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A Contrast Effect Between the Concurrent Production and Perception of Movement Directions

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Abstract

With three experiments we explored the nature of specific interference between the concurrent production and perception of movements. Participants were asked to move one of their hands in a certain direction while simultaneously trying to identify the direction of an independent and non-biological stimulus motion. Perceived direction of the stimulus was assessed with either above/below judgments (Experiment 1), same/different judgments (Experiment 2), or the adjustment of a line (Experiment 3). The results revealed a form of contrast effect: Perceived directions were repulsed by produced directions. Moreover, the size of the effect was comparable across the three experiments, which points to its robustness and allowed us to control for potential confounds associated with some of the perceptual measures. These results alleviate concerns regarding the interpretation of related findings and demonstrate that effects of this type are not tied to the processing of biological motion, as previously proposed.

A Contrast Effect Between the Concurrent Production and Perception of Movement Directions

There are countless studies that have focused on how perception and action work in (relative) isolation (e.g., Marshak & Sekuler, 1979; Rauber & Treue, 1999; Swinnen, Dounskaia, Levin, & Duysens, 2001). In everyday life, however, we seldom, if at all, merely perceive or act at a given moment in time. Rather, we almost always have to simultaneously deal with multiple perceptual and (self-generated) motor events. The view that perception and action may nonetheless operate independently under such conditions has been challenged by a variety of observations. For example, when people have to perceive a stimulus while concurrently selecting or producing a response, an overall decrement in perceptual performance has been observed (e.g., De Jong, 1993; Jolicoeur, 1999; Makeig, Müller, & Rockstroh, 1996). *Unspecific interference* effects of this type are generally thought to reflect structural or central capacity limitations, as also revealed by the typical increase in response times that is observed when people try to perform two independent tasks at the same time (e.g., Meyer & Kieras, 1997; Pashler, 1994).

The view that perceptual and action-related processes are largely independent has also been challenged by studies that have explored *specific interference* effects (for reviews, see Prinz & Hommel, 2002; Ward, 2002). Specific interference relates to changes in performance that are determined by the relationship or degree of feature overlap (at a representational level) between what needs to be perceived and produced (Müsseler, 1999). A well-known example of specific interference comes from studies on stimulus-response compatibility, where it has been repeatedly shown that movements are initiated faster and more accurately when the location of a stimulus corresponds to that of the required response (Hommel & Prinz, 1997; Proctor & Reeve, 1990). In addition to spatial locations, specific interference effects have been found for a variety of stimulusresponse dimensions, such as velocity (Kerzel, 2001), amplitude, (Schubö, Aschersleben, & Prinz, 2001; Schubö, Prinz, & Aschersleben, 2004), and weight (Hamilton, Wolpert, & Frith, 2004). Therefore, the presence of feature overlap is crucial for understanding whether and how perception and action interact. According to many theories, such effects support the notion that a common set of processes and/or representations underlie perception and action (Hommel, Müsseler, Aschersleben, & Prinz, 2001; Prinz, 1990; Rizzolatti, Riggio, & Sheliga, 1994; Wolpert, Doya, & Kawato, 2003).

Specific interference effects have generally been studied in the context of reaction time experiments, in which a response *follows* the presentation of an imperative stimulus. In these *sequential* paradigms, evidence of facilitation or assimilation between perception and action has usually been obtained (Hommel & Prinz, 1997; Proctor & Reeve, 1990). Interestingly, more recent studies have shown that opposite (i.e., inhibitory or contrastive) effects arise when people try to perceive a stimulus while *concurrently* producing movements (Hamilton et al., 2004; Müsseler & Hommel, 1997; Schubö et al., 2001; but see Wohlschläger, 2000). Under such conditions, the challenge for the cognitive system is to perform a given action while encoding a *functionally independent* stimulus, i.e., a stimulus that in no way specifies what type of movement needs to be concurrently produced. It has been argued, however, that such conditions lead to an occupation or mutual inhibition of representational elements that are employed by/for both action and perception, thereby resulting in contrastive effects between what is produced and perceived (Hamilton et al., 2004; Hommel et al., 2001; Schubö et al., 2001).

The purpose of the present study was to further our understanding of specific interference effects that arise in concurrent perception-action paradigms. To this end, participants were asked to move one of their hands in a certain direction while simultaneously trying to identify the direction of an independent stimulus motion. On the basis of this paradigm, we sought to address three specific aims. The first aim

was to establish the nature of specific interference (i.e., assimilation vs. contrast) of production on perception when direction was the overlapping motion/movement dimension. We chose this dimension because it is well defined and has already been employed in the study of perception-perception (e.g., Rauber & Treue, 1999; Westheimer, 1990), perception-action (e.g., Chua & Weeks, 1997; Ehrenstein, Cavonius, & Lewke, 1996; Michaels & Stins, 1997), and action-action interactions (e.g., Heuer & Klein, 2006). More critically, those studies that have focused on concurrent perception-action interactions along the dimension of direction have typically reported facilitation effects, and therefore a form of assimilation of perception on production (e.g., Chua & Weeks, 1997; Ehrenstein et al., 1996; Michaels & Stins, 1997). In these paradigms action and perception were functionally dependent. As mentioned above, however, more recent studies have reported contrastive effects of action on concurrent, but functionally independent, perception. Thus, it is unclear whether the nature of specific interference in concurrent paradigms depends on the overlapping dimension or on the functional relationship between perception and action.

The second aim was to establish a specific interference effect that does not suffer from the type of confounds that have rendered the interpretation of related effects problematic. Indeed, among the various types of concurrent perception-action interactions that have been examined (e.g., Jacobs & Shiffrar, 2005; Kilner, Paulignan, & Blakemore, 2003; Müsseler & Hommel, 1997), two effects obtained in paradigms similar to our own have already been reported. Schubö et al. (2001) and Schubö et al. (2004) found an influence of produced amplitudes on concurrently perceived motion amplitudes, whereas Hamilton et al. (2004) observed an influence of lifting weights on the judgment of weights carried by other people. However, as we will argue below, the results of those studies could be accounted for without postulating an influence of action on perception because of potential confounds.

Finally, given that Schubö et al. (2001, 2004) and Hamilton et al. (2004) presented their participants with relatively complex biological stimulus motions, we tested whether such effects generalize to the processing of simple non-biological stimulus motions (i.e., motions with constant velocity profiles, see e.g., Viviani & Stucchi, 1992). Showing that specific interference effects can nonetheless be obtained with non-biological motions is of interest in this context because it is well known that biological motions are processed differently than non-biological motions (e.g., Viviani, 2002). Moreover, as argued by Hamilton et al. (2004) and others (Jacobs & Shiffrar, 2005; Kilner et al., 2003; Wolpert et al., 2003), perception-action interactions of this type may relate to the involvement of the motor system in the perceptual processing of biological motion.

Before considering the paradigm we employed and the predictions we derived, we begin by considering the experiments of Schubö et al. (2001, 2004) and Hamilton et al. (2004) in more detail and pointing out some concerns with those studies the present study sought to alleviate.

Contrast Effects Between Action and Perception

In a series of studies by Schubö and colleagues (Schubö et al., 2001, 2004), participants were asked to draw (without visual feedback) sinusoidal trajectories of varying amplitude while observing sinusoidal motions of a dot that could also vary in amplitude. The stimulus motions were biological in that they were generated on the basis of previously recorded drawing movements and therefore had biological velocity profiles. On a given trial, the stimulus motion specified the amplitude of the movement that had to be produced on the subsequent trial, whereas the current movement amplitude was specified by the amplitude of the stimulus motion of the previous trial. The results revealed a contrast effect (CE): When people were required to produce a medium-amplitude trajectory (and therefore had watched a medium-amplitude trajectory on the previous trial), there was an *increase* in movement amplitude when participants had been required to produce a smallamplitude trajectory on the previous trial, whereas there was a *decrease* in movement amplitude when participants had been required to produce a largeamplitude trajectory on the previous trial. The attribution of this effect to an influence of action on perception relied on the assumption that the movement produced on a given trial did not only reflect the influence of the simultaneously perceived motion, but also the manner in which the perception of the motion on the previous trial was influenced by the concurrently produced movement.

Although Schubö et al. (2004) were able to rule out the possible influence of motor carry-over effects by inserting an irrelevant movement task between trials, it remains unclear to what extent their effect could nonetheless be attributed to perceptual carry-over effects. That is, because the sequence of movement amplitudes was always specified by the previously seen motion amplitudes, it could be that their CE reflects an interaction between the perceived motion amplitudes on successive trials rather than an interaction between production and perception (for a similar argument in the context of research on action-effect blindness, see Stevanovski, Oriet, & Jolicoeur, 2003). Indeed, both of these accounts would predict the same pattern of results. For example, a medium-amplitude motion could have been perceived as larger when it was preceded on the previous trial by a small-amplitude motion and perceived as smaller when it was preceded by a large-amplitude motion, independent of the produced movements. More generally, by relying on the kinematics of subsequently produced movements, they employed a rather indirect way of assessing perceptual performance and thereby could not exclude perceptual confounds.

In a related study, Hamilton et al. (2004) explored how our own actions influence the perception of other peoples' actions. They asked individuals to lift and

hold a light or heavy weight while simultaneously observing short films of another person lifting (identical-looking) boxes of different weights. At the end of each film, participants had to judge the weight of the boxes they had observed on a rating scale. A CE was again obtained, in that people *overestimated* the weight of the boxes when they had concurrently held a light weight and *underestimated* the box weights when they had held a heavy weight. In a later study, they also established that the visual cue that people rely on to judge weights lifted by other people is the duration of the lifting movement (de C. Hamilton, Joyce, Flanagan, Frith, & Wolpert, 2005). Thus, strictly speaking, their CE was based on judgments along a dimension (i.e., weight) that differed from the dimension (i.e., duration) that was considered to be affected by concurrent movement production. Unfortunately, in yet another study aimed at identifying the neural correlates of these effects, de C. Hamilton, Wolpert, Frith, and Grafton (2006) failed to replicate the CE obtained by Hamilton et al. (2004), which calls its robustness into question (for a discussion of why this may have occurred, see de C. Hamilton et al., 2006).

A more general problem could be that not the action, *perse*, influenced the judgments, but that having lifted the weight prior to seeing the film provided an anchor at one end of an imaginary weight continuum. Weight judgments could have then been repulsed from this anchor (e.g., Brewer & Chapman, 2003). Such anchoring effects have indeed been shown to lead to CEs in the context of weight judgments. DiLollo (1964) asked participants to judge the weights of bottles they were asked to lift. Conditions differed with respect to the range of weights that had to be judged in separate phases of the experiment. When participants began with heavy weights and then shifted to light weights, the latter were judged as being lighter than when participants began with light weights in the first phase as well. The opposite pattern of results was obtained when participants began with light weights and then switched to heavy weights. Thus, such anchoring effects could

have lead to, at least part of, the CE reported by Hamilton et al. (2004). We now turn to the paradigm we employed and how we attempted to deal with the issues raised above.

Current Paradigm and Predictions

The purpose of the present paradigm was to establish whether and how the direction of a produced movement influences the perceived direction of a concurrently presented stimulus motion. Figure 1 illustrates the basic structure of the paradigm. Participants were asked to produce an upward (M_u) or downward (M_d) movement while simultaneously observing a reference stimulus (RS) motion that either moved upwards, horizontally or downwards. As illustrated in the figure, the movements deviated from the horizontal axis by larger amounts than all of the RS motions.¹ To avoid potential carry-over effects associated with visually cueing the movements, movement directions were blocked. That is, participants produced movements in a given direction for one half of the experiment before switching to the other movement direction.

The velocity profile of the stimulus motion was constant and therefore nonbiological. (A biological velocity profile would, in the present case, involve a relatively smooth transition between an acceleration phase and a subsequent deceleration phase.) Once participants had finished their movement, they were presented with a test stimulus (TS) motion to asses how they had perceived the RS. The TS was either identical to the RS motion or deviated upwards or downwards from it. The task of the participants was then to judge the relationship between the TS and the RS motions. Since no movement on the part of the participants was allowed during the judgment phase, their judgments of the TS should not be influenced by the recently produced movements and should therefore only reflect how those movements had affected their perception of the RS motion direction. Although movement-based anchoring effects could potentially arise in this paradigm as well, such effects would be present for the perception of the RS as well as the TS. Therefore, even if present, such effects should "cancel out" because the perceptual judgments are based on a comparison between the two types of stimuli.

The nature of the perceptual judgment was varied between experiments. Experiment 1 involved above/below judgments, same/different judgments were used in Experiment 2, and the adjustment of a rotating line (as a alternative form of TS) was introduced in Experiment 3. This was done in order to provide converging ways of assessing the influence of action on perception and to differentiate between competing interpretations of the effects that were obtained. Importantly, all types of perceptual judgments allowed us to either estimate or directly measure the size of interference effects in the units of the manipulated variables, i.e., degrees. Thus, the dimension that was supposed to be influenced by action (i.e., direction) was also the dimension that had to be judged.

If the CEs obtained in earlier studies (Hamilton et al., 2004; Schubö et al., 2001, 2004) are not tied to biological motion perception and particular stimulusresponse dimensions, then the perceived direction of the RS should be repulsed by the direction of the produced movement. That is, as shown in Figure 2, upward movements should lead to perceived RS motions that are shifted downwards (upper panel of the figure) and downward movements should lead to perceived RS motions that are shifted upwards (lower panel of the figure). In the context of the present task, the RS should therefore be perceived as more similar to a downward deviating test stimulus (TS_1) when it was observed during an upward movement and more similar to an upward deviating test stimulus (TS_5) when it was observed during a downward movement.

Experiment 1

Experiment 1 employed a two-alternative forced-choice procedure in which participants had to indicate whether they perceived the TS motion as *above* or *below* the RS motion. Based on the logic outlined above, if a CE occurs, perceived directions should be repulsed by the direction of the produced movements (see Figure 2). With the present perceptual measure, this CE should translate into a higher proportion of "above" judgments for upward movements than for downward movements. This pattern of results should be reversed if assimilation, instead of contrast, arises between the produced and perceived directions.

Method

Participants. Sixteen right-handed individuals (mean age = 24.94 years; age range = 21-35 years; 4 males, 12 females) participated in the experiment. In this, as well as in the subsequent experiments, all participants reported normal or corrected-to-normal vision and no motor impairments, were not aware of the purpose of the study, and received 8 Euro for their time.

Apparatus. The experiment was conducted in a dimly-illuminated and soundattenuated chamber. Stimulus presentation and data collection were controlled by an IBM-compatible microcomputer connected to a 21" color monitor. Movement data were collected with a Wacom Ultrapad A3E graphics tablet that sampled the *x* and *y* positions of a hand-held stylus in synchrony with the monitor's refresh rate, which was set at 70 Hz. The graphics tablet was placed directly below and centered with respect to the monitor, and was covered with a board such that no on-line visual feedback of the stylus/hand was available.

Stimuli and Movements. A red circle with a diameter of 6mm was used for the RSs and TSs. The start position of the circle was always vertically centered and shifted 9.5cm to the left of the vertical midline of the display area (see Figure 1). The circle moved to the right along a straight 20cm line on a black background

without leaving a trace on the display. Motion duration was held constant at 500ms and the circle disappeared at motion offset. For the RS, the direction of the circle motion deviated by either 0 or $\pm 15^{\circ}$ from a horizontal motion. The subsequently presented TS motion was identical to the RS motion except that it deviated in direction from it by either 0, ± 2 , or $\pm 4^{\circ}$ (the differences between the different TSs are exaggerated in Figure 1 for the purpose of illustration). At the approximate viewing distance of 60cm, the circle subtended 0.57° of visual angle and traversed a path of 18.92° at a constant velocity of 37.84 °/s.

For the movements, participants were asked to draw with their right hand straight-line trajectories on the graphics tablet. The start position for the hand movements was also held constant and was horizontally aligned with the start position of the stimuli. The required trajectories deviated by 25° upward or downward from the horizontal axis. Given that the stylus was moved within the horizontal plane, "upward" and "downward" trajectories actually involved hand movements that went away from and toward to the participant's body, respectively. The mapping between these latter trajectories and those presented on the display was learned during a training phase in which off-line feedback of the produced movements was provided (see the *Procedure* section for more details).

Design. Three variables were manipulated within participants: movement direction (upward, downward), RS direction (upward, horizontal, downward), and TS direction deviation (i.e., the angular difference between TS and RS directions: - 4° , -2° , 0° , $+2^{\circ}$, $+4^{\circ}$). Movement direction was blocked and counterbalanced across participants, such that half of the participants started with upward/downward movements and switched half-way through the experiment to downward/upward movements. Each movement direction was performed for 9 consecutive blocks. In each block, all 15 RS direction x TS direction deviation combinations appeared

once in a new pseudorandom order. This resulted in a total of 270 trials.

Procedure. To ensure that participants always started their movements from the same position, they began each trial by moving a cursor inside the RS start position. The cursor was a white disk with a diameter of 2mm (0.19° of visual angle) that represented on-line the movement of the stylus on the graphics tablet. The gain was adjusted such that there was a 1:1 mapping between the movement of the stylus and the corresponding movement of the cursor on the screen. One second after the participants had moved into the start position, a tone (1760 Hz, 15ms) signaled that they could start drawing whenever they felt ready. As soon as the participants had left the start position, the cursor disappeared and the RS motion started. The end of the RS motion (after 500ms) was marked by the disappearance of the RS and the onset of a second tone (880Hz, 15ms). The recording of the stylus movement lasted for another 500ms (i.e., for a total of 1000ms), at which time a third tone was played (440Hz, 15ms). As shown in Figure 1, as soon as the movement recording had finished, one of the five TSs was displayed. At TS motion offset, the screen went blank and participants were asked to indicate whether the TS motion had been "above" or "below" the RS motion by pressing the up or down arrow keyboard key, respectively, with their left hand. No time limit was placed on this perceptual judgment. The next trial started after an inter-trial interval of 1000ms.

Each series of 9 blocks of the experiment was preceded by a training phase in which participants practiced making either a 25° upward or downward movement trajectory. In each training trial, the to-be-produced trajectory was presented as a red line for 2000ms and then erased. Participants then had to move the cursor into the start position and wait for 1000ms, after which the first tone indicated that they could start to move whenever they felt ready. The rest of the tone sequence was identical to that used in experimental trials and it was stressed to the participants

that the third tone indicated the end of the movement recording and the time by which the movement should be finished. After each movement, the required and the actually produced trajectories were presented for 2000ms as red and white lines, respectively. This off-line feedback was provided to help participants learn the movements and was not available during the experimental blocks. If participants kept on moving after the third tone, an error message was displayed to that effect. Additionally, throughout the training and experimental phases, participants received an error message whenever they lifted the pen or reversed movement direction during drawing. Error messages were displayed after the off-line feedback in the training phase and after the perceptual judgment in the experimental phase. The training phase came to an end when the participants had produced a sufficient number of acceptable trajectories (as determined by a point system based on the below-mentioned criteria) or when 30 training trials had been completed. On average, participants needed about 17 trials to complete the training. The entire experiment lasted between 45-55 minutes.

Data Analysis. Each movement trajectory was analyzed by first realigning the *x* and *y* stylus values to a common (0,0) coordinate position. Tangential velocity profiles were then obtained through numerical derivation and low-pass filtered at 8Hz using a fourth-order and zero-lag Butterworth filter. Movement onset was defined as the first moment at which 5% of peak tangential velocity was reached. Similarily, movement offset was defined as the first moment at which tangential velocity. Based on these temporal markers, movement end angle (as defined by the angle with respect to the horizontal axis of the line connecting the start position to the position of the stylus at movement offset) and trajectory length (from movement onset to offset) were determined for each condition and participant. In order to only include trials that complied with the movement instructions, trials were excluded when one of the

following hierarchical criteria was met: (a) the pen was moved after the tone that signaled the end of the movement and before the perceptual judgment was provided (late movement), (b) the pen was lifted during movement (pen lift), (c) participants reversed the direction of drawing (movement reversal), (d) the movement end angle deviated by more than 20° to the outside, 9° to the inside of the required movement angle, or the produced trajectory length was shorter than 10cm (trajectory failure). If these exclusion criteria led to zero observations in any of the conditions for a given participant, all of their data were discarded from the analysis.

Perceptual judgments were analyzed by computing the proportion of "above" judgments for each condition and participant. These values were then arcsine transformed to deal with the non-normality of proportions (e.g., see Winer, 1971) and subsequently averaged across the three RS directions to increase statistical power. To establish the influence of movement production on perceived motion direction, a two-way repeated-measures ANOVA on the arcsined values with movement direction (downward, upwards) and TS direction deviation (-4°, -2°, 0°, +2°, +4°) as within-participants factors was performed. Whenever necessary, violations of sphericity were corrected for using the Greenhouse-Geisser ϵ (to facilitate reading, the uncorrected degrees of freedom are provided).

Finally, to determine the size of the CE in perception, psychometric functions were fit to the perceptual judgment data in order to determine the point of subjective equality (PSE) for each movement direction. Figure 3A shows the proportion of "above" judgments as function of TS direction deviation and movement direction for one participant. It was assumed that perceptual sensitivity as a whole would not be affected by produced movement directions and therefore the slopes of the psychometric functions should not differ for the two movement directions. In contrast, the effect of movement production should manifest itself as a shift in the

PSE for each movement direction, that is the TS direction deviation at which participants provide an equal proportion of "above" and "below" judgments. To determine the PSEs, a separate logistic function was fit for each movement direction and participant using a maximum-likelihood estimation method assuming binomial distributed choices (see Figure 3A). The fitted function is given in Equation 1:

$$p = \frac{1}{1 + e^{\frac{a-x}{b}}}$$
(1)

where *p* denotes the probability of responding "above", *x* is a given TS direction deviation, *b* is related to the slope of the psychometric function (with higher values indicating a lower slope), and a corresponds to the value on the abscissa which gives a value of 0.5 on the ordinate, i.e., the PSE. To test the adequacy of the assumption that the functions for each movement direction only differed in their PSEs and not in their slopes, we compared the fits of Equation 1 when *b* was allowed to vary with movement direction ("unrestricted" model) to the fits obtained when *b* was fixed for both movement directions ("restricted" model). The quality of the fits was assessed with the goodness-of-fit χ^2 and the normed-fit index (*NFI*). Finally, to show that the perceived directions differed for upward and downward movements, the PSEs for the two movement directions were compared using a paired-samples t test and the size of the CE was calculated as half the difference in mean PSEs between downward and upward movements.

Results

The data of two participants had to be excluded. One participant had at least one condition with zero observations because of more than 38% of excluded trials, with 95% of those involving trajectory failures. The other participant was excluded because of an apparent failure to follow the instructions, as evidenced by exclusively responding "above" or "below", irrespective of the TS direction deviation. For the remaining participants (N = 14), the mean percentages of excluded trials were 1.64%, 1.61%, 0.77%, 6.98%, for late movements, pen lifts, movement reversals, and trajectory failures, respectively, resulting in a total percentage of discarded trials of 11.01%.

The mean proportion of "above" judgments as a function of TS direction deviation and movement direction are presented in Figure 3B. Negative values on the abscissa refer to a TS that was below the RS and positive values refer to a TS that was above the RS. As shown in the figure, the proportion of "above" judgments increased with TS direction deviation and was higher for upward than for downward movements by a similar amount across TS direction deviations. In support of this, there were significant main effects of TS direction deviation (F(4, 52) = 215.14, MSE = 0.02, p < .001) and movement direction (F(1, 13) = 5.30, MSE = 0.06, p < .05), but no interaction between these two factors (F(4, 52) = 0.11, MSE = 0.01, p > .90).

In order to determine the size of the CE in perception, we began by fitting the "restricted" model, which lead to acceptable overall fits (mean $\chi_{(7)}^2 = 2.46$, p > .20, for all participants). To test the adequacy of our assumption that perceptual sensitivity remained constant across the two movement directions, the fits of the "restricted" model were compared to those of the "unrestricted" model. The difference in the quality of the fits between these models did not reach significance for any participant (mean $\chi_{(1)}^2 = 0.72$, p > .05, for all participants, mean *NFI* = 0.24), suggesting that perceptual sensitivity did not vary with movement direction.

Using the "restricted" model, the mean PSEs for upward and downward movements were -0.21° and -1.05°, respectively, and the difference between these

means (0.84°) was significant (t(13) = 2.09, p < .05, one-tailed²). The estimated CE therefore corresponds to half of this difference: 0.42°. Given the RS trajectory length of 20cm, this corresponds to about 1.5mm of arc length on the screen.

Discussion

The results of Experiment 1 support the notion that perceived motion directions are repulsed by concurrently produced movement directions. Consistent with a CE interpretation, the proportion of "above" judgments was overall higher for upward than downward movements. Moreover, the TS direction deviation at which people provided an equal proportion of "above" and "below" judgments (i.e., the PSE) was lower for upward than for downward movements, with the estimated size of this CE being 0.42°. It is also worth noting that participants were indeed able to perform the judgment task required of them, as evidenced by the increase in the proportion of "above" judgments with increases in TS direction deviation.

Although the present results are consistent with the idea that movement production has a repulsing effect on motion perception, there is an alternative explanation of these results that does not rely on an influence of action on perception. According to this explanation, producing an upward/downward movement makes the perceptual judgment "above" more/less likely because of an abstract feature overlap between the movement directions and the judgment categories. As this response-bias explanation could in principle account for the results, the next experiment was performed.

Experiment 2

The goal of Experiment 2 was to replicate the perceptual CE found in Experiment 1 and rule out the response-bias explanation that could have accounted for that effect. To this end, the same experiment was performed, except that the nature of the perceptual judgment was changed such that there was no longer any feature overlap between the judgment categories and the direction of the produced movements. This involved replacing the "above"/"below" judgments with "same"/"different" judgments. If the produced movement directions actually lead to a repulsion of the perceived RS motions directions (as illustrated in Figure 2), then TSs that deviate away from the direction of the produced movement should be judged more often as "same" than TSs that deviate toward the direction of the produced movement. This, in turn, should result in an interaction between movement direction and TS direction deviation.

Method

Participants. Seventeen right-handed individuals (mean age = 24.29 years; age range = 19-32 years; 4 males, 13 females) took part in the experiment. The number of participants was increased with respect to the previous experiment in order to replace the data of one participant that had to be excluded (see *Results* section for details). None of the participants had taken part in Experiment 1.

Apparatus, Stimuli and Movements, Design, and Procedure. Everything remained the same as in Experiment 1, except that participants were asked to judge whether the TS motion was the "same" as or "different" from the RS motion, rather than "above" or "below" it. Moreover, to further prevent any form of feature overlap between the movement directions and the perceptual judgments, participants made these judgments by pressing with their left hand one of two horizontally arranged keyboard keys (i.e., the numbers 5 and 6 on the numeric pad, which were labeled "different" and "same", respectively). The entire experiment lasted between 45-60 minutes.

Data Analysis. The data analysis was identical to that of Experiment 1, except that the proportion of "same" judgments was taken as the perceptual measure and a different form of psychometric function was employed to determine the PSEs and,

thereby, the size of the CE. Figure 4A shows the data of one participant as a function of TS direction deviation and movement direction. The basic reasoning was the same as in Experiment 1. That is, the psychometric function for downward movements should correspond to that for upward movements, but shifted to the right. It was again assumed that movement direction should not influence perceptual sensitivity and, thus, the width of the psychometric function. Given the change in perceptual measure, the PSE now corresponds to the TS direction deviation at which participants provided the maximum number of "same" judgments (see dotted lines in Figure 4A). In order to estimate this value, Equation 2 was chosen as the underlying psychometric function. This function is the first derivative of Equation 1 with one additional free parameter, *c*, that was included to allow for variations in the height of the function:

$$p = \frac{c}{b} \frac{e^{\frac{a-x}{b}}}{(1+e^{\frac{a-x}{b}})^2}$$
(2)

where *p* is the probability of responding "same", *x* denotes a given TS direction deviation, *b* is related to the width of the psychometric function (with higher values indicating a wider width), and *a* is the value on the abscissa which leads to the maximum value on the ordinate, i.e., the PSE. As in Experiment 1, to test whether perceptual sensitivity varied with movement direction, we compared the fits of a "restricted" model, in which the *b* parameter was fixed for both movement directions, to those of an "unrestricted" model, in which all parameters were allowed to vary.

Results

The data of one participant had to be discarded because of conditions with zero observations. This resulted from more than 48% of trials being rejected, with nearly 98% thereof being trajectory failures. For the remaining participants (N =

16), the mean percentages of discarded trials were 1.62%, 1.27%, 0.49%, 4.86%, for late movements, pen lifts, movement reversals, and trajectory failures, respectively, leading to a total of 8.24% of excluded trials.

The mean proportion of "same" judgments as a function of TS direction deviation and movement direction are shown in Figure 4B. The probability of responding "same" decreased with increases in TS direction deviation and, more critically, was slightly higher for TS directions that deviated away from, as opposed to toward, the direction of the produced movement. Movement direction alone had no apparent effect. In accordance with these observations, the ANOVA yielded no effect of movement direction (F(1, 15) = 2.98, MSE = 0.01, p > .10), a significant main effect of TS direction deviation (F(4, 60) = 65.87, MSE = 0.03, p < .001), and a significant interaction between these two factors (F(4, 60) = 2.95, MSE = 0.02, p < .05).

To estimate the size of the CE in perception, we again began by fitting the "restricted" model, which yielded acceptable fits for all participants (mean $\chi_{(6)}^{2} = 3.35$, p > .20). The "unrestricted" model did not significantly improve upon the fits of the "restricted" model (mean $\chi_{(2)}^{2} = 0.83$, p > .20, for all participants, mean *NFI* = 0.29), which suggests that perceptual sensitivity as a whole did not vary with movement direction. The "restricted" model was therefore used to estimate the PSEs and the difference between the mean PSE for upward (-0.36°) and downward (0.33°) movements was significant (t(15) = 2.52, p < .05, two-tailed). The size of the CE can therefore be estimated at 0.35°, which corresponds to about 1.2mm of arc length on the screen.

Discussion

Experiment 2 lends further support for the notion that perceived motion directions are repulsed by produced movement directions. The expected interaction

between movement direction and TS direction deviation on the proportion of "same" judgments was present, and, as in Experiment 1, the PSE for upward movements was lower than for downward movements. The estimated CE of 0.35° was also similar in size to that found in the previous experiment (0.42°). More generally, the decrease in the proportion of "same" judgments with increasing TS direction deviations indicates once again that participants could perform the judgment task required of them.

As there was no feature overlap between the perceptual judgment categories and the movement directions in this experiment, the response-bias explanation of Experiment 1 can be ruled out. Even if for some reason responding "same" became systematically associated with only upward or only downward movements, the fact that the main effect of movement direction was not significant further excludes this account.

Taken together with the findings of Experiment 1, another alternative interpretation for the CE can be discarded. According to this interpretation, perception should be facilitated or enhanced in the space surrounding the (endpoint of the) hand trajectories (e.g., see Humphreys, Riddoch, Forti, & Ackroyd, 2004; Schneider & Deubel, 2002). Although the movement trajectories were not visible to the participants, they could have nonetheless imagined what their movement trajectories would have looked like on the screen, had they been displayed. If this was the case, then RS and, more critically, TS motions that deviated in the direction of the movement trajectories would have from the movement trajectories. This would lead to a decrease in the probability of judging the TS as "same" when it differed from the RS and deviated in the direction of the movement trajectory. The interaction between TS direction deviation and movement direction that was obtained in Experiment 2 could thereby be explained. However, the absence of such an interaction in

Experiment 1 and, as will be seen, the consistency of the estimated CE sizes across experiments suggests that such an action-based enhancement of perception cannot, at least by itself, account for the present effects.

Experiments 1 and 2 assessed the effects of movement production on motion perception by relying on categorical judgments and fitting psychometric functions to estimate the size of the CEs. Moreover, by employing TS motions that were very similar to the RS motions, the observed effects cannot be attributed to differences in the stimulus material between the reference and test phases. Having consistently found effects under such conditions, Experiment 3 was performed to provide further converging evidence for the size of the effects obtained until now by employing a more "direct" way of measuring the CE.

Experiment 3

To corroborate the size estimates of the CEs obtained in the first two experiments, a more "direct" way of measuring perceptual performance was introduced in Experiment 3. Instead of employing a TS motion that resembled the RS motion and asking participants to provide categorical judgments, the TS now consisted of a line that rotated around the previously seen RS motion direction. The participants' task was to stop the line when they believed it matched the direction of the RS motion. This measure has two advantages over those used in the previous experiments. First, by employing perceptual judgments that are already in angles, there is no need to assume and fit various types of psychometric functions. Second, the presence of an effect measured in this way cannot be accounted for via a response-bias, as was the case in Experiment 1. With this new type of perceptual measure, a CE should be reflected in higher TS end angles for downward movements than for upward movements.

Method

Participants. Seventeen right-handed individuals (mean age = 23.06 years; age range = 18-30 years; 3 males, 14 females) participated in the experiment. As in the previous experiment, the number of participants was increased with respect to Experiment 1 in order to compensate for the loss of data from one participant (see *Results* section for details). None of the participants had taken part in any of the other experiments.

Apparatus, Stimuli and Movements, Design, and Procedure. The only changes with respect to Experiments 1 and 2 related to the nature of the TS and the associated perceptual judgment. The TS now consisted of a line composed of 5 equally spaced circles, with the first and last circle located at the start and end positions of (potential) motion trajectories. The circles were identical in size and color to the RS circle. At movement recording offset, the line appeared 15° above or below the angle of the previously presented RS motion and immediately started to rotate downwards or upwards, respectively, around the (fixed) circle located at the start position. The line moved by 0.2° every refresh of the monitor (i.e., after about 14ms). The direction in which the line started to rotate was varied pseudo-randomly and balanced within each block. When the line had rotated 30° (i.e., 15° beyond the angle of the RS motion), it changed direction of rotation. Participants were asked to press the space bar on the keyboard with their left hand as soon as they believed the line matched the direction of the RS motion. As soon as they did so, the rotating line disappeared. No correction of the perceptual judgment was possible once the key had been pressed. The experiment lasted between 30 and 55 minutes.

Data Analysis. The data analysis was identical to that of the previous experiments, except that the size of the CE was determined on the basis of the end angles at which the TS line motions were stopped by the participants. These *perceived* angles were computed separately for each movement direction (and, as before, averaged across RS directions) and submitted to a one-way repeatedmeasures ANOVA with movement direction (upward, downward) as the withinparticipants factor.

Results

One participant was excluded because of conditions with zero observations due to more than 64% of excluded trials. Nearly 90% thereof were trajectory failures. For the remaining participants (N = 16), the mean percentages of excluded trials were 0.40%, 0.97%, 0.60%, and 16.02%, for late movements, pen lifts, movement reversals, and trajectory failures, respectively, resulting in a total of 17.98% discarded trials.

For both movement conditions, the TS motions were stopped equally often during upward and downward rotations. More importantly, downward movements led to higher perceived angles (-0.36°) than upward movements (-0.97°) and the ANOVA revealed that this difference of 0.61° as significant (F(1, 15) = 5.38, *MSE* = 0.56, *p* < .05). The size of the CE was thus estimated at 0.31°, which corresponds to 1.1mm of arc length on the screen.

Discussion

Using a more "direct" perceptual measure, Experiment 3 once again shows that the direction of a produced movement has a repulsing effect on the direction of perceived motions. The perceived motion angles were lower for upward than downward movements and the estimated CE of 0.31° was similar in size to those found in Experiments 1 (0.42°) and 2 (0.35°). This observation is consistent with the absence of a significant main effect of Experiment when the CE estimates were submitted to an additional one-way between-participants ANOVA (F(2, 43) = 0.13, MSE = 1.51, p > .80). The fact that the observed CE sizes did not differ significantly across experiments points to the robustness of the CE and the reliability of the different perceptual measures.

General Discussion

Previous studies have suggested that the perception of amplitude (Schubö et al., 2001, 2004) and weight (Hamilton et al., 2004) are subject to repulsion effects from concurrently produced movements. However, the paradigms they employed suffered from confounds that have rendered the interpretation of their results in terms of an influence of action on perception potentially problematic. Namely, the presence of perceptual carry-over effects and anchoring effects could have partly led to the findings they observed. In the present study, we introduced a paradigm in which such confounds were absent and focused on the overlapping motion/movement dimension of direction. The use of direction as the overlapping dimension was of interest because studies that have focused on the influence of perception on concurrent action along this dimension have typically reported facilitation effects, and therefore a form of assimilation of perception on production (e.g., Chua & Weeks, 1997; Ehrenstein et al., 1996; Michaels & Stins, 1997).

Consistent with the studies of Schubö et al. (2001, 2004) and Hamilton et al. (2004), we also observed CEs: Perceived motion directions were repulsed by simultaneously produced movement directions. Moreover, the estimated size of the CEs was similar across experiments, despite the use of different types of perceptual measures. This latter result points to the robustness of the effect and allowed us to exclude various interpretations of the CE. In particular, that it may reflect a judgment bias induced by a categorical overlap between movement and perceptual judgment categories (Experiment 1) or an action-based enhancement of perceptual processing in the space surrounding the (endpoint of the) movement trajectories (Experiment 2).

The fact that CEs were also found for the overlapping dimension of direction suggests that the nature of specific interference depends on the functional unrelatedness of perception and action in the paradigm in question, rather than on

the particular overlapping dimension under study. However, the nature of specific interference also seems to be contingent upon the concurrent nature of the perception-action task. For example, in a study by Kerzel (2001) participants were asked to encode a stimulus motion that could vary in velocity, then produce a functionally independent fast or slow movement themselves, and finally judge the velocity of the previously presented motion by comparing it to the velocity of a test stimulus motion. Under these sequential conditions, the results revealed a form of assimilation effect in that the remembered velocities were biased in the direction of produced velocities. Thus, functional unrelatedness between what needs to be perceived and produced does not, by itself, determine the type of specific interference that will be observed. What still remains unclear, however, is which aspects of action (e.g., planning, execution, and/or the integration of proprioceptive information) are critical for inducing CEs.

Unlike previous studies (Hamilton et al., 2004; Schubö et al., 2001, 2004), the current findings also show that such effects are not tied to the perceptual processing of complex biological motion. It points therefore to the generality of the CE in concurrent action-perception paradigms. This result is noteworthy because biological motions are known to be processed differently than non-biological motions (e.g., Viviani, 2002) and it has been argued that perception-action interactions of this type may relate to the involvement of the motor system in the processing of biological motion (Hamilton et al., 2004; Jacobs & Shiffrar, 2005; Kilner et al., 2003; Wolpert et al., 2003).

For example, in the context of weight perception, Hamilton et al. (2004) accounted for their CE by proposing that there are multiple weight modules (one for each weight) that play a role in the perception and production of actions (for more details concerning their theoretical framework, see Wolpert et al., 2003). Each of these modules is responsible for generating a prediction of the kinematics associated with lifting/holding a corresponding weight. The predictions of each module are then compared to the kinematics of observed lifting movements and the resultant discrepancies provide the basis for the perceptual judgment. The critical assumption here is that the module that corresponds to the weight held by the observer does not contribute to the perceptual judgment, such that perceived box weights are biased in a direction opposite to the held weight. In order to apply this model in the present context, one could simply replace the weight modules with direction modules. However, to the extent that the comparison process is tied to the prediction of biological motion, it is unclear how this model would deal with visual motions that have non-biological velocity profiles.

An alternative account of CEs was proposed by Schubö et al. (2001). Although they also employed biological stimulus motion, their model was not formulated in a way that is specific to biological motion processing. Figure 5 illustrates an adaptation of their model for the overlapping movement/motion dimension of direction (instead of the original dimension of amplitude). They assumed that perception and action share a common representational system (Prinz, 1997) in which movement and motion directions are represented in a distributed fashion. That is, produced movements and perceived motions not only activate their corresponding directions, but also neighboring directions, with the mean of each distribution determining what is perceived and produced at a given moment in time. When, however, people have to simultaneously engage in distinct perceptual and motor activities, they hypothesized that the codes underlying each activity must be "kept separate" from one another in order to minimize interference. This is achieved via a form of mutual partial inhibition of the codes that are activated by both perception and action (gray area in the figure), which causes the means of the underlying distributions to "shift away" from each other within the common representational space. Hence the repulsion effect between action and

perception.

The applicability of these two models to the present data may ultimately depend on assumptions related to biological motion processing. However, their merit should also be evaluated on the basis of specific predictions. For example, both models make a strong claim about the CE that has yet to be tested: The size of the CEs should increase monotonically with the amount of similarity (feature overlap) between what is produced and perceived. Even though different RS motion directions were used in the current experiments, it was not possible to test this "distance prediction" here because the CE was defined as the difference in perceived motion directions during upward and downward movements and a larger angular difference between a given RS motion and movement direction was always associated with a smaller angular difference for the other movement direction. The distance prediction, however, is of interest because it is consistent with a wellstudied perception-perception interference effect: The motion repulsion effect (Marshak & Sekuler, 1979). This phenomenon refers to the finding that the directions of two simultaneously presented visual motions have a contrasting effect on each other, i.e., the angle between the two motion directions is perceived as larger than it actually is. It has also been shown that the size of the repulsion effect depends on the angular distance between two motions/lines, with larger distances leading to smaller repulsion effects (Marshak & Sekuler, 1979; Rauber & Treue, 1999; Patterson & Becker, 1996; Westheimer, 1990).

A distance effect has also been reported for the influence of static object perception on action. Tipper, Howard, and Jackson (1997) asked participants to point to a target object as fast and as accurately as possible while trying to ignore near/far non-target objects. The kinematics of the hand movements revealed that movements veered away from non-target objects that were close to the target and veered toward non-target objects that were farther away from the target. Given these results, an aim for future research should be to test the distance prediction for action-perception interactions, and, thereby, determine to what degree they relate to their perception-perception and perception-action interaction counterparts. In this way, it may be possible to integrate models of specific interference in the perceptual domain and across the perceptual and action domains.

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Notes

¹This choice of Ms and RSs was necessary to reliably measure specific interference effects of production on perception. As a consequence, however, the current paradigm did not allow us to obtain a similar measure for effects of perception on production. That is, given that all of the RSs lay on the same "side" of the Ms, any potential influence of the perceived motions on the produced movements could not be interpreted in terms of assimilation or contrast.

²The fact that this difference only reached significance with a one-tailed test led us to corroborate this result with a different, non-parametric, estimation method: The Spearman-Kärber method (Miller & Ulrich, 2001, 2004; Ulrich & Miller, 2004), which does not make any assumptions about the underlying psychometric functions. When comparing the PSEs obtained with this method, the *t* test reached significance two-tailed (*t*(13) = 3.02, *p* < .05).

Figure Captions

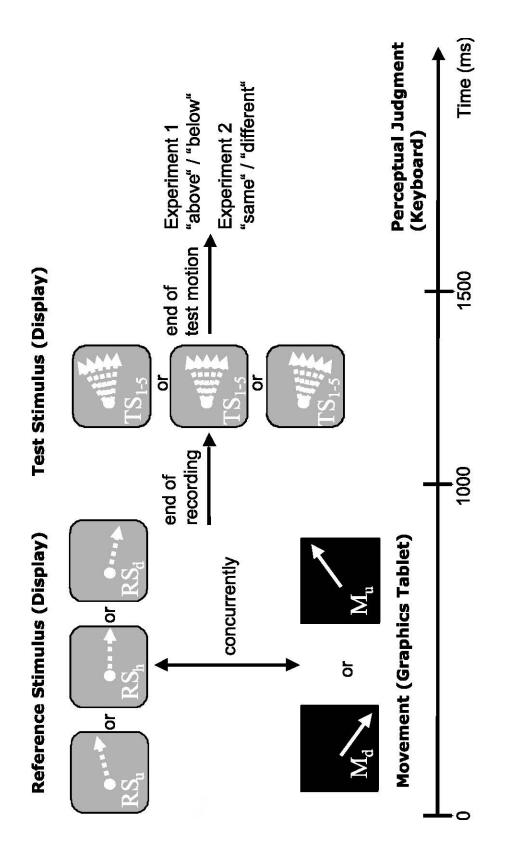
Figure 1. The paradigm employed in Experiments 1and 2. Upward (M_u) and downward (M_d) movements deviated from the horizontal axis by +25° and -25°, respectively. The reference stimulus (RS) moved +15° upwards (RS_u), 0° horizontally (RS_h), or -15° downwards (RS_d), and the test stimulus (TS) deviated in direction from the presented RS motion direction by -4°, -2°, 0°, +2° or +4° (TS_{1-5}). Movement recording lasted 1000ms, whereas RS and TS durations were both 500ms.

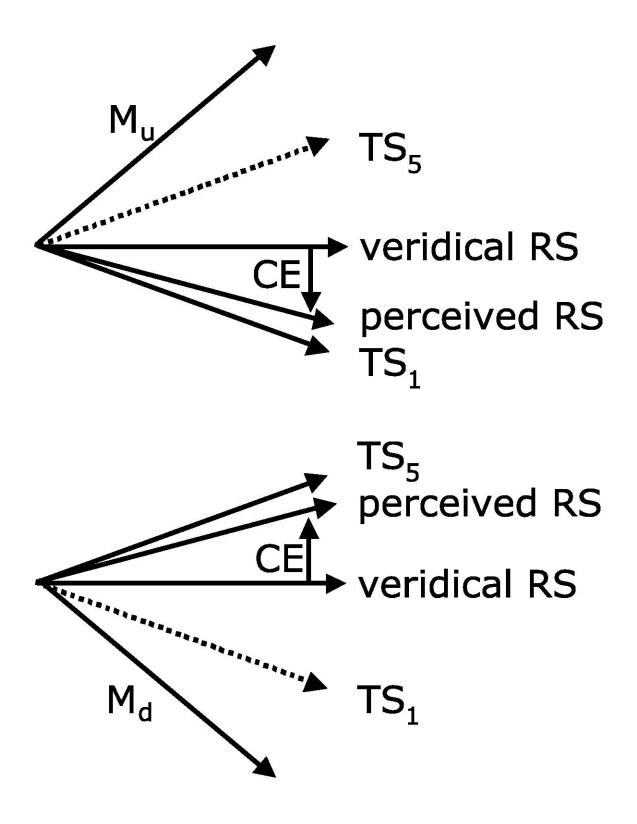
Figure 2. Illustration of how the direction of upward (M_u) and downward (M_d) movements should affect the perceived direction of a reference stimulus (RS) as assessed by participants' judgment of the test stimuli (TS_{1..5}). Two TS direction deviations are included in each panel of the figure exclusively for illustration purposes, since there was actually only one TS presented on a given trial of the experiments (see text for details). CE = contrast effect

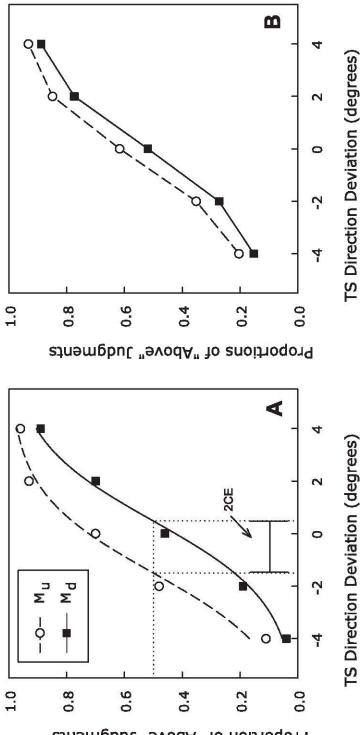
Figure 3. Proportion of "above" judgments as a function of test stimulus (TS) direction deviation (-4° , -2° , 0° , $+2^{\circ}$, $+4^{\circ}$) and movement direction (M_u : upwards, M_d : downwards) for Experiment 1. (A) Data from one participant with the best-fitting psychometric functions and a depiction of how the contrast effect (CE) was defined (see text for details). (B) Mean proportion of "above" judgments for all participants.

Figure 4. Proportion of "same" judgments as a function of test stimulus (TS) direction deviation (-4°, -2°, 0°, +2°, +4°) and movement direction (M_u : upwards, M_d : downwards) for Experiment 2. (A) Data from one participant with the best-fitting psychometric functions and a depiction of how the contrast effect (CE) was defined (see text for details). (B) Mean proportion of "same" judgments for all participants.

Figure 5. A depiction of the model proposed by Schubö et al. (2001) for the overlapping movement/motion dimension of direction (see text for details).







Proportion of "Above" Judgments

