REVIEW

Assimilation and contrast: the two sides of specific interference between action and perception

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Abstract Perception and action have long been treated as relatively independent and serial processes. More recent views, however, consider perception and action as relying on a common set of processes and/or representations. The present paper will focus on a variety of specific (content-based) perception–action interactions that have been taken as support for such views. In particular, the following aspects will be considered: direction of influence (perception on action vs. action on perception), temporal type (concurrent vs. non-concurrent), functional relation (related/unrelated), and type of movements (biological vs. non-biological). Different extant models of the perception-action interface are discussed and a classification schema proposed that tries to explain when contrast and when assimilation effects will arise.

Introduction

The interplay of perception and action lies at the heart of successful behavior. While perception delivers information about the environment relevant for action, action is what brings about changes in the environment. Given this importance of action in everyday life, it is not surprising that actions also play a prominent role in the cognitive

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architecture. For example, actions are represented as integrated properties in working memory quite independent from object and spatial information (Wood, 2007); actions influence short-term memory (Wilson & Fox, 2007), the selection of objects based on their action relation (Riddoch, Humphreys, Edwards, Baker, & Willson, 2003; Mahon et al., 2007), object recognition (Helbig, Steinwender, Graf, & Kiefer, 2010), and actions also bias visual search (Bekkering & Neggers, 2002; Fagioli, Hommel, & Schubotz, 2007; Hannus, Cornelissen, Lindemann, & Bekkering, 2005). Likewise, memory for actions is better when the actions have to be produced later instead of being simply recalled (Freeman & Ellis, 2003). Moreover, a close association between mental imagery and motor processes exists (Decety & Michel, 1989; Graf et al., 2007; Parsons, 1987; Wohlschläger & Wohlschläger, 1998).

Interestingly, perhaps owing to a computer metaphor and to reduce the complexity of scientific investigation, action and perception have been treated as separate entities for a long time (Sanders, 1983; Pylyshyn, 1999). This is so despite their close functional relationship, with one delivering information and the other acting based on the information. This clean theoretical distinction, however, has not held up to empirical scrutiny (Hommel, Müsseler, Aschersleben, & Prinz, 2001; Müsseler, 1999; Prinz, 1997; Schütz-Bosbach & Prinz, 2007; Ward, 2002).

Even the long-held view that the perceptual system is organized into two streams, one for action and a separate one for perception, which do not act on common representations (Goodale & Milner, 1992) is now under challenge (Franz, Gegenfurtner, Bülthoff, & Fahle, 2000; Glover, 2002; Mantas, Evdokimidis, & Smyrnis, 2008). Instead, a view has evolved that acknowledges the highly interwoven processing of actions and perceptions (e.g., Blaesi & Wilson 2010; Hamilton, Wolpert, & Frith, 2004;

Hommel et al., 2001; Lindemann & Bekkering, 2009; Schubö, Aschersleben, & Prinz, 2001; Zwickel, Grosjean, & Prinz, 2010a).

Views on action–perception interactions

Different theoretical views have incorporated the close associations between action and perception processes (see for an overview Hommel et al. 2001; Schütz-Bosbach & Prinz, 2007; Viviani, 2002). While interactions between action and perception are now generally accepted, it is still an open question what the interface between action and perception looks like. The coding of common distal properties (Prinz, 1997), attention (Schneider & Deubel, 2002; Rizzolatti & Craighero, 1998), motor codes (Gallese & Goldman, 1998), and affordances (Gibson, 1979) have all been proposed as common "currency" of action and perception.

According to the *common coding* approach (Prinz, 1997), action and perception share commensurate codes at a certain processing stage. Codes at this stage are activated by perceived and produced events. The common currency is achieved by coding actions in terms of their perceptual consequences. In themselves, these cognitive codes are neither perceptual nor motor in nature (Müsseler, 1999, p. 129) but connected to motor and perceptual codes. This assumption is supported by the mirror neuron approach (Gallese, Fadiga, Fogassi, & Rizzolatti, 1996), which stresses the large overlap of neuronal mechanisms when observing an action or performing the same action. This overlap is found in neurons in area F5 of the premotor cortex in monkeys. However, evidence of motor cortex activation during action observation has also been found in humans using brain activity related measures like electro-encephalography (EEG; Rizzolatti & Craighero, 2004), magnet-encephalography (MEG; Rizzolatti & Craighero 2004) and functional magnetic resonance imaging (fMRI; Buccino et al. 2001).

In the papers by Schneider and Deubel (2002) and Rizzolatti and Craighero (1998) *attention* acts as the interface between action and perception. According to their view, planning of an action leads to increased attention to action-congruent features. While earlier studies have stressed the importance of action-congruent spatial features (Rizzolatti & Craighero, 1998; Schneider & Deubel, 2002), later studies have generalized this to other action-congruent features as, for example, "hand posture" (Craighero, Bello, Fadiga, & Rizzolatti, 2002).

Other approaches placed more emphasis on motor codes as the common currency for action and perception interactions. The mirror neuron approach (Gallese et al., 1996) places the main interface at the premotor cortex. Motor

processes play an even more prominent role in affordances approaches (Gibson, 1979), as, for example, in Tucker and Ellis (1998) and Witt and Proffitt (2008). According to these theories, affordances of objects automatically activate associated motor processes (without overt execution) to act on these objects.

These approaches differ in the extent to which they assume mutual interactions between action and perception to occur. While a common coding approach would make no principled difference between influence of action on perception and perception on action, attentional approaches like "vision-for action" (Schneider & Deubel, 2002) or "premotor-theory" (Rizzolatti & Craighero, 1998) would place more emphasis on the influence of action on perception than vice versa. Strict motor theories that argue that perception is motor-based and goals play only a minor role would assume that stimulus processing is based on motor codes. Perception can thus be influenced by the occupation of motor codes by either other actions or perceptions. This leads to the prediction that influences between action and perception should depend on the similarities in motor coding properties (Fowler, Galantucci, & Saltzman, 2003).

Some evidence against a strict motor theory without goal representations can be found in studies as, for example, Wallace (1971). Participants were instructed to respond with their right or left hands to shapes that could occur to the right or left of a fixation point. Crucially, responses were carried out with crossed hands and therefore allowed the dissociation of anatomical and goal-space. The results showed that response time was influenced by the spatial location of the keys and responses were faster in compatible situations. A strict motor theory, in contrast, would predict that only the motor code activating the hand responding should interact with the perceptual location of the target stimuli and therefore the left hand should be faster for stimuli on the left side. Not surprisingly, most motor theories therefore acknowledge the importance of goal representations at the interface between action and perception (Rizzolatti, Fogassi, & Gallese, 2001; Wilson & Knoblich, 2005; Witt & Proffitt, 2008; Wolpert, Doya, & Kawato, 2003).

Action perception paradigms

In the following, we will evaluate evidence of influences of action on perception and perception on action and finally, will discuss results that show mutual influences within the same experiment. In doing so, we will mainly focus on specific interference effects (Müsseler, 1999) and largely ignore unspecific interference effects (e.g., Kahneman, Beatty, & Pollack, 1967).

Unspecific versus specific interference

Unspecific interference is typically "attributed to more general demands of action control" (Müsseler, 1999, p. 132) and associated with interactions between neural processing mechanisms (Wickens, 1984). The amount of unspecific interference is seen as a result of the similarity of tasks with respect to, for example, modalities or stages of processing; content variables on the other hand, are normally not varied or of little interest (Wickens, 1980, 1984). In contrast, specific interference is caused by the content of processing and attributed to the number of shared features between two tasks. In other words, unspecific interference relates to the similarity in operations while specific interference is caused by the features of these operations. For example, when steering a car and talking on the phone, there are at least two main operations going on: one operation would be to encode the visual scene and map this to appropriate steering actions. The other operation would be to encode speech, evaluate it, and finally produce a (hopefully) appropriate oral output to it. Unspecific interference would arise between concurrent operations of encoding information or mechanical operations for talking and steering. Specific interference, on the other hand, would arise between the features. For instance, steering to the right (feature 1) to avoid an obstacle while encoding verbal information to take the next exit to the left (feature 2).

Manipulating content or processing variables addresses different questions. Due to the supposed origin of unspecific interference, limitations and errors in dual-task situations are informative about processing similarities and resource allocation between tasks. A different question is addressed with specific interference paradigms, because here not the processes but the contents of the tasks are manipulated; as a result, the focus is on the overlap of content and hence the underlying codes. As will become clear from the following, in addition to understanding which content combinations lead to increased errors, the direction of the errors can be predicted. As a consequence of focusing on the influence of content, interference is demonstrated between levels that are commonly seen as separate, relatively independent processing stages like encoding and acting (Wickens, 1984).

There are essentially two ways interference can occur. Interfering features can make the action and perception events more or less similar to each other. Both effects can be explained within a common coding framework by two different approaches. According to a code-occupation approach (e.g., Hamilton et al., 2004; Hommel et al. 2001; Müsseler, 1999), the engagement of a feature by one event binds the feature and thus makes it less available for the other event. For example, producing a hand-movement to the right binds the feature(s) that represent "right" and in doing so, prevents the access of this by the perceptual representation of a stimulus. This causes the stimulus to be perceived more to the left than if no rightward codes were bound by the action. However, after the binding has been dissolved, the feature codes are available again with some remaining activation. This remaining activation enhances the representation of the features in the next binding (e.g., for perception of a stimulus). Therefore, the stimulus is perceived as more similar to the action.

According to an inhibition account (e.g., Schubö et al., 2001; Zwickel et al., 2010a), common codes are inhibited and thus lead to an underrepresentation of the common features in the perceived and produced events, which makes it easier to discriminate between the two events. Random exchange of features would increase the similarity between two events if no inhibition takes place. In the following, the attenuation of common features in the representation of an event will be called contrast effect (CE) and the enhancement of similarity, assimilation effect (AE). Until now there is no clear consensus when CEs and when AEs arise. At the end of this paper, we will develop a classification schema along which these effects might be structured. The overview is thus structured according to this schema.

Paradigms on specific interference between action and perception

The following overview of interactions between action and perception will distinguish between the direction of influence (action on perception or perception on action), the temporal type (concurrent, non-concurrent), meaning whether a movement occurs during the need for *ongoing* perception or not, and the functional relationship (related, unrelated), that is, whether the actions were performed in response to the stimuli or independent of the stimuli (see Table 1). The distinction between the direction of the effect is owing to the informal observation that AEs seem to prevail when actions are influenced. The reason why we distinguish between functionally related and unrelated paradigms is that the latter case allows separation of the action and perception tasks, and it has been argued previously (Schubö et al., 2001; Zwickel et al., 2010a) that whether CEs occur or not depends on whether two tasks have to be kept separate from each other. Only when there is no functional relation between the action and perception tasks can the two tasks be kept separate. Further, the need for keeping two tasks separate only arises when a temporal overlap between action and perception events exists, which led us to classify studies according to whether the two tasks occur concurrently or not.

Table 1 Classification of discussed studies on specific interference and observed effects (AE = assimilation effect; CE = contrast effect; ? = unclear with respect to AE/CE)

Related	Unrelated
Perception on action/non concurrent	
Brass et al. (2001) (AE)	Chartrand and Bargh (1999) (AE)
Greenwald (1972) (AE)	Craighero et al. (1998) (AE)
Simon (1968) (AE)	Edwards et al. (2003) (AE)
	Ellis and Tucker (2000) (AE)
Perception on action/concurrent	
Chua and Weeks (1997) (AE)	Grosjean et al. (2009) (CE)
Kilner et al. (2003) (AE)	Repp (2006) (AE)
	Richardson et al. (2007)(AE)
	Schubö et al. (2001) (CE)
	Tipper et al. (1997) (CE)
	Zwickel et al. (2010a) (CE)
Action on perception	
Beets et al. (2010b) (AE)	Hamilton et al. (2004) (CE)
Craighero et al. (1999) (AE)	Jacobs and Shiffrar (2005) (?)
Keller et al. (2007) (?)	Miall et al. (2006) (?)
Lindemann and Bekkering (2009) (AE)	Müsseler and Hommel (1997) (CE)
	Repp and Knoblich (2007) (AE)
	Wohlschläger (2000) (AE)
	Zwickel et al. (2007, 2008, 2010a, b) (CE)

Brass et al. (2001): Faster finger movements in response to compatible visual stimuli. Greenwald (1972): Compatible S-R mappings reduce PRP effect between two tasks. Simon (1968): Faster hand movements in directions compatible with side of verbal instruction. Chartrand and Bargh (1999): Incidental mimicking of behavior mannerisms of confederate. Craighero et al. (1998): Faster grasp responses when unrelated grasp-congruent stimulus is presented prior to go signal. Edwards et al. (2003): Faster hand reaches after seeing a compatible reach. Ellis and Tucker (2000): Faster grasps in response to tone when object encoded prior to go signal was grip congruent. Chua and Weeks (1997): Better synchronization between arm and dot motion for compatible movement end points. Kilner et al. (2003): Less variable arm movements that are made in time with compatible observed movements. Grosjean et al. (2009): Produced movements veer away from concurrent independent dot motions. Repp (2006): Tapping temporally attracted to distractor tones. Richardson et al. (2007): incidental synchronization between rocking frequency when sitting in chairs. Schubö et al. (2001): Smaller/larger produced movement amplitudes while watching larger/smaller motion amplitudes. Tipper et al. (1997): Arm reaches veer away from close static distractors. Beets et al. (2010b): Ambiguous stimulus is perceived longer rotating in direction congruent with hand rotation. Craighero et al. (1999): Faster prepared grasp responses to congruent go signal. Keller et al. (2007): Better synchronization between playing and listening to pre-recorded music sequence of oneself than of someone else. Lindemann and Bekkering (2009): Faster prepared hand rotations when go signal induces congruent apparent motion. Hamilton et al. (2004): Observed boxes judged to be lighter/heavier when lifting heavier/lighter boxes. Jacobs and Shiffrar (2005): Walking speed discrimination worse during walking than cycling. Miall et al. (2006): Faster detection of stimulus in observed hand movement sequence that is congruent with performed hand movement. Müsseler and Hommel (1997): Worse discrimination of masked arrow direction while preparing compatible button press. Repp and Knoblich (2007): Ambiguous tone sequence in terms of rising or falling is perceived as rising/falling during ascending/descending movements on piano.Wohlschläger (2000): Direction of ambiguous motion is perceived rotating in direction congruent with concurrent independent hand rotation. Zwickel et al. (2007, 2008, 2010a, b): Perceived and produced movement directions veer away from each other

Perception on action

Perception on Non-concurrent/Functionally Related Action Paradigms that measure the influence of perception on non-concurrent and functionally related actions are typically found in the stimulus-response compatibility literature (for reviews Hommel & Prinz 1997; Kornblum, Hasbroucq, & Osman, 1990; Proctor & Reeve, 1990). For example, button presses are faster when performed on the same side as the stimulus relative to fixation. Also, high stimulus–response compatibility can reduce interference between two response tasks (Greenwald, 1972) and speed up

responding (Brass Bekkering, & Prinz, 2001). These effects are found for biological (Brass et al., 2001) and non-biological stimuli (Simon, 1968). To the extent to which facilitation of response codes can be seen as examples of AEs, these studies provide unequivocal evidence of AEs in functionally related paradigms.

Perception on Non-concurrent/Functionally Unrelated Action Similar AEs have been found for independent actions. Craighero, Fadiga, Rizzolatti, and Umiltà (1998) asked participants to prepare a grasp response to one of two differently oriented bars that were visually occluded. Grasping responses were faster when a bar of the same

orientation was presented shortly before the go signal. This was interpreted as showing that visual stimuli prime actions. Similarly, Ellis and Tucker (2000) reported faster responses to a tone when the response was grip congruent (power/precision grip) to an object that was presented before the go signal and had to be memorized for later recognition (the object stayed visible until response). Not only congruent objects but also observed congruent actions prime actions in the observer as Edwards, Humphreys, and Castiello (2003) were able to show. Participants saw a movement either towards the same or a different object that they had to grasp themselves after a go signal. Observing congruent actions led to faster movements than observing incongruent actions.

Visual stimuli not only increase the speed of congruent responses but also the likelihood that congruent responses will occur (Chartrand & Bargh, 1999). In their study, the authors showed that participants incidentally mimicked behavioral mannerisms (e.g., rubbing one's nose) of a confederate during a cover task. Again, influences were found for biological (Chartrand & Bargh, 1999; Edwards et al., 2003) and non-biological stimuli (Craighero et al., 1998; Ellis & Tucker, 2000).

Perception on Concurrent/Functionally Related Action AEs also arise in concurrent paradigms when a functional relationship exists. In one condition of a study reported in Kilner, Paulignan, and Blakemore (2003), participants made sinusoidal arm movements in time with an observed arm movement. These movements could either be along the same dimension (e.g., both performed horizontally) or along different dimensions (e.g., observer horizontal, observed vertical). Participants' movements were less variable in congruent than incongruent conditions. Another example of concurrent functionally related tasks with non-biological stimuli was provided by Chua and Weeks (1997). Here, people were better at synchronizing their movements with dot motions when movement and motion endpoints corresponded spatially.

Perception on Concurrent/Functionally Unrelated Action While, in functionally related paradigms, AEs seem to prevail, the results are more mixed in functionally unrelated paradigms: Richardson, Marsh, Isenhower, Goodman, and Schmidt (2007) reported that two people incidentally synchronize their rocking behavior in a rocking chair when a cover task required them to watch each other. These types of effects are not restricted to the observation of biological stimuli. As Repp demonstrated in his study (2006), irrelevant distractor tones influenced the tapping behavior in that finger taps were temporally attracted to the distractors. However, participants were all trained musicians, which could explain their tendency to synchronize with a rhythmic sequence.

CEs have also been reported in this kind of paradigm. Schubö et al. (2001) asked participants to perform movements of certain amplitudes on a graphics tablet. The concurrent visual trajectories on a screen were not relevant for the current trial but had to be reproduced in later trials and therefore attended to. The amplitude of the concurrently perceived motions produced a CE on the hand movement amplitude; amplitudes produced were smaller while watching large amplitudes than while watching small amplitudes. In this paradigm, visual motions were dot movements that followed biological movement profiles.

However, even dots without a biological movement profile but with constant velocity produced similar effects (Grosjean, Zwickel, & Prinz, 2009). Here, participants produced straight line movements while watching a movement in a different direction. Again, the concurrent visual movement was made relevant by the need to reproduce it later. As in Schubö et al. (2001), the movements produced were made less similar to the observed motions (i.e., the direction of movements veered away from the observed directions). However, because the motion differed from the movement from the beginning, it was possible to evaluate the unfolding of this CE. Interestingly, the final CE in movement production was preceded by an assimilation during approximately the first 200 ms. A CE has also been found to static distractors for arm reaches[1] (Tipper, Howard, & Jackson, 1997).

Action on perception

One way action influences perception is through action competency and knowledge. For example, in Casile and Giese (2006), blindfolded participants practiced a new movement which led to better visual discrimination performance of the corresponding movements afterwards (see also Beets, Rösler, & Fiehler, 2010). Also, patients who have lost their proprioception and sense of cutaneous touch have trouble in interpreting others' kinematics (Schütz-Bosbach & Prinz, 2007), which shows that motor competency influences perception. Further, knowledge about certain motor properties influences perception (Viviani, 2002) and judgments (Grosjean, Shiffrar, & Knoblich, 2007). For example, a dot moving at different speeds along an elliptic trajectory was judged as moving at a constant speed if the acceleration/deceleration pattern followed the typical profile of motor movements (the so-called two-thirds power law). Also, participants tended to perceive a biologically plausible rather than a biologically implausible

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[1] Attraction was found to far away distractors. This pattern was explained within a competitive model and is consistent with the current account, assuming that distance controls amount of overlap (see Zwickel et al. 2010a).

movement in an ambiguous situation (e.g., an arm moving around an object instead of passing through it), which demonstrates that movement knowledge changes perception (Shiffrar & Freyd, 1990). However, these effects concern long-term effects of action experience instead of concurrent influences and are not considered further below.

When looking at influences of action on perception, at least two phases of action can be distinguished: planning and execution. After-effects after movements have ended have rarely been considered (cf. Kerzel, 2001; Stevanovski, Oriet, & Jolicoeur, 2002).

Action on Concurrent/Functionally Related Perception
In a functionally related and concurrent paradigm, Keller, Knoblich, and Repp (2007) asked skilled pianists to synchronize their playing with a pre-recorded music sequence. Participants were better able to synchronize when the concurrent recorded music was a record of their own earlier playing. This argues for a close interaction between the motor and perceptual processes. Another example is the study of Beets, 't Hart, et al. (2010). In one condition participants used a manipulandum to indicate the perceived direction of a rotating ambiguous stimulus. The stimulus could be perceived as either rotating clockwise or counterclockwise. When participants reported clockwise rotations with clockwise rotations and vice versa for counterclockwise rotations they perceived the congruent rotation for a longer time interval than when motion directions were reported by incongruent movement directions. Interestingly, no influence on perceived directions was found when participants were asked to rotate the manipulandum in one direction over the whole block and to report the perceived rotation direction instead by a key press. This disappearance of an influence from action on perception shows the importance of changes in actions between trials which increases the need for planning of and attending to actions.

Action on Concurrent/Functionally Unrelated Perception More studies have used concurrent and independent paradigms. For example, participants in a study by Jacobs and Shiffrar (2005) were asked to discriminate between different observed gait speeds while walking, cycling, or standing. Only concurrent walking reduced performance, arguing for a specific influence of movements produced on the perception of similar motions. Similarly, in a detection task by Miall et al. (2006), participants detected a stimulus faster in a depicted hand movement sequence when they were concurrently performing the same movement as compared with another hand movement. However, because the time course of the action and perception events was not tightly controlled in these studies, these effects are difficult to interpret in terms of contrast or assimilation effects. The interpretation that the authors provided was unrelated to this distinction. According to their explanation, performing

a congruent movement allows better prediction of what should be observed, and it was this improved prediction that made the odd stimulus stick out.

Wohlschläger (2000) investigated the influence of directional hand movements on the perception of an ambiguous motion that could be interpreted as a rotation in a clockwise or counterclockwise direction. To create the ambiguous motion, dots were arranged around an imaginary circle with a 60° distance between each adjacent dot on a screen. Apparent motion was then achieved by rotating the dots along the imaginary circle. Because all the dots looked identical, the direction of motion was ambiguous. Concurrent with observing the dot motions, participants were required to turn a knob either clockwise or counterclockwise. Stimulus rotation was started by the hand movement which might have induced a relation between the two tasks.[2] However, this relation would be rather temporal than functional because the hand movement did not change the stimulus. The perceived direction of the ambiguous motion was influenced by the turning direction in that clockwise turns of the knob led to a higher rate of perceived clockwise motions and turning the knob counterclockwise increased the chance of perceiving a counterclockwise motion.

A similar effect was reported for auditory perception by Repp and Knoblich (2007). In this paradigm, participants listened to two tones in sequence. These tones were selected so that the probability of perceiving a rising or falling sequence was expected to be equal. When participants performed a left to right movement on a piano or computer keyboard, they were more likely to perceive a rising sequence than when moving from right to left. This was what would be expected because left is associated with low, and right with high tones (e.g., Rusconi, Kwan, Giordano, Umiltà, & Butterworth, 2006). Interestingly, the AE was found only in skilled pianists and not in a control group of untrained students, which suggests that learned movement effects might play a role in this effect.

However, the opposite effect of an increased difference between the perceived and produced events was also observed in concurrent independent paradigms. Hamilton et al. (2004) had participants lift boxes of different weights while they judged the weight of boxes that were lifted by another person. Lifting heavy boxes led to lower weight judgments of the boxes participants merely observed than lifting light boxes. Thus, the perceived motion was made less similar to the produced event. Similarly, Zwickel, Grosjean, and Prinz (2008) asked participants to produce either upward or downward movements with a pen on a graphics tablet while observing a concurrent horizontal dot motion to the right. Participants judged the horizontal

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[2] We thank an anonymous reviewer for raising this point.

motion as deviating upwards more when producing downward movements than when producing upward movements, again showing a CE. Moreover, not only concurrent action execution influences perception but already the *planning* of movements:

Movement Planning/Functionally Related Perception Functionally related paradigms also led to AEs in the case of planning. Craighero, Fadiga, Rizzolatti, and Umiltà (1999) had participants prepare to grasp and lift bars of different orientations. They had to withhold their action until a go signal. The go signal could be either congruent or incongruent with the prepared action. Responses were faster in congruent than incongruent conditions, which was interpreted as showing priming of the visual stimulus by the planned action. This interpretation was supported by a control experiment in which participants also responded faster in congruent trials if they had to make an unprepared foot response. Similar effects of movement planning on apparent motion perception have been found by Lindemann and Bekkering (2009).

Movement Planning/Functionally Unrelated Perception Mixed results in terms of AEs and CEs have been reported for the influence of action planning on the perception of a functionally unrelated stimulus. Müsseler and Hommel (1997) reported that participants were worse at detecting a masked rightward or leftward pointing arrow while planning a congruent button press. For example, planning to press a button on the right increased the difficulty to detect a masked error pointing to the right when compared with planning a left button press. This was explained by common codes which can only be bound to either action or perception, for example, of the direction "right". Therefore, planning a rightward action bound rightward codes and made them less available for the perception of rightward pointing arrows. This led to a CE: the perception representation was less similar to the action representation. On the other hand, Wohlschläger (2000) also reported the same effects on ambiguous motion perception as discussed earlier for planned hand movements.

Interference in both directions

All studies mentioned above reported either an influence on action or an influence on perception. However, none tested whether both effects could be found within the same experiment. Finding effects in action and perception at the same time would be a strong indication that there is no unidirectional information flow and that action and perception share common representational elements. This was addressed in a study by Zwickel et al. (2010a). In this study, participants made hand movements in different directions with a pen on a graphics tablet. As soon as they started their movement, a dot motion started a vertical trajectory on a screen. The starting point of the dot motion corresponded to the starting point of the hand movement (see Fig. 1) and ended before the hand movement ended. The participants' task was to report the perceived direction of the dot motion. This resulted in CEs for hand movement directions above the horizontal midline (when an upward component was present); that is, perceived directions were biased away from the directions produced. This was measured by comparing judged motion direction for hand movements to the right and left. Hand movements to the right led to judgments of motion direction that were biased to the left, and vice versa. This CE was reversed for hand movements with a downward component. More importantly, hand movements also veered away from the stimulus motion; that is, hand movements had a stronger rightward and leftward component when a dot trajectory was displayed that lay between the hand movement directions. Therefore, CEs in action and perception were observed within the same paradigm.

The fact that effects in this paradigm constitute concurrent influences on ongoing perception and not aftereffects in memory was demonstrated by Zwickel, Grosjean, and Prinz (2007). Here, participants had to detect a deviation of the stimulus motion from its vertical trajectory. Detection of deviations to the left was faster during concurrent hand movements to the right than during movements to the left. Similarly, deviations to the right were detected faster during leftward hand movements. This is what would be expected if producing a movement attenuates the contribution of action congruent features and by
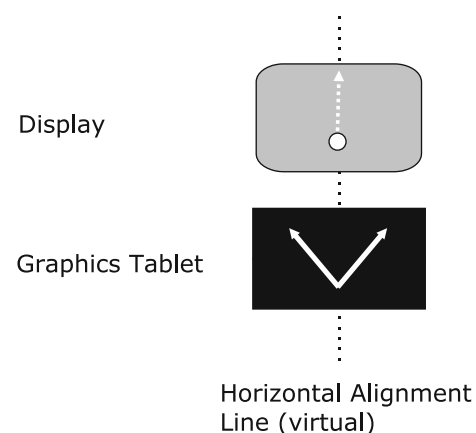

Fig. 1 Experimental setup of Zwickel et al. 2010. *Lower part* shows one example of right and left movement direction that had to be performed on the graphics tablet. *Upper part* depicts example motion on screen. Start point of motion and movements were horizontally aligned. Motion deviations from the vertical were always smaller than required movement angles

this, enhances the relative contribution of action incongruent features (left).

Finally, a modification of the paradigm allowed testing of which part of an action caused this interference effect (Zwickel, Grosjean, & Prinz, 2010b). To test whether proprioceptive information alone would be sufficient to produce this change in perception, participants' hands were passively transported in some trials by a motor. In these trials, no CE was observed, which reveals that proprioceptive information about the position of the hand is not sufficient to cause the effect. In another experiment, participant's movements were blocked in some trials by fixing the pen with the force of a motor. In these trials, participants had planned and prepared the movement and already applied the force to move the pen but could not execute the movement. In this condition, assimilation was observed in that perceived motions were biased in the direction of the intended movements. This supports the view that intention alone does not produce the CEs but later processes of movement execution do. Assimilation in this paradigm seems to be the default consequence of intending to perform a movement that is turning into a contrast effect during movement execution. This effect in perception nicely mirrors the effect on movements as reported by Grosjean et al. (2009). Here, the influence of a presented movement direction made the hand movements veer towards the observed motion at first, and later repelled them, resulting in a reliable CE at the end of the movement (see Gomi, Abekawa, & Nishida, 2006; Whitney, Westwood, & Goodale, 2003).

Status of biological stimuli in interference effects between action and perception

Interference effects have been found with and without biological stimuli. Therefore, the question arises whether biological stimuli have a special status in interference effects. This question is of interest 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.

In the previously described study by Kilner et al. (2003), in which participants showed interference effects when performing arm movements that were incongruent to observed motions, another condition involved a robot performing the observed motion instead of a human. In the robotic condition, some biological features critical for activating the mirror neuron system seemed to have been missing because no interference effect was found.

However, in a more recent study (Kilner et al., 2007) as well as in other studies discussed in this article (Grosjean et al., 2009; Zwickel et al., 2010a), even a moving dot with a non-biological movement profile has been found to interfere with movement execution. One interpretation offered by Kilner and colleagues was that the mirror system only responds if the observed stimuli combined with the observed movement patterns are sufficiently familiar, which was assumed to be the case for moving dots, but not for robots.

However, the relevance of physical attributes of biological stimuli is further questioned by a number of findings that point to the importance of abstract "features" of actions, in particular, goals or interpretations, in the activation of the mirror neuron system (Gazzola, Rizzolatti, Wicker, & Keysers, 2007). In the study by Gazzola and colleagues, a robot action was found to activate the mirror neuron system only if the observed action had a familiar goal. The influence of interpretation was underscored by Stanley, Gowen, and Miall (2007), who reported that the same moving dot stimuli did or did not lead to interference, depending on whether participants were made to believe that the dot motion was biological or non-biological in origin.

These studies therefore nicely show that interference is not only influenced by the physical properties of biological motions but also by the observer's knowledge and beliefs about them (see Liepelt et al. 2010). The studies above reported contrast and assimilation effects in similar paradigms. This raises the question of what determines which kind of effect is observed.

What leads to assimilation or contrast?

According to a common coding approach, CEs are assumed to arise between *concurrent* perceptual and motor processing if the action and perceptual processes are interpreted as functionally *unrelated* but *feature overlap* occurs. In this case, the features are bound to the action and perceptual representations and/or become inhibited. By this, the features are made less available. In contrast, AEs arise when (a) processing is seen as belonging to functionally related tasks or (b) action and perception processing do not lead to feature overlap, or (c) no concurrent perception is required. AEs could be explained within a code-occupation account by assuming that bound features are rapidly dissolved, leaving some remaining activation that biases the new event for which the feature is needed. For example, a movement feature is quickly dissolved and bound into a perceptual representation of a stimulus and the stimulus thus made more similar to the action event. According to an inhibition account, if no inhibition of common elements

occurs in these situations, random exchanges of features between the perception and action representations increase their similarity.

In the following we will discuss how this proposal relates to empirical data. In studies by, for example, Jacobs and Shiffrar (2005), Kilner et al. (2003), and Miall et al. (2006), a change in performance was reported, but it is not clear whether this change was caused by an enhanced or attenuated contribution of the overlapping features. We will therefore, in the following, look at the tasks for which it is easier to see whether CEs or AEs occurred.

Single tasks, like standard stimulus–response tasks or even continuous stimulus–response tasks, do not induce an overlap of two concurrent events that belong to independent tasks. Therefore, facilitative interference should be expected. To the extent that AEs can be related to facilitation, stimulus–response studies confirm the prediction. Similar effects were found in functionally unrelated and non-concurrent paradigms (e.g., Craighero et al. 1998). Craighero et al. (1998)'s task of responding with a prepared movement to a go signal did not involve overlapping tasks in the sense that further visual processing was not needed after movement start and, as expected, better processing of overlapping features was found.

The expected facilitation effect was also found in concurrent and functionally related tasks (e.g., Chua & Weeks, 1997). In functionally unrelated and concurrent paradigms, CEs were observed (e.g., Grosjean et al., 2009) again in line with the argument outlined above. Similar observations apply to the influence of action on perception: CEs were found for concurrent and unrelated tasks (e.g., Hamilton et al., 2004). In addition, the influence of planning on perception seems to mirror this distinction between AEs for related (e.g., Craighero et al., 1999) and CEs for unrelated (e.g., Müsseler & Hommel, 1997) tasks.

What might be problematic for this account are the findings of Wohlschläger (2000), Repp (2006), Repp and Knoblich (2007) and Richardson et al. (2007). As described earlier, Wohlschläger (2000) found AEs in the judgment of the direction of rotating dots when concurrently and unrelated to the judgments, participants rotated their hands. Repp and Knoblich (2007) found AEs in the perception of ambiguous (in terms of rising or falling, the tritone paradox) tone sequences, when concurrently but unrelated to the tone height pressing keys on a keyboard either in a rising or falling order. A major difference from the other studies reported, however, was that one concurrent event involved an ambiguous stimulus. Two different reasons could therefore be advanced to explain the AEs. First, the ambiguous stimulus might have led to such a weak representation that binding of the features of the stimulus did not work properly and included features of the other task to a high degree. This reason seems unlikely on introspective grounds because at each point in time one direction clearly dominates and the other direction is not perceived at all. Thus, it seems unlikely that the ambiguous motion was represented in a weaker fashion than non-ambiguous motions.

Therefore, a second reason seems more viable. While in the experiments of, for example, Hamilton et al. (2004) and Zwickel et al. (2010a), further perceptual processing of a stimulus could improve decisions about the stimulus, ambiguous situations need additional information to disambiguate them. For example, when Wohlschläger (2000) asked individuals to judge the direction of the rotation of a stimulus, even having exact knowledge of the dot locations would not resolve the ambiguity. Only the application of additional criteria, for example, preferring shorter paths between the dots, could lead to a directional judgment. The situation is different, for example, in the study by Hamilton et al. (2004), where participants judged the weight of boxes that were lifted by someone else while hefting boxes themselves. In this experiment, having detailed visual information would allow for a veridical judgment of the weights. Therefore, it might be helpful to also integrate information from other sources in the former case, when the stimulus does not provide sufficient information, but not in the latter case. While additional information is needed to disambiguate the situation in the former case, in the latter case, adding information from another task would distort the veridical perception.

It seems that processes that control the occurrence of CEs not only take into account whether two tasks are functionally unrelated but also whether one stimulus is ambiguous and therefore needs additional information. In this case, sensory processing seems to not be protected against other concurrent tasks and AEs arise. Another difference between the findings of Repp and Knoblich (2007) and other studies described here is that they reported an influence of task experience; only trained musicians showed the AE effect. Likewise, the studies by Richardson et al. (2007) and Repp (2006) are special in that they involved rhythmic movements [and experienced musicians in the case of Repp (2006)]. There might be a general tendency in humans to synchronize with rhythmic movements that causes this kind of AE. Figure 2 summarizes the conditions under which AEs or CEs are expected to arise.

According to this schema, CEs occur only when two functionally unrelated tasks are performed at the same time, no perceptual ambiguity or rhythm is involved, and the tasks share common features. In addition, the results of Stanley et al. (2007) that whether interference occurs or not depends on participants' beliefs about the biological/non-biological origin of a motion points to the importance of the interpretation that participants have about observed
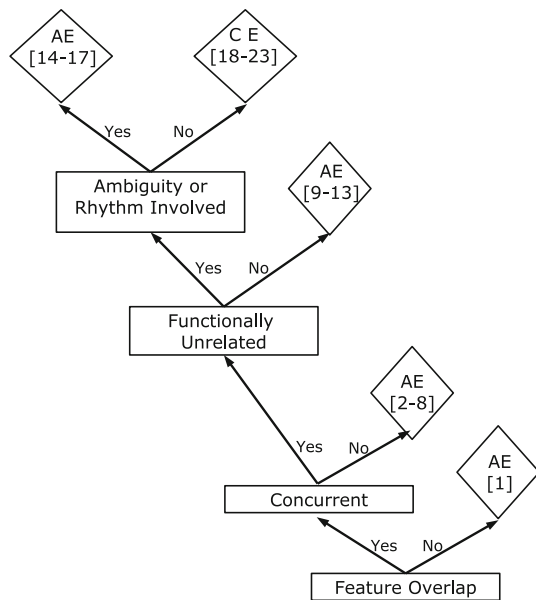
Fig. 2 Action and perception conditions that lead to AEs and CEs. *Number in brackets* refer to exemplar studies, from Table 1 that could be classified as either showing CE or AE effects. [*1*] Zwickel et al. (2010a) with movements below horizontal; [*2*] Brass et al. (2001); [*3*] Greenwald (1972); [*4*] Simon (1968); [*5*] Chartrand and Bargh (1999); [*6*] Craighero et al. (1998); [*7*] Edwards et al. (2003); [*8*] Ellis and Tucker (2000); [*9*] Chua and Weeks (1997); [*10*] Kilner et al. (2003); [*11*] Beets et al. (2010b); [*12*] Craighero et al. (1999); [*13*] Lindemann and Bekkering (2009); [*14*] Repp (2006); [*15*] Richardson et al. (2007); [*16*] Repp and Knoblich (2007); [*17*] Wohlschläger (2000); [*18*] Grosjean et al. (2009); [*19*] Schubö et al. (2001); [*20*] Tipper et al. (1997); [*21*] Hamilton et al. (2004); [*22*] Müsseler and Hommel (1997); [*23*] Zwickel et al. (2007, 2008, 2010a, b)

motions. Whether feature overlap occurs or not depends not so much on physical properties of the stimuli, as for example the kinematic differences between biological and non-biological movements, but on the interpretation of the stimuli by the observer. With these restrictions however, contrast effects occur in action and in perception.

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