14	5.52 ± 4.86	5.68 ± 5.79	4.04 ± 4.17	5.71 ± 8.77	6.42 ± 4.10	4.32 ± 4.06

Values are median dominance duration in seconds. ± SD gives the standard deviation within each observer. Observers marked in gray did not perform well in the catch blocks and their data were left out of the analyses, but are included here for the interested reader.

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