On the effects of action on visual perception

&

How new movement types are learned

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Table of contents

Study I: Beets I.A.M., Rösler F. and Fiehler K. (accepted for publication). **Non-visual motor learning improves visual motion perception: Evidence from violating the two-thirds power law.** *Journal of Neurophysiology*

Study II: Beets I.A.M., 't Hart B.M., Rösler F., Henriques D.Y.P., Einhäuser W. and Fiehler K. (under review). **Online action-to-perception transfer: only percept-dependent action affects perception.** *Vision Research*

Study III: Beets I.A.M., Rösler F. and Fiehler K. (submitted for publication). **Acquisition of a bimanual coordination skill after active and passively guided motor training.** *Experimental Brain Research*

I. Cumulus

1. Introduction

In order to enhance our ability to survive, we need to act upon the environment appropriately. To be able to fine-tune our actions to the environment, we have the ability to perceive the environment accurately with vision, hearing, smell, touch, and proprioception. Any sensory and cognitive processes can be viewed as inputs which later create motor outputs (Wolpert, Ghahramani & Flanagan 2001). In turn, the generation of motor output always results in feedback in vision and proprioception (Wolpert & Ghahramani 2000). But what happens when we rule out the visual feedback by viewing one's own actions? In what ways and to what extent the motor system can influence vision without the direct confounding factor of viewing one's own actions, and how new movements are learned, are questions which have only been partly investigated. In this thesis, these questions are investigated more closely. First, the main topics are introduced in part I. A review on previous literature is given, providing the rationale for conducting Study I-III. At the end of the first part, the specific research questions and the methodology are delineated after which the general conclusions are discussed. In the second part, Study I-III are described into more detail. In the third and fourth part, a summary in German and in Dutch are given.

1.1 Theory of event coding (TEC)

The ideomotor principle, already described by Lotze (1852) and James (1890) posits that observing an action activates neuronal representations of the human motor system:

> "…every representation of a movement awakens in some degree the actual movement which is its object; and awakens it in a maximum degree whenever it is not kept from doing so by an antagonistic representation present simultaneously in the mind." (James 1890, Vol. 2, p. 526).

This influential idea has been taken up later to provide a basis for the common coding approach (Prinz 1997) and the theory of event coding (TEC) (Hommel, Müsseler, Ascherleben & Prinz 2001). These theories state that the final stages of perception and the initial stages of action control share a

common representational domain. Planned actions are thus represented in the same format as perceived events. Three core principles underlie the TEC. First, action and perception are coded in a common representational domain. Consequently, action effects can be induced by response- or action-contingent perceptual events. Second, perceived and produced events are represented as individual feature codes, instead of as a unitary entity. There is no special brain area for each specific action, but instead, fragments belonging to actions are coded in different cortical areas and need to be integrated upon action execution or action perception. Third, event features are distally coded. That is, features like exact size, object distance and location of the stimulus only need to match in a distal context where action is executed by the "peripheral" motor system (i.e., distal system). In the central system however (i.e., the proximal or 'common coding' system), these features do not need to match, as the central system only needs the representational features in order to plan actions and the peripheral system automatically matches these features to the given context. Figure 1 describes the structure of how sensory and motor systems interact in a common coding system according to the TEC. It shows us how two different sensory systems and two different motor systems interact. The two sensory systems can for example be vision (s_{1-3}) and audition (s_{4-6}), while the two motor systems could be driving eye movements (m_{1-3}) and driving hand movements (m_{4-6}) in order to act upon the stimulus. The information of the peripheral system enters the proximal system by the two sensory systems. This information is used to build feature codes. These could for example be the location (f_1) and pitch (f_2) of a tone. The auditory system can make up the pitch best, but also a bit of location (coded as s_4). The visual system can in turn make up location best, but also a little bit of pitch when for example, a violin is shown (coded as s_3). These feature codes are then used to send commands to the motor systems; for example to make a button press to decide whether it was a high- or a low-pitched tone, or to make an eye movement toward the location of the auditory stimulus. However, perception and action-planning can only interact if the codes refer to the same feature of a distal event (Hommel et al. 2001).

The TEC implies that changes in the visual system should lead to changes in the motor system, and vice versa (Schütz-Bosbach & Prinz 2007). Therefore, the motor system should be recruited in observing movements that it can execute. This idea is supported by the recent discovery of the mirror neuron system (MNS) (di Pellegrino, Fadiga, Fogassi, Gallese & Rizzolatti 1992; Gallese, Fadiga, Fogassi & Rizzolatti 1996; Rizzolatti, Fadiga, Gallese & Fogassi 1996) in the macaque. These neurons specifically fire during the observation *and* during the execution of the same action. This implies that the observed action is simulated by the monkeys' own motor system,
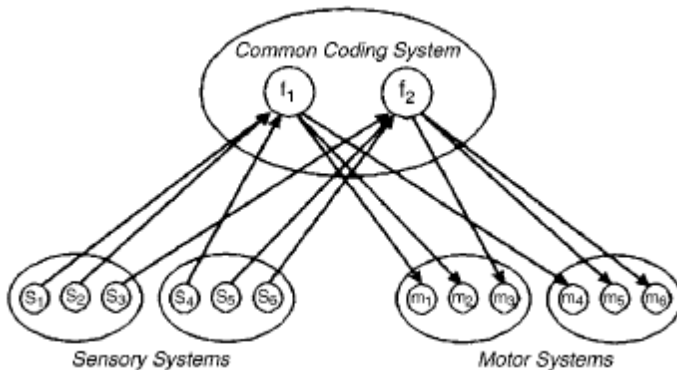
Figure 1. Feature coding according to TEC. Sensory information coming from two different sensory systems (s_1, s_2, s_3, and s_4, s_5, s_6) converges into two abstract feature codes (f_1 and f_2) in a common-coding system. These again spread their activation to codes belonging to two different motor systems (m_1, m_2, m_3, and m_4, m_5, m_6). Sensory and motor codes refer to proximal information, feature codes in the common-coding system refer to distal information. (Text has been modified. Source: Hommel et al. 2001, p. 862).

which may enhance action understanding and even the assessment of motor intentions of the perceived actor (Rizzolatti & Craighero 2004). Some studies have found indirect neurophysiological evidence that a MNS also exists in humans. For example, when expert dancers watched the movements belonging to their own dancing style, the brain areas associated with the human MNS (which mainly are: the ventral premotor area and the rostral part of the inferior parietal lobe) showed stronger activity as measured by functional magnetic resonance imaging (fMRI) than viewing a different dancing style (Calvo-Merino, Glaser, Grezes, Passingham & Haggard 2005). Of course, one may assume that these dancers also have more visual experience with their own dancing style. Therefore, a follow-up study was conducted in which gender-specific moves in ballet were viewed. The assumption here was that dancers would have equal visual experience with male as with female movements. Still, the human MNS resonated more strongly when observing the own, gender-specific moves (Calvo-Merino, Grezes, Glaser, Passingham & Haggard 2006). A problem with the design of these studies is that they still do not rule out whether any confounding factors played a role in these results, as there are too many variables during the course of acquiring such movement skills over life. To investigate the effects of motor skills on the effect of MNS resonance more directly, some studies have trained specific pre-defined movements. Before and after motor training, these movements were viewed while brain activity was measured using fMRI (Engel, Burke, Fiehler, Bien & Rösler 2008; Reithler, van Mier, Peters & Goebel 2007). These studies also found an enhanced activity in brain areas associated with the human MNS for trained movements compared to newly encountered movements. Consequently, the motor system is thought to play a key role in the observation of a movement by 'simulating' the seen action as if one would be executing it (Jeannerod 1994, 2001).

1.2. Action-to-Perception transfer

The previous section already pointed out that action and perception share a common representational domain and that both influence each other. More specifically, effects of perception on action can be called perception-to-action transfer, and effects of action on perception can be called action-to-perception transfer (Hecht, Vogt & Prinz 2001). This section discusses into more detail how action influences movement perception. To illustrate the interactions between perception and action and their consequences, figure 2 shows an example of social interaction between two people in which one individual observes the actions of the other. The action performed by the actor leads to motor resonance in the observer. It is thus as if the observer mentally simulates the action he or she sees. The action performed by the actor in turn, leads to perceptual resonance in the actor himself. This means that the actor builds a perceptual representation of the action he or she performs, which leads to an increased sensitivity to seeing this type of movement. Thus, seeing an action leads to recruitment of motor areas in order to understand and anticipate this action, and performing an action leads to perceptual sensitivity for this action and sensory feedback (Schütz-Bosbach & Prinz 2007).
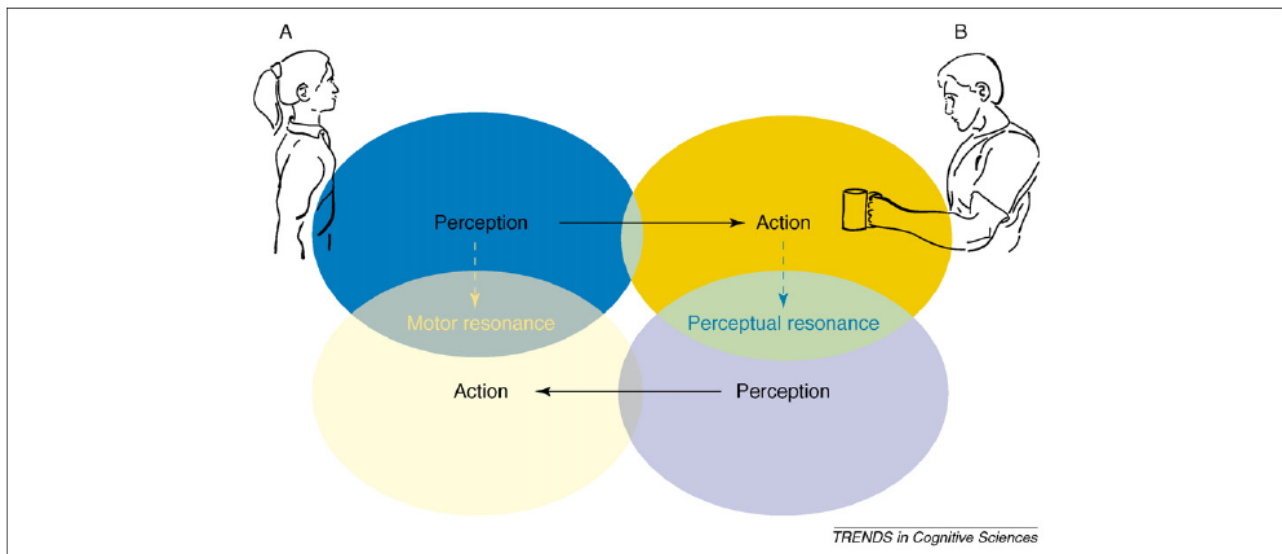

Figure 2. Motor and perceptual resonance. Modern theories which argue that observed actions are mapped onto a motoric representation of the same action in the perceiver (individual A, who perceives actions of individual B). Perceiving action can thus induce motor resonance and a disposition to execute what one observes. A common representation of action and perception, however, also suggests that action production will prime perception in the actor (individual B). Namely, his perceptual sensitivity is increased for those actions of other individuals that are similar to his own action (perceptual resonance). (Text has been modified. Source: Schütz-Bosbach & Prinz 2007).

Although there is a great body of research on the effects of perception on action, in for example, 'observational learning' (e.g. Hecht et al. 2001; Massen & Prinz 2007; McCullagh, Weiss & Ross 1989), research on how action influences perception is still scarce. This may be due to the difficulty in ruling out confounding factors by the immediate sensory consequences that follow from executing an action (Wolpert & Ghahramani 2000). Therefore, research on how action affects perception needs paradigms in which there has been no previous experience with the movement and in which the online visual feedback of one's own movement is ruled out. In the first study reporting direct effects of action on perception, participants were trained to execute cyclical hand movements while being blindfolded, before and after which visual perception ability was measured (Hecht et al. 2001). Training of this movement led to a perceptual improvement in seeing the same movement. The other previously described studies (Calvo-Merino et al. 2005, 2006; Engel et al. 2008; Reithler et al. 2007) also suggested such a direct influence of action on perception. However, these studies all base their training on movements which could either be explicitly memorized (e.g., cyclical movements or specific trajectories) or on movements which were trained over the course of life. To minimize confounding effects, it would be more ideal when any previous visual or motor experience can be ruled out. To assure this, learning to execute a-typical movements which do not intrinsically exist in the human motor system would provide an ideal methodology. Up until now, only one study has followed such an approach (Casile & Giese 2006). In their study, participants where blindfolded while they were trained to execute a gait pattern (moving the arms only) with a phase difference of 270°. In everyday life, humans only execute symmetric (0°) or asymmetric (180°) inter-limb oscillations. When a 270° phase shift pattern is executed, one limb always lies a quarter ahead of the other. Even though this pattern is not intrinsic to the human motor system, such a-typical phase shifts can be learned after extensive training (Zanone & Kelso 1992, 1997). Before and after motor training (Casile & Giese 2006), a visual test was performed in which moving point-light walkers in different phase-shifts were discriminated from each other. These point light walkers were divided into three groups and featured gait oscillations of 135°, 180°, or 270°, which were compared either with the same or slightly deviating movements. The task was to decide whether two consecutive movements were the same or different. Compared to before training, hit-rate improved in the trained movement (i.e., 270°), but not in the non-trained a-typical movement (i.e., 135°). Thus, when a 270° phase shift was shown and was compared with the same movement, percentage correct increased. In conclusion, this study provided the first evidence that training of an a-typical movement could bring about improvements in the visual perception of the same

movement.

Although Casile and Giese (2006) did pioneering work and presented interesting results, their methodology could have biased the results. First, training was not standardized. That is, participants were trained personally by an experimenter who gave verbal and haptic feedback, without any form of automation. Also, training duration and the number of movement cycles varied among participants, leading to differences in motor experience with the movement. Second, perhaps because of these problems, only two participants were actually able to produce a stable movement pattern after training. Third, only hit-rate was taken into consideration when analyzing the improvement in visual discrimination ability, leaving out the false alarm rates which could also have increased due to a simple shift in bias (Swets & Picket 1982; Macmillan & Creelman 2005). Fourth, a second training group should have been tested who were trained on the other 135° movement type, before a claim can be made that motor training results in a *specific* visual perception improvement of the trained movement type.

Study I will attempt to overcome these problems. It has a similar overall design, with a visual test at the beginning and at the end of the experiment, with motor training in between. Here, a different a-typical movement type is trained which allows highly standardized motor training, and the study consists of two training groups to investigate the specificity of action-to-perception transfer. Additionally, a control group is trained on a simple linear movement, not related to the visual stimulus. Finally, d-prime (d') is used to provide a more reliable indication of visual discrimination ability in which hit-rate is corrected for the false alarm rate (Swets & Picket 1982; Macmillan & Creelman 2005). In sum, Study I will provide a more reliable method for investigating action-to-perception transfer, also in the case of the specificity of this effect.

Besides the influence that motor expertise can have on visual perception of movements, action can also influence perception on-line. That is, action perception can be biased due to concurrent action execution (Müsseler 1999; Schütz-Bosbach & Prinz 2007). For example, the mere intention of grasping a bar with a certain orientation facilitates the detection of visual stimuli with the same orientation (Craighero, Fadiga, Rizzolatti & Umiltà 1999). Also, hand movements can facilitate the concurrent visual discrimination of congruent hand postures (Miall, Stanley, Todhunter, Levick, Lindo & Miall 2006). These studies however, show effects of action on the perception of objects which can be 'potentially' manipulated. That is, these objects may evoke a neural representation of how the object may be manipulated. To overcome this problem, a moving (structure from motion) rivalry stimulus provides an excellent opportunity. In rivalry, the stimulus is

always constant the stimulus information is ambiguous. Namely, two interpretations are equally likely, causing the perceptual interpretation of the stimulus to alter between these two possibilities, while only one interpretation can dominate at any given time (Blake & Logothetis 2002; Leopold & Logothetis 1999; Wohlschläger 2000). Figure 3 shows the well-known Necker cube (Necker 1832) which can be interpreted as having either the left vertical plane in front, or the right. Rivalry covers not only the visual system; it has also been observed for auditory (van Noorden 1975), olfactory (Zhou & Chen 2009), and tactile (Carter, Konkle, Wang, Hayward & Moore 2008) stimuli. Moreover, unambiguous information given into one modality can influence the perception of an ambiguous rivalry stimulus in the other. For example, Blake, Sobel and James (2004) showed that an unambiguous rotating tactile stimulus could bias the perception of a similar but ambiguous visual rivalry stimulus in the direction of the cutaneous input. Therefore, action should also have an influence on the perception of rivalrous stimuli.
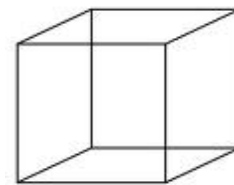

Figure 3. Necker cube. Either the left or the right vertical plane can be perceived to be in front (Necker 1832). Perception alters between these two equally likely interpretations over time. (Source: Wikipedia)

Two studies have investigated the immediate effects of action on the perceptual interpretation of rivalry stimuli. In Wohschläger (2000), rotating dots were presented which could be perceived as rotating clockwise or counterclockwise. During stimulus presentation, participants executed actions by turning a knob in specified directions. The perceptual interpretation of the stimulus was biased in the direction of the concurrently performed movement. The drawback of this study however, was that the stimulus was presented upon action initiation. Consequently, the action itself already influenced the visual stimulus, thereby confounding the true effects of action on perception. In a more recent study (Maruya, Yang & Blake 2007) binocular rivalry stimuli were presented in which one stimulus showed gratings and the other consisted of a cloud of moving dots. When actions were performed, the stimulus containing the moving cloud of dots was seen more often. However, in this study too, stimulus and action itself were tightly linked. Participants needed to be trained in order to execute these movements, and the velocity of the moving dots was driven by the actor's own movement velocity. Thus, more research is needed to rule out that these effects have been found due to the dependence of the visual stimulus on the executed action.

In Study II, a moving perceptual rivalry stimulus is presented in which stimulus presentation

is independent of action. Simultaneously, either no actions are performed; actions are performed which are not related to the stimulus; actions are performed which are related to the stimulus but not to the current perceptual interpretation; or actions are performed which are both related to the stimulus and also to the current perceptual interpretation (i.e., action is dependent on the stimulus interpretation). This study thus disentangles effects of action which are percept-related from actions which are independent from percept, and investigates whether the action should be percept-related before it can induce action-to-perception transfer.

1.3. The human motor system

This section will discuss how motor skills can be developed and how we interact with the world around us. It is also discussed how our motor system is subjected to certain constraints and how these constraints can affect motion perception but also whether we can violate these by learning a-typical movements. The motor system can be seen as a loop system where motor commands induce motor contractions, which generate sensory feedback due to changes in the muscles, tendons and joints, which in turn leads to changes in future motor commands (Wolpert & Ghahramani 2000). In this way, the motor system stays (unconsciously) up to date about body position and current movements, so that it can correct any deviations quickly (Wolpert et al. 2001). In order to act upon the environment appropriately, the sensory system and the motor system must interact. The central nervous system transforms sensory signals into motor signals, while the transformation from motor to sensory signals is done by the musculoskeletal system and sensory receptors (Wolpert & Ghahramani 2000). When the central nervous system decides to make a movement, it needs to represent the external world so that it can predict the consequences of the action. This is called an 'internal model' in which the central nervous system estimates the parameters of sensorimotor system in the environment (Wolpert & Ghahramani 2000; Wolpert, Ghahramani & Jordan 1995). Indeed, feedback from the outside world is delayed which is especially problematic in fast movements. Therefore, feed forward models are thought to predict the future position and velocity of for example, a tennis ball when playing tennis (Wolpert & Ghahramani 2000). Using this model, we can act upon moving objects before the exact end position is known.

Also in the case of motor learning, we are dependent upon feedback from the consequences of our actions. Here too, feedback models are not always effective, as the appropriate training signal, the motor command error, is not directly available (Wolpert & Ghahramani 2000). In Figure

4, a model is described which deals with this problem. First, a goal needs to be reached by learning an 'inverse model' that generates motor commands to reach a 'desired state'. Then, a 'feed forward' motor command is sent in order to reach this goal. Note that a *feed forward* model indicates the causal direction, in which for example, motor commands are mapped onto their sensory consequences, whereas an *inverse model* indicates the opposite direction in which the predicted sensory consequences are mapped onto motor commands in order to achieve these sensory consequences (Wolpert et al. 2001). Once the action is executed, the achieved goal (i.e., state) is
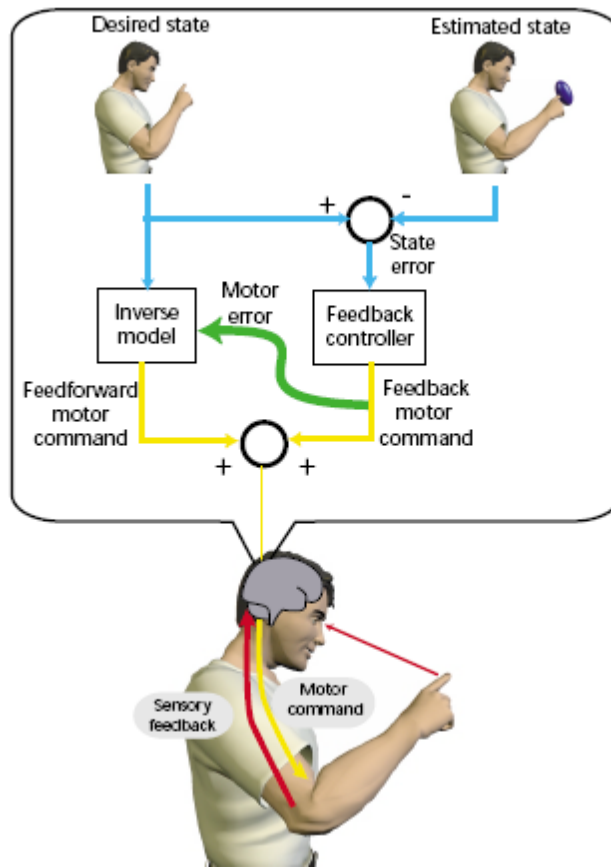

Figure 4. A schematic of feedback-error learning. The aim is to learn an inverse model that can generate motor commands given a series of desired states. A hard-wired and low-gain feedback controller is used to correct for errors between desired and estimated states. This generates a feedback motor command that is added to the feedforward motor command generated by the inverse model. If the feedback motor command goes to zero, then the state error, in general, will also be zero. Therefore, the feedback motor command is a measure of the error of the inverse model and is used as the error signal to train it. (Source: Wolpert & Ghahramani 2000).

estimated. Subtracting the desired state from the estimated state gives out a state error. Because the real feedback on the consequences of the motor command is too slow, this first passes a hard-wired (i.e., non-learned), feedback controller which computes a motor command based on the estimated

discrepancy between the desired and the estimated states. The feedback controller then corrects the estimated errors between desired and estimated states. This loop continues and should improve performance over time. This learning mechanism has been supported by neurophysiological evidence in the cerebellum for creating ocular responses in eye-movements (Shidara, Kawano, Gomi & Kawato 1993). A more detailed review of this mechanism is described in Wolpert & Ghahramani (2000).

The possible ways in which a movement can be executed are as good as infinite. Two movements are hardly ever the same. In spite of the huge amount of degrees of freedom, the motor system generally chooses prototypical movement paths with the least amount of noise (Wolpert & Ghahramani 2000). These types of movement paths have been explained by several optimal control models proposing that hand trajectories are executed with the highest degree of smoothness (Flash & Hogan 1985). Another highly influential optimal control model is the two-thirds power law (Lacquaniti, Terzuolo & Viviani 1983; Viviani, Baud-Bovy & Redolfi 1997; Viviani & Schneider 1991; Viviani & Stucchi 1992). The model describes the relation between curvature and velocity, and states that these are inversely related. That is, at points of high curvature, velocity is low, and vice versa. To describe this relation more clearly, figure 5 depicts a trajectory and its characteristics from a related model; the Isogony principle (Viviani & McCollum 1983; Viviani & Terzuolo 1982). When one wants to draw the trajectory illustrated in panel A without interruptions, drawing the top part takes about the same amount of time as drawing the bottom part of the trajectory. Panel C illustrates the position expressed in angle, which changes over time as the trajectory is drawn. The timeline shows that the top and the bottom part take up about the same amount of time even though the trajectory length differs. Consequently, velocity is low at the top part, where curvature is high, and vice versa. When the logarithm of the radius of curvature is plotted against the logarithm of the tangential velocity, the slope of the regression coefficient (1-β) is about $^1/_3$, which can be expressed by the formula V = K$R^{1-\beta}$ in which β lies around $^2/_3$ (Lacquaniti et al. 1983; Viviani et al. 1997; Viviani & Schneider 1991; Viviani & Stucchi 1992). Note that the radius of curvature is the inverse of curvature (1 / curvature).   Study I demonstrates this relation in more detail.

The two-thirds power law has also been observed to be effective in motion perception. When a dot traveling along an elliptic path was viewed, its velocity was only perceived to be uniform if the movement path and its velocity profile corresponded to the two-thirds power law (Viviani & Stucchi 1992). Any discrepancies between curvature and velocity resulted in the perception of a non-uniform velocity. In line with this finding, movement anticipation is highly influenced by the
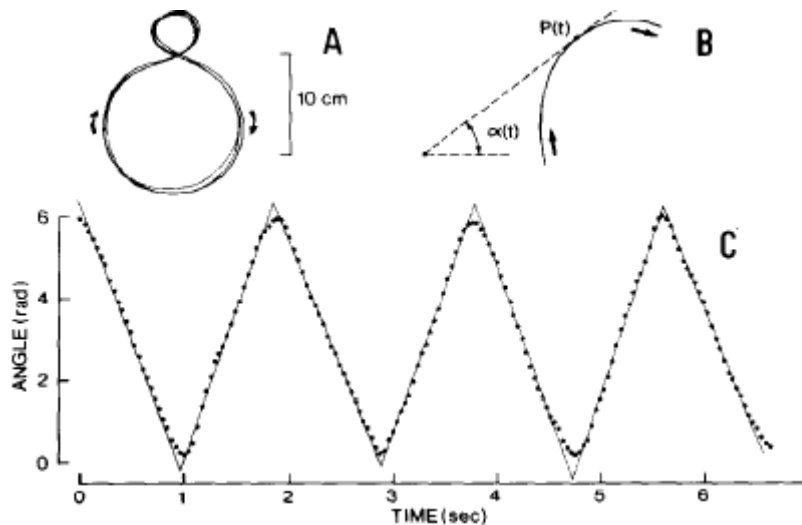
Figure 5. Isogony. The Isogony Principle is illustrated in a simple closed pattern (A). The principle states that, in drawing movements, equal angles are described in equal times. In panel C the time course of the angle α(*t*) is shown in which the tangent to the trajectory forms with an arbitrary reference (see panel B). A linear interpolation (continuous lines) fits quite accurately both the increasing and decreasing portions of the graph corresponding to the larger and smaller loop of the pattern, respectively. The average angular velocity in the two loops (slope of the corresponding graphs) differs by less than 20%. Thus, the time of execution of the loops tend to be independent of their size. Note that the example illustrated is somewhat extreme. In general, the extent to which the angular velocity is independent of the radius of curvature is a function of the coupling between the execution of the two parts of the pattern. (This text has been modified. Source: Lacquaniti, Terzuolo & Viviani 1983).

two-thirds power law (Flach, Knoblauch & Prinz 2004). A recent fMRI study has found a neural network which shows increased activity during the observation of movements obeying the two-thirds power law. The areas were located in left dorsal premotor, dorsolateral prefrontal and medial frontal cortex, suggesting that these regions compare the observed actions with the observers' own motor program (Casile, Dayan, Caggiano, Hendler, Flash & Giese 2010). In several experiments, attempts have been made to make people generate movements which violate the two-thirds power law. Yet, findings have indicated that it is impossible to reproduce predictable (Viviani and Mounoud 1990) and unpredictable (Viviani, Campadelli & Mounoud 1987) two-dimensional movements that violate the natural relation between curvature and velocity. In a later study (Viviani et al. 1997), passively presented movements that violated the two-thirds power law to the right hand could not be reproduced with the left hand. However, task conditions in these studies made it difficult for a real generation of movements deviating from the two-thirds power law. In the latter study for example, the real time reproduction done by the opposite hand could have imposed increased task difficulty. More importantly, these studies did not have a training phase in which one and the same movement could be remembered in order to form an internal representation of the movement. On the other hand, some studies have reported that deviations from the two-thirds power

law are possible in simple, slow, and harmonic movements (Wann, Nimmo-Smith & Wing 1988; Viviani & Flash 1995) and that other models like for example, the minimum jerk model and the 3D power law explain movement data consistently better (e.g., Maoz, Berthoz & Flash 2009; Viviani & Flash 1995). Thus, motor constraints seem to be more refined and not easily explained by a model. A more interesting question however is, what happens when we train one specific movement which violates the two-thirds power law consistently, so that a more solid internal representation of this movement can be built? Study I also addresses this question.

From the motor learning literature, there is evidence that other types of a-typical movements can be learned after intensive training. Natural inter-limb movements usually encompass symmetric or asymmetric patterns. That is, either two limbs oscillate in phase, with a phase shift of around 0° (e.g., during rowing), or they oscillate out-of-phase with a phase shift of around 180° (e.g., during walking). Producing other types of phase lags is usually not intrinsic, but they can be learned by intensive motor training (e.g., Debaere, Wenderoth, Sunaert, van Hecke & Swinnen 2004; Rémy, Wenderoth, Lipkens & Swinnen 2008; Zanone & Kelso 1992, 1997). In Zanone & Kelso (1992) for example, a phase shift of 90° between both hands was trained, in which one hand always lies a quarter phase ahead of the other. Training took five days in which participants were guided by a visual metronome which led to improvements in movement accuracy and movement stability (i.e., smaller within-trial standard deviation of phase shift). This type of motor constraint thus seems not to be fixed and referring back to the previous paragraph, it is the question whether this could be generalized to the two-thirds power law. Because Study I found that passively guided motor training leads to successful motor learning, the question arises whether passive and active training would lead to any differences in training success.

Usually humans move their limbs actively. During movement reproduction, an efference copy is thought to be sent back to the sensory system (which is also called reafference) so that the exact movement parameters can be estimated (Gallistel 1980; Robinson, Gordon & Gordon 1986). This efference copy can be useful in the acquisition of new movements as it provides an extra source of feedback. Whereas training these a-typical inter-limb phase shifts has only been done actively, there is no literature on whether this is also possible after passive training. For patients who need motor-rehabilitation for example due to stroke which caused paralysis however, the generation of active movements is not possible. For this group of people, passive motor training can provide enhanced outcomes in rehabilitation (Hesse, Schulte-Tigges, Konrad, Bardeleben & Werner 2003; Nelles Spiekermann, Jueptner, Leonhardt, Müller, Gerhard & Diener 1999). Although passive

movements can induce an improved outcome for patients, results are mixed about their exact value in comparison with active movements. On the one hand, active movements have been found to lead to superior performance in pointing tasks (Féry, Magnac & Israel 2004; Kaelin-Lang, Sawaki & Cohen 2005; Paillard and Brouchon 1968, 1974) while on the other hand, active and passive movements seem to rely on similar neural mechanisms as active movements (Gerardin, Sirigu, Lehericy, Poline, Gaymard, Marsault, Agid & Le Bihan 2000; Jeannerod and Decety 1995; Weiller, Juptner, Fellows, Rijntjes, Leonhardt, Kiebel, Muller, Diener & Thilmann 1996) and affect behavior in pointing tasks (Chokron, Colliot, Atzeni, Bartolomeo & Ohlmann 2004) just as well as active movements. Passively guided eye movements can even produce similar reductions in perceived motion smear as actively executed saccades (Tong, Stevenson & Bedell 2008). Investigating the role of passive motor training in the acquisition of novel movement skills can provide more insight in the exact differences between active and passive movements.

Surprisingly, apart from Study I, the effect of passively guided training has rarely been investigated in the acquisition of new movement patterns. Therefore, Study III provides a methodological design in which active and passively guided training can be directly compared in the acquisition of a bimanual coordination skill in which both hands are moved with a phase shift of 90°. As visual information is another feedback source, visual information was occluded to avoid any confounding effects in investigating passive versus active training. The exclusion of visual feedback however, does lead to a general decrease in performance (Swinnen, Lee, Verschueren, Serrien & Bogaerds 1997). For this study, a device has been built which could apply rotational movements to both hands either passively or actively. This allows testing two training groups in very similar settings, and allows participants to actively reproduce their movements on the same device in order to assess training success over days.

2. Overview

The two main issues that are addressed in this thesis are the effects of action on visual perception and the issue of motor learning. The following questions are addressed in this thesis:

1. Does successful learning of a novel movement type lead to improvements in the visual perception of the same and of related movements?

2. How does online action influence perception? Do the stimulus and the action need to be related as a prerequisite for action to be able to influence perception?

3. Can passive motor training lead to successful motor learning and how successful is it compared to active motor training in the acquisition of a novel movement skill?

In Study I, the question whether learning an a-typical movement in which the two-thirds power law is violated can influence the visual perception of the same and related movements, is addressed. Furthermore, the progress in learning such a movement is investigated. In order to address this question, an experiment is conducted consisting of a motor training phase and a visual discrimination test before and after motor training, in which participants are blindfolded to prevent any visual feedback to confound the results. First, training success of the learned movements is assessed, after which the influence of motor learning on visual perception is tested by comparing visual discrimination ability after training with the discrimination ability before training separately for each group. One group is trained to produce a movement with a weak violation of the two-thirds power law; a different group is trained to produce a movement with a strong violation of the two-thirds power law. This is the first study to report this type of motor training in the investigation on the effects of action on perception. Moreover, it tries to overcome flaws of other studies described earlier in section 1.2. Here, training is standardized and consists of an equal amount of training cycles across participants. Second, two training groups are tested, to provide a double dissociation in the case of action-to-perception transfer to assess whether learning a movement results in visual discrimination improvements *specific* to the learned movement. Finally, the discrimination index d' is reported as a measure for discrimination ability, thus correcting for any changes in response bias. In sum, this study provides more reliable evidence on the effects of motor learning on visual perception of the same and related stimuli using a new type of motor training.

In Study II, the question is addressed whether in online action-to-perception transfer, the action needs to be dependent on the current perceptual representation. As described in section 1.2, action-to-perception transfer not only occurs due to motor learning, but action also influences perception online. That is, the interpretation of visual information may be biased in the direction in which a concurrent movement is performed. In previous studies (Maruya et al. 2007; Wohlschläger 2000), the stimulus presentation depended on the executed action, which already produces effects of action on perception. In Study II, the stimulus presentation is always independent of the executed

action, but either the action is not related to the stimulus; is related to the stimulus but not to the current perceptual representation; or is related to both the stimulus and the perceptual representation. A structure from motion perceptual rivalry stimulus in the form of a cylinder is viewed which can be perceived as rotating clockwise or counterclockwise. For the first time, the effect of action is disentangled between where the action is relevant or not relevant to the current perceptual state. In this way, confounds in which the stimulus depends upon participants' action are overcome in order to compare the effects of stimulus-irrelevant versus stimulus-relevant action on visual perception.

In Study III, the question whether passively guided motor training leads to the same degree of motor learning as active motor training is addressed. Whereas Study I found that passive motor training could lead to successful motor learning, a direct comparison between active and passively presented movements in the acquisition of a new motor skill is still lacking. To allow for such a direct comparison, the acquisition of a new bimanual coordination skill is investigated, using an apparatus which can apply movements passively and actively under the same conditions. Participants in two training groups (passively guided vs. active) and a group which does not receive training, attempt to produce movements in which the two hands rotate with a phase-shift of 90°. Directly after training, the learned movement is actively reproduced to assess accuracy and movement stability. The group with no training only actively 'reproduces' this movement type. The learning curves between groups are compared over four consecutive days.

2.1. Study I

Beets I.A.M., Rösler F. and Fiehler K. (accepted for publication). **Non-visual motor learning improves visual motion perception: Evidence from violating the two-thirds power law.** *Journal of Neurophysiology*

In Study I, the direct effect of motor learning of a new movement type on the visual perception of the same and related movements is investigated. The experiment consisted of a visual discrimination test performed directly before and after motor training. Each trial of the visual test consisted of two consecutive movements which needed to be compared with each other. The movement was illustrated by a white dot on a black screen. The movements could either be the same (50% of trials) or different. Visual stimuli belonged to three categories (i.e., prototypes). One

prototype featured a natural movement, in which the geometry of the trajectory was circular and the velocity was constant. Thus, geometry (i.e., curvature) and velocity matched and obeyed the two-thirds power law. The geometry of the trajectory of the second prototype was also circular but the velocity profile belonged to a weakly elongated vertical ellipse, in which the velocity was relatively fast at the sides of the trajectory and relatively slow at the top and bottom of the circular trajectory. Thus, curvature and velocity did not match, and therefore there was a weak violation of the two-thirds power law. The geometry of the trajectory of the third prototype was also circular but the velocity profile belonged to an extremely elongated vertical ellipse, in which the velocity was very fast at the sides of the trajectory and very slow at the top and bottom of the circular trajectory. Thus, curvature and velocity formed a strong mismatch, and therefore the two-thirds power law was strongly violated.

In half of trials, the one of the three prototypes was compared with itself (i.e., same trial); in the other half, the comparison stimulus featured a slightly stronger or a slightly weaker violation of the two-thirds power law (i.e., the velocity profile belonged to a slightly more or a slightly less elongated ellipse than the prototype itself). Participants indicated their subjective perception of whether the movements were the same or different by using the keyboard. The data could be divided into cases where movements were the same in which the response could be correct (i.e., hit) or incorrect (i.e., miss) and into cases where movements were different in which the response could be correct (i.e., correct rejection) or incorrect (i.e., false alarm). The signal detection theory (e.g., MacMillan & Creelman 2005; Swets & Picket 1982) takes the standardized (z-) value of the proportion of hits minus the standardized value of the proportion of false alarms (d'). This is necessary because an increase in hit-rate does not provide any information whether false alarms also increased due to a shift in response bias (MacMillan & Creelman 2005; Swets & Picket 1982). This provides an optimal measure of discrimination ability independent of participants' own bias. Thus, this measure was used to determine discrimination ability over different grades of two-thirds power law violation, comparing between visual pre- and post-test.

During motor training, a programmable manipulandum passively guided the participants' arm in order to learn a new movement type. Participants were blindfolded during any presentation or reproduction of movement to avoid visual experience with the trained movement. One group was trained to execute a movement trajectory with a circular geometry and a velocity profile belonging to a weakly elongated vertical ellipse (i.e., identical to the second visual test prototype). The other group was trained to execute a circular movement with a velocity profile belonging to an extremely

elongated vertical ellipse (i.e., identical to the third visual test prototype). After each training session (2 times 80 movement cycles), the trained movement was actively reproduced and recorded (2 times 15 movement cycles) by an ultrasound device to assess training success. For reproduction, a cuboid device (similar to the training manipulandum) was freely moved on a horizontal plane on which a sensor was placed for recording by the ultrasound system. The system recorded sensor positions every 20 ms. Motor training lasted four days so that improvements in acquiring this new motor skill could be assessed. After motor training, the same visual discrimination test as before training was performed. Improvements in visual discrimination ability were assessed per prototype to see whether visual discrimination improvement would be selective to the learned movement or whether it would also transfer to the non-trained but related prototype.

The results show that motor training brought about learning effects. Circular trajectory was kept constant, while the velocity profile grew more elliptic over sessions in the extreme elliptic training group. In the weak elliptic training group, the velocity profile did not grow significantly more elliptic over sessions, and a subset of participants was not able to identify and reproduce the elliptic velocity profile. In both training groups, the slope of the regression coefficient between the radius of curvature and tangential velocity deviated from the naturally found $\frac{1}{3}$. Visual discrimination ability in both groups improved for the learned prototype but also for the non-learned but related, elliptic prototype. Discrimination ability of the non-elliptic prototype did not improve. Participants who did not learn the new movement (in the weak elliptic training group) and a control group of participants who were trained on an unrelated (i.e., linear) movement, did not show any visual discrimination changes after motor training. In sum, these results provide evidence for a direct effect of motor learning on visual perception. However, motor expertise does not lead to visual discrimination improvements specific to the learned movement, but can probably be recruited to perceive related movements with an elliptic velocity profile.

2.2. Study II

Beets I.A.M., 't Hart B.M., Rösler F., Henriques D.Y.P., Einhäuser W. and Fiehler K. (under review). **Online action-to-perception transfer: only percept-dependent action affects perception.** *Vision Research*

In Study II, an experiment was conducted in which participants viewed a structure-from-motion

stimulus in the shape of a vertically oriented cylinder which consisted of moving white dots on a black screen. Because the velocities were sinusoidal (i.e., maximum velocity in the center of the stimulus and minimum velocity at the edges of the stimulus), and the amount of left and rightward movements was 50/50, the stimulus was fully ambiguous. Thus, the cylinder could be perceived to be rotating clockwise or counterclockwise. The experiment consisted of several blocks in which this cylinder was viewed. Stimulus presentation was always independent of participant's action under all task conditions. In the 'no movement' condition, participants merely reported the subjective rotation direction (i.e., perceptual interpretation) by key presses. In other conditions, actions were performed during the viewing of the stimulus. The movements were also recorded using an ultrasound device, which recorded the position of an electrode placed on the manipulandum or stylus every 10 ms. The performed movements were always occluded so that participants had no visual information of the self-produced action. First, there was a condition in which vertical movements, which were not related to moving direction of the stimulus, were performed. For these actions, a stylus was used which was moved up and down along the cardboard tunnel through which participants viewed the stimulus. Then, there was a condition in which pre-defined movements which were related to the stimulus were performed. These movements were performed using a manipulandum which could be either clockwise or counterclockwise. Movement direction did not change within one block. While performing these actions (vertical, clockwise or counterclockwise), the current percept was reported using the keyboard. Finally, there were conditions in which movements were related to the stimulus *and* the current perceptual state. Here, participants reported their current perceptual state using the manipulandum. They moved either congruently or incongruently with their current percept. Percept durations (i.e., dominance durations) were extracted from keyboard and movement data (depending on condition) of each participant. To verify that participants could veridically report their percept, we also presented an unambiguous stimulus which had a bar drawn over it, which participants had to track by moving the manipulandum congruently or incongruently.

The results indicate that dominance durations of perceptual interpretation are the same for all conditions in which no action, an unrelated, or a related pre-defined action is performed. However, when the action becomes dependent upon the current perceptual state, the findings are different. When movements incongruent with the current percept are performed, the dominance durations are significantly shorter than in congruent movements. Thus, percept destabilizes as a function of moving incongruently with perceptual state, but only when the action is related to the current percept. Movement data from tracking the red bar of the unambiguous stimulus indicate a

high accuracy for both congruent and incongruent tracking. The movement data in conditions where current perceptual state was reported were investigated around the transition points (i.e., when the participant changed direction). No differences were found when the congruent and the incongruent condition were compared with each other, nor when a switch from clockwise to counterclockwise and vice versa was compared. Thus, the effects that moving incongruently leads to shorter dominance durations cannot be explained by differences in movement characteristics. The results strongly indicate that action can only affect visual perception when the action is percept-dependent. In the case of rivalry, actions in which the visual stimulus is not relevant cannot induce action-to-perception transfer.

2.3. Study III

Beets I.A.M., Rösler F. and Fiehler K. (submitted for publication). **Acquisition of a bimanual coordination skill after active and passively guided motor training.** *Experimental Brain Research*

In Study III, an experiment is performed which directly compares passively guided training with active training in the acquisition of an a-typical bimanual coordination skill, controlling the effects by a group which does not receive any training. The procedure took four days in which accuracy and movement stability were compared between groups. During motor training, participants were blindfolded to avoid visual feedback to confound the effects between active and passively guided training. A device was built which could apply passive and active movements under identical conditions, and the same device movements could be used to actively reproduce the trained movement. The device consisted of two turntables which could be coupled with each other. In that way, the phase shift between both would stay constant. During training, the turntables were locked within a phase-shift of 90° and were both rotated clockwise, so that participants could be trained to execute this a-typical movement pattern. During active training, the turntables were actively rotated by the participant. During passively guided training, a motor was attached to the turntables which rotated the turntables so that the same movement type, in which the turntables rotated with a phase-shift of 90°, was presented. Following training, the learned movement was actively reproduced in which the two turntables were decoupled from each other and from the driving motor. Movements were recorded during this phase using an ultrasound device measuring the position of the two

electrodes attached to the vertical handles of the turntables every 10 ms. A metronome was used at a frequency of 1.25 Hz to indicate the pace in all phases of the experiment. Before the first training session started, a baseline measurement was taken in which participants were instructed to perform this movement as accurately as possible, to rule out pre-training differences between groups. The group who did not receive training underwent the same procedure as the others; they only skipped the training phase. Participants in each group were unaware that there were groups receiving other types of training. In the no training group it was generally believed that a new movement was learned, as they were not aware that training was not present and thought that reproduction was training in itself.

As dependent measures, position of both sensors was coded into angles of which the phase-shift could be calculated. The accuracy was measured by taking the root mean squared error of the target relative phase (90°), and movement stability was calculated by taking the standard deviation of relative phase-shift within each trial. Thus, lower scores indicated more accurate and more stable performance, respectively. The results indicate that active training leads to a higher overall accuracy than passively guided training. Over days, accuracy increases in the passively guided training group. While accuracy in the passively guided training group is not different from the group who did not receive training during the first three sessions, accuracy improves to such an extent that it is different from the no training group and comparable to accuracy in the active group during the fourth session. While variability decreases significantly in all groups, and no overall difference between groups is found, the improvement is much larger in the active and passively guided group. Effect size of stability increase was comparable between the active and passively guided group.

2.4. General conclusions

In this thesis, two main topics stand central: the effects of action on visual perception and motor learning of a-typical movements. Here, the general and most important conclusions of the three studies are discussed. For a more detailed discussion, see the experimental studies in part II of this thesis.

In the discussed studies, some new effects of action on perception are found. In line with previous literature (e.g., Casile & Giese 2006; Engel et al. 2007; Hecht et al. 2001; Reithler et al. 2007), successful motor learning has resulted in improved perception of the same movement. When the movement was not successfully acquired, no improvement in visual perception occurred. Another group which was trained on an unrelated, linear movement did not improve on visual perception either,

ruling out any possible motivational factors or effects due to the training procedure in itself. Although most studies (e.g., Casile & Giese 2006; Reithler et al. 2007) claim that action-to-perception transfer is specific to the learned movement, this study indicates that motor expertise in one movement may generalize to related movements. The reason for this could well be that the qualitative movement type was similar in all elliptic velocity profiles, and that only the quantitative strength of two-thirds power violation was different. The fact that visual perception did not change in the non-elliptical movement indicates that this generalization holds for movements with vertical elliptic velocity profiles only. Further research on different types of constraint violation should investigate whether this effect can be generalized.

Another new finding in the case of action-to-perception transfer was that online action could only influence perception when the stimulus was relevant to the action. Actions that were executed in a pre-defined direction were probably cognitively separated from the visual stimulus presentation, even when actions were related to the stimulus (when rotational clockwise or counterclockwise movements were executed). Perception and action-planning can only interact if the codes refer to the same feature of a distal event (Hommel et al. 2001). Because the action could be cognitively separated from the visual stimulus, the feature codes were probably not shared, which is probably why the action did not act upon the stimulus representation in pre-defined movements. Although this seems to contradict previous studies who found an effect of pre-defined actions on the stimulus representation (Maruya et al. 2007; Wohlschläger et al. 2000), these studies have not completely separated the stimulus representation from the performed action. The stimulus presentation in these previous studies was always dependent upon action initiation and in Maruya et al. (2007) the velocity of the visual stimulus was driven by the self-produced actions. Therefore, action already had an effect on the visual stimulus, which is a confounding factor when one is interested in the effects of action on perception. Instead, when actions were dependent on the current perceptual interpretation, the stimulus and the action could not be separated from each other. Only when this is the case, the action is able to exert an influence on the perceptual interpretation. That is, when the current percept is indicated by incongruent movements, perceptual durations are significantly shorter than when the current percept is indicated by congruent movements. Thus, the percept is destabilized when actions are incongruent with vision, which indicates that the perceptual interpretation favors the direction in which the action is executed. Study II has cleared the confounding factors of immediate effects of action on perception by for example initiating or driving a certain stimulus by participants' own action, and thus provides a clear distinction as to what happens when an action and the stimulus are coupled and when these are independent and

irrelevant to each other. In conclusion, action can only induce action-to-perception transfer when the stimulus representation drives the action. When the task does not require an active coupling between action and perception, no such transfer seems to occur. These effects could not be explained by differences in movement characteristics.

In the case of motor learning, it has been found that it is possible to learn a-typical movement patterns which did not belong to the motor repertoire beforehand. First, the two-thirds power law, which is an important movement constraint, can be violated by learning simple movements following a circular trajectory but featuring an elliptic velocity profile. Although the slope was different from the natural $\frac{1}{3}$, it was not different from slopes found in other studies in which simple, elliptic movements were executed (Viviani & Flash 1995; Wann et al. 1988). It may thus well be that these data can be explained more precisely by other models stressing smoothness of trajectories (Gribble and Ostry 1996; Harris and Wolpert 1998; Maoz, Berthoz & Flash 2009; Schaal and Sternad 2001; Todorov and Jordan 1998), and that a non-parsimonious outcome may be possible when the system has been able to deal with the increased noise resulting from the non-smooth trajectory (Wolpert & Ghahramani 2000). The movement characteristics as measured by circular geometry and elliptic velocity profile changed over sessions. While the geometry of the trajectory stayed equally circular, the velocity profile became more elliptic over sessions in a group in which the extreme elliptic velocity profile was trained. In the group which was trained on the weak elliptic velocity profile, the change in velocity profile over sessions was not significant. This could be due to the smaller room for improvement and also because of difficulties in estimating the exact ratio between maximum and minimum velocity (i.e., the velocity profile was much more ambiguous than the one of the extreme elliptic velocity profile). Future research is needed to investigate whether training can lead to violations of the two-thirds power law in different movement types.

Second, learning effects are brought about by training a bimanual coordination skill in which both hands are moved with a phase-shift of 90°. In both Study I and Study III, passive training has led to successful learning. However, in the second study, where active and passively guided motor training are directly compared, active training is found to be superior. Nevertheless, the learning effects seemed to be relatively large in the first study, which could be due to a slower movement for which only one hand was needed, and the concept of the movement was probably clearer to build. Thus, training success of passively guided motor training seems to be different for different movement types. In line with the literature, active movements are superior to passively guided movements (Féry et al. 2004; Kaelin-Lang et al. 2005; Paillard & Brouchon 1968, 1974) in the acquisition of a new bimanual

coordination skill. However, whereas passively guided training leads to improvements in accuracy, no training does not. Moreover, the increase in movement stability over days, and accuracy on the fourth day, are comparable to the active group. This again is in line with other studies which found equal effects of passive movements on behavior compared to active movements (Chokron et al. 2004; Jones, Cressman & Henriques in press; Tong et al. 2008). Passive and active movements may be grounded on similar neural mechanisms which are mainly sensitive to afferent information (Weiller et al. 1996). Passively guided movements may thus have given rise to building an internal model increasing the vividness of motor imagination during training which leads to brain activity which overlaps to a great deal with active execution of movements (Gerardin et al. 2000; Jeannerod & Decety 1995). The data indicate that the consolidation process is slower in passively guided training than in active training. Passive training may therefore continue to bring about further improvements when training is done over an extended period of time. However, the fact that passively guided training leads to the same outcome as active movements verifies that passive training may be a useful tool in motor-rehabilitation. Although electromyographic (EMG) activity has probably not played a role in passively guided motor training (due to the big overall difference in active and passively guided training in the first three sessions), it should be controlled for in future studies. In sum, this thesis has resulted in the following conclusions:

1. Successful learning of a novel movement type leads to an improvement in the visual perception of the same and of related movements.

2. It is possible to produce movements with deviations from the typical two-third power law relation.

3. Online action-to-perception transfer is possible, but only when the action is dependent on the current perceptual interpretation of the visual stimulus.

4. Passive motor training can lead to successful motor learning, but active motor training leads to faster improvements in the acquisition of a new bimanual coordination skill.

3. References

Beets I.A.M., 't Hart B.M., Rösler F., Henriques D.Y.P., Einhäuser W. and Fiehler K. (under review). Online action-to-perception transfer: only percept-dependent action affects perception. *Vision Research*

Beets I.A.M., Rösler F. and Fiehler K. (accepted for publication). Non-visual motor learning improves visual motion perception: Evidence from violating the two-thirds power law. *Journal of Neurophysiology*

Beets I.A.M., Rösler, F. and Fiehler K. (submitted for publication). Acquisition of a bimanual coordination skill after active and passively guided motor training. *Experimental Brain Research*

Blake R. and Logothetis N.K. (2002). Visual competition. *Nature Reviews Neuroscience, 3:* 13-21.

Blake R., Sobel K.V. and James T.W. (2004). Neural synergy between kinetic vision and touch. *Psychological Science, 15:* 397-402.

Calvo-Merino B., Glaser D.E., Grezes J., Passingham R.E. and Haggard P. (2005). Action observation and acquired motor skills: an FMRI study with expert dancers. *Cerebral Cortex, 15:* 1243-1249.

Calvo-Merino B., Grezes. J, Glaser D.E., Passingham R.E. and Haggard P. (2006). Seeing or doing? Influence of visual and motor familiarity in action observation. *Current Biology, 16:* 1905-1910.

Carter O., Konkle T., Wang Q., Hayward V. and Moore C. (2008). Tactile rivalry demonstrated with an ambiguous apparent-motion quartet. *Current Biology, 18:* 1050-1054.

Casile A., Dayan E., Caggiano V., Hendler T., Flash T. and Giese M.A. (2010). Neuronal encoding of human kinematic invariants during action observation. *Cerebral Cortex, 20:* 1647-1655.

Casile A. and Giese M.A. (2006). Nonvisual motor training influences biological motion perception. *Current Biology, 16:* 69-74.

Chokron S., Colliot P., Atzeni T., Bartolomeo P. and Ohlmann T. (2004). Active versus passive proprioceptive straight-ahead pointing in normal subjects. *Brain Cognition, 55:* 290-294.

Craighero L., Fadiga L., Rizzolatti G. and Umiltà, C. (1999). Action for perception: a motor-visual attentional effect. *Journal of Experimental Psychology: Human Perception and Performance, 25:* 1673-1692.

Debaere F., Wenderoth N., Sunaert S., Van Hecke P. and Swinnen S.P. (2004). Changes in brain activation during the acquisition of a new bimanual coodination task. *Neuropsychologia, 42:* 855-867.

di Pellegrino G., Fadiga L., Fogassi L., Gallese V. and Rizzolatti G. (1992). Understanding motor events: a neurophysiological study. *Experimental Brain Research, 91:* 176-180.

Engel A., Burke M., Fiehler K., Bien S. and Rösler F. (2008). Motor learning affects visual movement perception. *European Journal of Neuroscience, 27:* 2294-2302.

Féry Y.A., Magnac R. and Israel I. (2004). Commanding the direction of passive whole-body rotations facilitates egocentric spatial updating. *Cognition, 91:* B1-10.

Flach R. Knoblich, G. and Prinz W. (2004). The two-thirds power law in motion perception: when do motor anticipations come into play? *Visual Cognition, 11:* 461-481.

Flash T. and Hogan N. (1985). The coordination of arm movements: an experimentally confirmed mathematical model. *Journal of Neuroscience, 5:* 1688-1703.

Gallese V., Fadiga L., Fogassi L. and Rizzolatti G. (1996). Action recognition in the premotor cortex. *Brain, 119* (Pt 2): 593-609.

Gallistel C. (1980). *The Organization of Action: A New Synthesis.* Erlbaum, Hillsdale, New Jersey.

Gerardin E., Sirigu A., Lehericy S., Poline J.B., Gaymard B., Marsault C., Agid Y. and Le Bihan D. (2000). Partially overlapping neural networks for real and imagined hand movements. *Cerebral Cortex, 10:* 1093-1104.

Gribble P.L. and Ostry D.J. (1996). Origins of the power law relation between movement velocity and curvature: modeling the effects of muscle mechanics and limb dynamics. *Journal of Neurophysiology, 76:* 2853-2860.

Harris C.M. and Wolpert D.M. (1998). Signal-dependent noise determines motor planning. *Nature, 394:* 780-784.

Hecht H., Vogt S. and Prinz W. (2001). Motor learning enhances perceptual judgment: a case for action-perception transfer. *Psychological Research, 65:* 3-14.

Hesse S., Schulte-Tigges G., Konrad M., Bardeleben A. and Werner C. (2003). Robot-assisted arm trainer for the passive and active practice of bilateral forearm and wrist movements in hemiparetic subjects. *Archives of Physical Medicine and Rehabilitation, 84:* 915-920.

Hommel B., Müsseler J., Aschersleben G. and Prinz W. (2001). The Theory of Event Coding (TEC): a framework for perception and action planning. *Behavioral Brain Science, 24:* 849-878; discussion 878-937.

James W. (1890). *The principles of psychology.* New York: Holt.

Jeannerod M. (2001). Neural simulation of action: a unifying mechanism for motor cognition. *Neuroimage, 14:* 103-109.

Jeannerod M. (1994). The representing brain: Neural correlates of motor intention and imagery. *Behavioral Brain Science, 17:* 187-245.

Jeannerod M. and Decety J. (1995). Mental motor imagery: a window into the representational stages of action. *Current Opinion in Neurobiology, 5:* 727-732.

Jones A.H., Cressman E.K. and Henriques D.Y.P. (in press). Proprioceptive localization of the left and right hands. *Experimental Brain Research.*

Kaelin-Lang A., Sawaki L. and Cohen L.G. (2005). Role of voluntary drive in encoding an elementary motor memory. *Journal of Neurophysiology, 93:* 1099-1103.

Lacquaniti F., Terzuolo C. and Viviani P. (1983). The law relating the kinematic and figural aspects of drawing movements. *Acta Psychologica, 54:* 115-130.

Leopold D.A. and Logothetis N.K. (1999). Multistable phenomena: changing views in perception. *Trends in Cognitive*

Sciences, 3: 254-264.

Lotze R.H. (1852). *Medicinische Psychologie oder Physiologie der Seele.* Weidmann.

Macmillan N. and Creelman C. (2005). *Detection Theory: A user's Guide.* Lawrence Erlbaum Associates, Inc., Mahwah, New Jersey.

Maoz U., Berthoz A. and Flash T. (2009). Complex unconstrained three-dimensional hand movement and constant equi-affine speed. *Journal of Neurophysiology, 101:* 1002-1015.

Maruya K., Yang E. and Blake R. (2007). Voluntary action influences visual competition. *Psychological Science, 18:* 1090-1098.

Massen C. and Prinz W. (2007). Activation of action rules in action observation. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 33:* 1118-1130.

McCullagh P., Weiss M.R. and Ross D. (1989). Modeling considerations in motor skill acquisition and performance: an integrated approach. *Exercise and Sport Sciences Reviews, 17:* 475-513.

Miall R.C., Stanley J., Todhunter S., Levick C., Lindo S. and Miall J.D. (2006). Performing hand actions assists the visual discrimination of similar hand postures. *Neuropsychologia, 44:* 966-976.

Müsseler J. (1999). How independent from action control is perception? An event-coding account for more equally-ranked crosstalks. In G. Ascherleben, T. Bachman and J. Müsseler (Eds.), *Cognitive contributions to the perception of spatial and temporal events* (pp. 121-147). Amsterdam: Elsevier.

Necker L. (1832). Observations on some remarkable optical phenomena seen in Switzerland, and on an optical phenomenon which occurs on viewing a figure of a crystal or geometrical solid. *London Edinburgh Philosophical Magazine and Journal of Science, 1*, 329-337.

Nelles G., Spiekermann G., Jueptner M., Leonhardt G., Müller S., Gerhard H. and Diener H.C. (1999). Reorganization of sensory and motor systems in hemiplegic stroke patients. A positron emission tomography study. *Stroke, 30:* 1510-1516.

Paillard J. and Brouchon M. (1968). *Active and passive movements in the calibration of position sense.* S.J. Freedman (ed), pp 37-55.

Paillard J. and Brouchon M. (1974). A proprioceptive contribution to the spatial encoding of position cues for ballistic movements. *Brain Research, 71:* 273-284.

Prinz W. (1997). Perception and action planning. *European journal of cognitive psychology, 9:* 129-154.

Reithler J., van Mier H.I., Peters J.C. and Goebel R. (2007). Nonvisual motor learning influences abstract action observation. *Current Biology, 17:* 1201-1207.

Rémy F., Wenderoth N., Lipkens K. and Swinnen S.P. (2008). Acquisition of a new bimanual coordination pattern modulates the cerebral activations elicited by an intrinsic pattern: an fMRI study. *Cortex, 44:* 482-493.

Rizzolatti G. and Craighero L. (2004). The mirror-neuron system. *Annual Review of Neuroscience, 27:* 169-192.

Rizzolatti G., Fadiga L., Gallese V. and Fogassi L. (1996). Premotor cortex and the recognition of motor actions. *Cognitive Brain Research, 3:* 131-141.

Robinson D.A., Gordon J.L. and Gordon S.E. (1986). A model of the smooth pursuit eye movement system. *Biological Cybernetics, 55:* 43-57.

Schaal S. and Sternad D. (2001). Origins and violations of the 2/3 power law in rhythmic three-dimensional arm movements. *Experimental Brain Research, 136:* 60-72.

Schütz-Bosbach S. and Prinz W. (2007). Perceptual resonance: action-induced modulation of perception. *Trends in Cognitive Sciences, 11:* 349-355.

Shidara M., Kawano K., Gomi H. and Kawato M. (1993). Inverse-dynamics model eye movement control by Purkinje cells in the cerebellum. *Nature, 365:* 50-52.

Swets J.A. and Pickett R.M. (1982). *Evaluation of diagnostic systems. Methods from signal detection theory.* Academic Press: Series in cognition and perception. New York.

Swinnen S.P., Lee T.D., Verschueren S., Serrien D.J. and Bogaerds H. (1997). Interlimb coordination: Learning and transfer under different feedback conditions. *Human Movement Science, 16:* 749-785.

Todorov E. and Jordan M.I. (1998). Smoothness maximization along a predefined path accurately predicts the speed profiles of complex arm movements. *Journal of Neurophysiology, 80:* 696-714.

Tong J., Stevenson S.B. and Bedell H.E. (2008). Signals of eye-muscle proprioception modulate perceived motion smear. *Journal of Vision, 8:* 7.1-6.

van Noorden L. (1975). *Temporal coherence in the perception of tone sequences.* Unpublished doctoral dissertation, Eindhoven University of Technology. Eindhoven, The Netherlands.

Viviani P., Baud-Bovy G. and Redolfi M. (1997). Perceiving and tracking kinesthetic stimuli: further evidence of motor-perceptual interactions. *Journal of Experimental Psychology: Human Perception and Performance, 23:* 1232-1252.

Viviani P. and Flash T. (1995). Minimum-jerk, two-thirds power law, and isochrony: converging approaches to movement planning. *Journal of Experimental Psychology: Human Perception and Performance, 21:* 32-53.

Viviani P. and McCollum G. (1983). The relation between linear extent and velocity in drawing movements. *Neuroscience, 10:* 211-218.

Viviani P. and Mounoud P. (1990). Perceptuomotor compatibility in pursuit tracking of two-dimensional movements. *Journal of Motor Behavior, 22:* 407-443.

Viviani P. and Schneider R. (1991). A developmental study of the relationship between geometry and kinematics in drawing movements. *Journal of Experimental Psychology: Human Perception and Performance, 17:* 198-218.

Viviani P. and Stucchi N. (1992). Biological movements look uniform: evidence of motor-perceptual interactions. *Journal of Experimental Psychology: Human Perception and Performance, 18:* 603-623.

Viviani P. and Terzuolo C. (1982). Trajectory determines movement dynamics. *Neuroscience, 7:* 431-437

Viviani P, Campadelli P and Mounoud P. (1987). Visuo-manual pursuit tracking of human two-dimensional movements. *Journal of Experimental Psychology: Human Perception and Performance, 13:* 62-78.

Wann J., Nimmo-Smith I. and Wing A.M. (1988). Relation between velocity and curvature in movement: equivalence and divergence between a power law and a minimum-jerk model. *Journal of Experimental Psychology: Human Perception and Performance, 14:* 622-637.

Weiller C., Juptner M., Fellows S., Rijntjes M., Leonhardt G., Kiebel S., Muller S., Diener H.C. and Thilmann A.F. (1996). Brain representation of active and passive movements. *Neuroimage, 4:* 105-110.

Wohlschläger A. (2000). Visual motion priming by invisible actions. *Vision Research, 40:* 925-930.

Wolpert D.M. and Ghahramani Z. (2000). Computational principles of movement neuroscience. *Nature Neuroscience, 3 Suppl:* 1212-1217.

Wolpert D.M., Ghahramani Z. and Flanagan J.R. (2001). Perspectives and problems in motor learning. *Trends in Cognitive Sciences, 5:* 487-494.

Wolpert D.M., Ghahramani Z. and Jordan M.I. (1995). An internal model for sensorimotor integration. *Science, 269:* 1880-1882.

Zanone P.G. and Kelso J.A. (1992). Evolution of behavioral attractors with learning: nonequilibrium phase transitions. *Journal of Experimental Psychology: Human Perception and Performance, 18:* 403-421.

Zanone P.G. and Kelso J.A. (1997). Coordination dynamics of learning and transfer: collective and component levels. *Journal of Experimental Psychology: Human Perception and Performance, 23:* 1454-1480.

Zhou W. and Chen D. (2009). Binaral rivalry between the nostrils and in the cortex. *Current Biology, 19:* 1561-1565.

II. Experimental part

Study I

Beets I.A.M., Rösler F. and Fiehler K. (accepted for publication). **Non-visual motor learning improves visual motion perception: Evidence from violating the two-thirds power law.** *Journal of Neurophysiology*

Study II

Beets I.A.M., 't Hart B.M., Rösler F., Henriques D.Y.P., Einhäuser W. and Fiehler K. (under review). **Online action-to-perception transfer: only percept-dependent action affects perception.** *Vision Research*

Study III

Beets I.A.M., Rösler F. and Fiehler K. (submitted for publication). **Acquisition of a bimanual coordination skill after active and passively guided motor training.** *Experimental Brain Research*

Study I

Beets I.A.M., Rösler F. and Fiehler K. (accepted for publication). **Non-visual motor learning improves visual motion perception: Evidence from violating the two-thirds power law.** *Journal of Neurophysiology*

Non-visual motor learning improves visual motion perception: Evidence from violating the two-thirds power law

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Running head: Motor learning improves visual motion perception

Abstract

Few studies have reported direct effects of motor learning on visual perception, especially when using novel movements for the motor system. A-typical motor behaviors that violate movement constraints provide an excellent opportunity to study action-to-perception transfer. In our study, we passively trained blindfolded participants on movements violating the two-thirds power law. Before and after motor training, participants performed a visual discrimination task, in which they decided whether two consecutive movements were same or different. For motor training, we randomly assigned the participants to two motor training groups or a control group. The motor training group experienced either a weak or a strong elliptic velocity profile on a circular trajectory which matched one of the visual test stimuli. The control group was presented with linear trajectories unrelated to the viewed movements. After each training session, participants actively reproduced the movement in order to assess motor learning. The group trained on the strong elliptic velocity profile reproduced movements with increasing elliptic velocity profiles while circular geometry remained constant. Furthermore, both training groups improved in visual discrimination ability for the learned movement as well as for highly similar movements. Participants in the control group, however, did not show any improvements in the visual discrimination task, nor did participants who did not acquire the trained movement. The present results provide evidence for a transfer from action to perception which generalizes to highly related movements and depends on the success of motor learning. Moreover, under specific conditions, it seems to be possible to acquire movements deviating from the two-thirds power law.

Introduction

Looking at other people performing an action can help one to acquire new motor skills, such as learning to perform a handstand, and even abstract skills like learning to work with a new computer program. However, can motor skills affect visual perception as well?

The common coding theory (Hommel et al. 2001; Prinz 1997) posits that the final stages of perception and the initial stages of action control share a common representational domain, where planned actions are represented in the same format as perceived events. The idea that perception affects action, including 'observational learning', has been supported by many studies (Hecht et al. 2001; for an overview see McCullagh et al. 1989). On the other hand, if perception and action share the same codes, it is predicted that changes in these codes due to motor learning, should lead to corresponding changes in perceptual skills (Hecht et al. 2001; Prinz 1997; for a review see Schütz-Bosbach and Prinz 2007). Only few studies have examined the effects of action on perception, probably due to problems in avoiding perceptual experience which immediately emerges from action performance (Wolpert and Ghahramani 2000).

The question whether action-to-perception transfer is possible, regained interest after the discovery of mirror neurons in monkeys which fire during the execution of an action but also during the mere observation of the same goal-directed action (di Pellegrino et al. 1992; Gallese et al. 1996). Indirect neurophysiological measures have supported the idea that such a mirror neuron system also exists in humans (for an overview see Rizzolatti et al. 2001). This suggests that the brain internally simulates an action during the observation of others' actions (Jeannerod 1994, 2001) which may yield action understanding (Gallese et al. 1996). An internal model, which merges motor and perceptual experience, is suggested to play a role in the anticipation of action effects (Wolpert and Ghahramani 2000; Wolpert et al. 1995; for an overview about biological movement perception see Giese and Poggio 2003). In summary, there is converging evidence that the motor system is involved in action perception. As a consequence, changes in the motor system should elicit changes in perception.

In recent years, some studies have already demonstrated a direct influence of action on perception. Hecht and colleagues (2001) showed effects of action-to-perception transfer using a timed movement task in which participants practiced cyclical movements while being blindfolded. Performance in a subsequent visual perception task was significantly enhanced for the trained movement. Using functional magnetic resonance imaging (fMRI), brain structures involved in motor-related processes have been observed to be active during the mere visual perception of movements

(Engel et al. 2008; Reithler et al. 2007). These brain areas were more active during the perception of trained than untrained movements suggesting a stronger resonance effect. Accordingly, expert dancers showed greater activity in premotor and parietal brain regions when they watched their own dance style compared to another dancing style (Calvo-Merino et al. 2005). To rule out that this effect was due to differences in visual experience, the authors conducted a follow-up study where they presented gender-specific ballet moves. In line with the previous results, enhanced activity was found when male and female ballet dancers viewed moves of their own motor repertoire (Calvo-Merino et al. 2006).

Further evidence for a tight link between action and perception comes from studies investigating motor constraints. Biological movements, i.e., movements humans are able to execute, are subjected to certain constraints. For example, curvature and velocity are inversely related, i.e., at points of low curvature, absolute velocity is high and vice versa. The two-thirds power law states that the instantaneous velocity V depends on the radius of the curvature R of the trajectory: $V = KR^{\beta}$ where K is a constant which depends on the tempo of the trajectory. The name of the two-thirds power law has been derived from the original literature in which the exponent was expressed as $1-\beta$ in which β lies around $^2/_3$. The value of exponent $1-\beta$ thus equals $^1/_3$ (Lacquaniti et al. 1983; Viviani et al. 1997; Viviani and Schneider 1991; Viviani and Stucchi 1992) and is here further referred to as β. This law has been shown to be effective in motion perception as well. The velocity of a dot travelling along an elliptic path was only perceived to be uniform if the movement path and its velocity profile obeyed the two-thirds power law (Viviani and Stucchi 1992). Movement anticipation also seems to rely greatly on the two-thirds power law (Flach et al. 2004). In line with these results, it was found that people are very sensitive to violations of the two-thirds power law (i.e., when velocity does not correspond with the curvature), and that even slight violations can be detected easily from natural movements (Bidet-Ildei et al. 2006). Moreover, it has been shown that motor-related brain areas (including primary motor cortex, premotor cortex, and supplementary motor areas) were much more active during movement perception in which the two-thirds power law was obeyed (Casile et al. 2010; Dayan et al. 2007), which supports the idea that the motor system resonates more strongly when movements which lay in our own motor repertoire, are perceived.

So far, most studies investigating action-to-perception transfer applied long-term skill learning with visual feedback (e.g. Calvo-Merino et al. 2005, 2006) or learning of specific movement trajectories under the use of explicit memory (e.g. Reithler et al. 2007). To rule out that visual experience of the movement or explicit motor learning mainly contribute to the transfer of action to perception, non-visual learning of an a-typical movement that does not belong to the person's motor

repertoire provides an excellent alternative. Casile and Giese (2006) followed this approach. They actively trained participants to execute a gait pattern in which their arms moved with an a-typical phase shift of 270°. During training, participants were blindfolded and received haptic and verbal feedback. There were four anchor points along which participants learned the relative positions of their hands. After motor training, visual recognition (i.e. hit-rate) of the learned movement was higher than before training. In this study, however, only 2 participants were able to learn the a-typical arm movement.

In the present study, we investigated action-to-perception transfer by applying a highly standardized passive motor training of hand movements violating the two-thirds power law. Thus, we presented a-typical movements which do not belong to the human motor repertoire. Blindfolded participants were trained on a fixed number of trials using a movement manipulandum. Such a passive motor training ensured a standardized training procedure without additional visual or verbal feedback. Motor training was executed over the course of four consecutive days on a movement exhibiting consistent properties. The trajectories were all circular and featured a velocity profile belonging to a vertical ellipse. Movements along a circle would normally be executed with a constant velocity due to constant curvature. Combining a circular geometry with an elliptic velocity pattern leads to an a-typical relationship of geometry and velocity. We repeatedly measured improvement in motor learning by a movement tracking system during active reproduction blocks. Before and after motor training, participants performed a visual discrimination task to assess whether learning of a specific movement skill improved visual perception. To test whether training effects on visual discrimination performance before and after training were due to learning of one specific novel movement; and not to motor training in general, a control group was tested who were trained to execute simple linear trajectories unrelated to the viewed movements of the visual discrimination task.

We demonstrate that successful learning of a novel movement improves visual discrimination ability of the learned movement as well as highly similar movements. In contrast to previous studies (Viviani 2002; Viviani et al. 1987; Viviani and Mounoud 1990), but similar to findings of Wann et al. (1988), the typical curvature-velocity relation as predicted by the two-thirds power law, seems to be altered after motor training.

Materials and Methods

Participants

Fifty-one healthy, right-handed participants took part in the experiment. Seven participants were excluded from further analyses because performance deviated more than 2 standard deviations from the norm in the visual pre-test or in any of the measured motor parameters (4 due to the visual pre-test; 2 due to motor performance; 1 due to both. Thus, the sample consisted of forty-four participants (9 male, 35 female) between the ages of 19 and 30 years (mean age, standard deviation: 22.8, ± 2.9 years). They performed the experiment over four consecutive days. All participants had normal or corrected-to-normal vision. Naïve participants were recruited from the Philipps-University Marburg, and were compensated with course-credits or money for their participation. The experiment was performed in accordance with the ethical standard laid down in the Declaration of Helsinki (2000).

Apparatus

A programmable movement manipulandum with two degrees of freedom (*x*- and *y*-plane) driven by two servo motors and controlled by LabVIEW (http://www.ni.com/labview) induced passive arm movements in the horizontal plane. The trajectory was circular, but the velocity varied over the trajectory according to the applied velocity profile. Participants sat facing the workspace and grasped the vertical handle of the motion device with a precision grip using their right thumb and index finger (Fig. 1*A*). A chin rest was used to keep body posture constant during each motor training session. The chair and chin rest were adjusted individually to assure a comfortable and stable position during motor training sessions.

As the movement manipulandum does not enable decoupling from the servo motors, its handle cannot be moved freely. Therefore, active movement reproduction was done in a separate room (due to space limitations) by sliding a smooth cuboid plastic device (width x length x height: 96mm x 65mm x 35mm) freely over a horizontal plane surface. The vertical handle on this device was comparable with that of the movement manipulandum. Movement trajectories were recorded with an ultrasound motion recording device (ZEBRIS CMS20, Zebris Medical GmbH, Isny im Allgäu, Germany). The data were sampled with 50Hz and analyzed offline. Participants were blindfolded during passive motor training and during the active movement reproduction blocks.
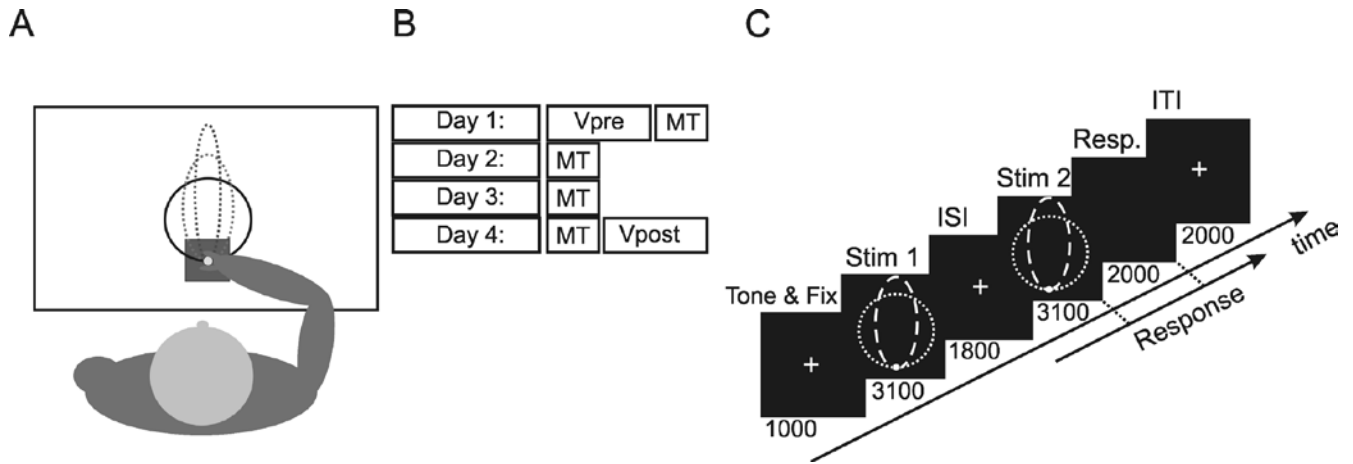
FIG. 1. Experimental protocol. A: Movement manipulandum by which participants were trained on a movement with a circular path (see solid line), but with a velocity profile of a weakly (light dotted) or an extremely (dark dotted) elongated ellipse. B: Experimental procedure over the 4 days. "V Pre" is visual pre-test; "V Post" is visual post-test; MT is motor training session (consisting of 2 passive training and 2 active reproduction blocks). C: Trial procedure for the visual discrimination task. ISI: inter-stimulus interval; ITI: inter-trial interval. During stimulus 2 and the response screen, participants could respond. Dotted lines in stimuli represent circular movement paths; striped lines represent the elliptic velocity profiles. The size of the icons here are arbitrary and do not correspond to real sizes in the experiment.

Procedure

Participants were randomly assigned to two experimental groups, or to the control group. One experimental group was trained on a trajectory with a circular geometry (geometric eccentricity, $\Sigma_g = 0$) with a velocity profile simulating an extremely elongated vertical ellipse (dynamic eccentricity, $\Sigma_d = -.92$). The other experimental group was trained on a trajectory with a circular geometry ($\Sigma_g = 0$) with a velocity profile simulating a weakly elongated vertical ellipse ($\Sigma_{d} = -.71$). In the following, we refer to the two experimental groups as *extreme elliptic condition* and *weak elliptic condition*. Twelve participants (2 male, 10 female; mean age, standard deviation: 24.3, 2.6 years), were allocated to the extreme elliptic condition and nineteen (3 male, 16 female; mean age, standard deviation: 23, 2.8) to the weak elliptic condition. Thirteen participants (4 male, 9 female) were assigned to the control group (mean age, standard deviation: 21.5 ± 2.6 years). They were passively trained on a linear movement along the body midline (*y*-plane) using the movement manipulandum.

The eccentricity parameter is conventionally applied in the movement literature (e.g. Viviani et al. 1997; Viviani and Stucchi 1989), and is used to describe the elongation of an ellipse. We distinguish here between geometric and dynamic eccentricity. The geometric eccentricity describes the shape of the trajectory. The dynamic eccentricity describes the velocity profile of the trajectory. In all of our

37

manipulations, the geometric eccentricity is set at 0 (for visual and passively presented movements). This means that each trajectory has a circular shape. The factor which is varied in our manipulations is the dynamic eccentricity, which was laid over these circular trajectories. The eccentricity, Σ, is defined as $\Sigma = [1 - (A_{xg} / A_{yg})^2]^{1/2}$, where A_{xg} and A_{yg} denote the horizontal and vertical axes of the ellipse, respectively. The *x-y* ratio is A_{xg} / A_{yg}, which thus denotes the width and the height of the ellipse (that is simulated by the velocity profile). The eccentricity of the velocity profiles of vertical ellipses is conventionally set to be negative throughout this paper (c.f. Viviani et al. 1997). For example, an ellipse with a width (*x*) of 4 cm and a height (*y*) of 10 cm. would have an *x-y* ratio of 0.4. The eccentricity of this ellipse would thus be -0.92. The trained trajectories in the weak and extreme elliptic conditions always had a circular geometry, while the velocity profiles belonged to ellipses with an eccentricity of -0.71 (*x-y* ratio = 0.7) in the weak elliptic condition, and an eccentricity of -0.92 (*x-y* ratio = 0.4) in the extreme elliptic condition. Note that the dynamic *x-y* ratio depicts the ratio between minimum and maximum speed in the velocity profile of the trajectory.

Polar plots of the geometry (dotted line) and velocity profiles (solid line) for the passively trained stimuli are depicted in Fig. 2. The dotted line depicts the geometry of the movement which is strictly circular due to the constant radius of curvature. The solid line illustrates the velocity profile which is inconsistent with the geometry. The radius of curvature of the solid line is low at the top and bottom portions of the movement, indicating the minimum velocity at these parts of the trajectory (see also fig. 2*C* in Viviani et al. 1997). The corresponding velocity profiles are illustrated in Fig. 4*A* (weak elliptic condition) and 4*B* (extreme elliptic condition).

To verify that participants in the experimental groups violated the curvature-velocity relation normally seen in circle drawing, we compared the unnatural movements acquired during motor training with natural circle drawing. To this end, an additional natural-movement-group (2 male, 4 female; mean age, standard deviation: 24.6 ± 2.7 years) was asked to actively produce circular trajectories while moving the cuboid plastic device over a horizontal plane surface (2 blocks of 15 movements; equivalent to data obtained in 1 motor training session in the other groups) without visual feedback.
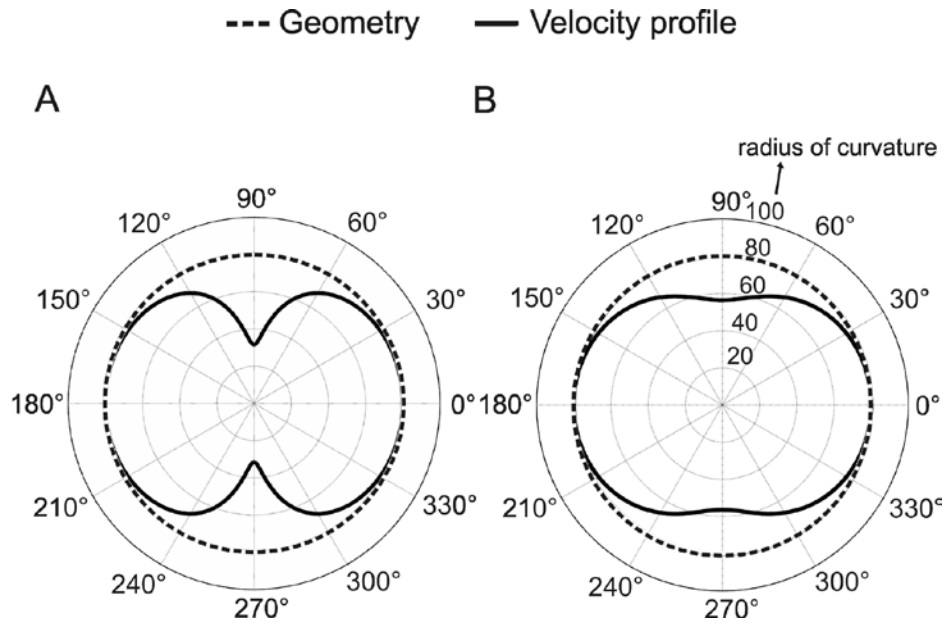
FIG. 2. Polar plots of geometry and velocity profiles in both kinesthetically presented movement trajectories. The radius of the striped line represents the radius of the trajectory (geometry); the radius of the solid line represents the varying radius of curvature of the corresponding simulated ellipse (velocity profile). Note that at points of low radius of curvature (where the line is located inwards), velocity is low. A: the extreme elliptic condition ($\Sigma d = -.92$); B: the weak elliptic condition ($\Sigma d = -.71$). Starting and ending point of all stimuli was at 270°.

All participants of the experimental groups and the control group performed a visual discrimination test before (pre-test) and after (post-test) motor training (Fig. 1*B*). The experiment was performed on four consecutive days. The visual test was accomplished on the first and the last day and took about 1.5 hours. Motor training was performed each day, which lasted about half an hour. Thus, the first and last experimental session took 2 hours in total and the second and third experimental session about half an hour.

Visual pre- and post-test followed the same experimental protocol (Fig. 1*C*). They consisted of 288 trials each, organized into six blocks. Between blocks, there was an obligatory 3-minute break. In each trial, two stimuli were presented consecutively with a short interval, upon which the participant indicated whether both movements were identical ("same") or different. Participants were instructed to press "different" only when they were sure that both movements were different. Buttons for "same" and "different" responses were counterbalanced across participants. To avoid inconsistent eye movements, participants were instructed to keep their eyes on the fixation cross located at the center of the screen.

Each trial started with a fixation cross for 1000 ms. Within the last 300 ms a tone was presented

indicating the onset of the first stimulus (3100 ms) in which one movement cycle was presented. Then, a fixation cross appeared for 1800 ms followed by the second stimulus (3100 ms). The stimuli were a white dot on a black background moving along circular trajectories centered in the middle of the screen. Participants had to respond as quickly and as accurately as possible. Responses could be given from the beginning of the second stimulus until 2000 ms after second stimulus presentation end. When participants did not answer within the requested time, the next trial was initiated, and the trial was counted as incorrect. No feedback about their responses was given.

Visual stimuli were divided into categories belonging to 3 prototypes. Identical to the kinaesthetic stimuli generated by the movement manipulandum, the geometry of movements of all prototypes was circular ($\Sigma_g = 0$), but varied in the velocity profile. Prototype P0 had a velocity profile belonging to a circle ($\Sigma_d = 0$). The velocity of this prototype was thus constant. Because the geometry and the velocity both belong to a circle, curvature and velocity matched, the two-thirds power law was obeyed. The velocity profile of prototype P-.71 corresponded to a weakly elongated vertical ellipse ($\Sigma_d = -0.71$; identical to the eccentricity presented in the weak elliptic training condition). The velocity was thus relatively high at the sides of the circular trajectory, but relatively low at the top and bottom of the circle. Because the velocity profile was slightly different from the geometry, i.e., curvature and velocity did not match, the two-thirds power law was weakly violated. The velocity profile of prototype P-.92 corresponded to an extremely elongated vertical ellipse ($\Sigma_d = -0.92$; identical to the eccentricity presented in the extreme elliptic training condition). The velocity was thus very high at the sides of the circular trajectory, but very low at the top and bottom of the circle. Because the velocity profile clearly differed from the geometry, the two-thirds power law was strongly violated. The weak and extreme elliptic visual prototypes were thus identical to the movements trained in the weak and extreme elliptic conditions during the motor training, respectively. To summarize, P0 obeyed the two-thirds power law (the curvature and the velocity is constant over the trajectory); P-.71 violated the two-thirds power law weakly (the geometric curvature is constant, but the velocity is distributed as if it were a weakly elongated ellipse); and P-.92 featured an extreme violation of the two-thirds power law (the geometric curvature is constant, but the velocity is distributed as if it were an extremely elongated ellipse). The velocity profile of both P-.71 and P-.92 can be seen in Fig. 4*A* and 4*B* (black line). The velocity profiles of comparison stimuli lay around these prototypical profiles; the ones with stronger eccentricities (i.e., more different from 0) exhibited a larger discrepancy between minimum and maximum velocity, and vice versa.

In half of the trials (48 per prototype), one of the three prototypes was presented with the same

prototype ("same" trial). In the other half of trials, the prototype was presented with one of its comparison stimuli ("different" trial). Comparison stimuli laid at .30 ("far"; less alike) or .15 ("near"; more alike) from each prototype (expressed in dynamic *x-y*-ratio [1]). The comparison stimuli either had more elliptic or less elliptic velocity profiles than the prototype which could differ in two degrees, i.e., near (small deviation from the prototype) or far (large deviation from the prototype). The two-thirds power law was obeyed only in P0 (dynamic *x-y* ratio = 0), and all other prototypes and all comparison stimuli violated the two-thirds power law to smaller or greater extent. For example, the prototype P-.92 has an *x-y* ratio of 0.4; an extremely elongated ellipse, and will thus have comparison stimuli with equally deviating *x-y* ratios (cf. de'Sperati and Viviani 1997), i.e., 0.10 and 0.25 (i.e., more extremely elongated ellipses), and 0.55 and 0.7 (i.e. less extremely elongated ellipses compared to P-.92). Each comparison stimulus appeared with equal probabilities, i.e., 12 trials per comparison stimulus and prototype. Thus, the visual stimulus set consisted of 15 different dot movements. The order of prototype, trial type (same or different), and comparison stimulus (far or near) were semi-randomized, i.e., the number of trial type occurrence was held constant over blocks.

After the visual pre-test, participants were passively trained on the movement according to their assigned condition. Due to the unnatural movement type which cannot be freely produced, we could not obtain a pre-training baseline. One motor training block consisted of 80 movement cycles on the motion device which were interrupted by 1000 ms breaks. The participants' task during motor training was to pay attention to both the shape and velocity distribution of the perceived movement, and to imagine performing the movement actively. No information was given about movement parameters. In order to assess effects of motor learning, passive motor training was followed by an active movement reproduction block. Participants were instructed to reproduce the previously felt movement for 15 movement cycles as accurately as possible regarding movement shape and velocity. Analogous to the manipulandum, participants stopped between every movement cycle. Overall, they performed 160 movement cycles on the motion device and 30 movement cycles of active movement reproduction per motor training session. The nature of the reproduced movements was very consistent within each reproduction session. The same procedure was maintained for participants in the control group (the linear movement data were not analyzed).

Stimuli

Visual and motor stimuli were programmed in Matlab 2007a (http://www.mathworks.com).

Coordinates (155 per movement) were refreshed every 20 ms. Presentation 11.0 (http://www.neurobs.com) was used to control the course of visual stimuli as well as passive-movement stimuli generated on the motion device. Both types of stimuli rotated clockwise along a circular path with a duration of 3100 ms and the same start and end location. Exactly one rotation was completed in this time. Thus, each stimulus consisted of one movement cycle only. The paths of both visual and motor stimuli were always circular, but their velocity profile varied, depending on which ellipse the velocity profile simulated. The dynamic eccentricity defined the distribution of the coordinates along the circular path through which the motion device, or the point light, traveled. The calculation and generation of the coordinates was performed in Matlab 2007a. We followed the same approach as in Viviani and Stucchi (1989). The speed of the motion device, or the point light, was defined by the distance between two consecutive coordinates, i.e., the time needed to travel from one coordinate to the next was always 20ms. Thus, the coordinates in which speed was higher lay further apart, and vice versa. The two-thirds power law was only obeyed when the dynamic eccentricity was zero and thus matched the geometric eccentricity. The more the dynamic eccentricity deviated from zero, the more the two-thirds power law was violated, and the greater the variability among the distances between coordinates was (thus featuring unequal velocity distributions).

The movement stimuli started at about 20 cm from the body midline. For the weak and extreme elliptic condition, the stimuli had a fixed radius of 80 mm (perimeter of 502.4 mm) and a variable velocity profile (see Procedure) with an average velocity of 0.16 m/s. For the control group, the motion device moved the participants' hand back and forth along a linear trajectory with a length of 200 mm and an average velocity of 0.13 m/s. Movement duration was kept identical between the experimental groups and the control group, i.e., 3100ms. Visual stimuli were presented on the center of a 16" screen (85 Hz; 1024 x 768 pixels) located about 50cm from the participant at eye-height. They consisted of a moving white dot (diameter: 0.23°) on a black screen. The diameter of the circular trajectory was 3.18°. Exactly one rotation was shown per stimulus.

Movement data pre-processing

Movement data pre-processing was executed in Java (Eclipse 3.3.2). Movement trajectories acquired during the active movement reproduction session were first fragmented into separate movement cycles (15 per reproduction block, i.e., 30 per reproduction session) and then smoothed using a weighted moving average filter that weighted data point x_i with 0.3; $x_{i \pm 1}$ with 0.25; and $x_{i \pm 2}$ with 0.1, to

minimize amplitude and phase distortion (Winter 1990). Then, x and y coordinates and angular velocity v (in °/s), the radius (in mm) per movement cycle and the deviation from radius of each movement cycle per time point were calculated to assess geometry. The pre-processed data were exported to SPSS for statistical analyses with a spatial resolution of 1 mm^2 and a temporal resolution of 20 ms. Note that the tangential velocity was calculated for curvature-velocity relationship only by using Matlab (see below).

Statistical analyses

Visual discrimination data. We calculated d' ($z_{(hits)} - z_{(false\ alarms)}$) and response bias (criterion, C = $z_{(hits)}$ + $z_{(false\ alarms)}$ / 2) per prototype and comparison stimulus to obtain a measure of visual discrimination ability, which is more reliable than hit-rate or percentage correct, because effects of response bias are excluded (Swets and Picket 1982; Macmillan and Creelman 2005). Especially here, where the instruction was to only press "different" when participants were sure that there was a difference, we expected the response bias to be significantly shifted toward "same" answers. Therefore, d' was used as it is independent of response bias (Tanner and Swets 1954; Swets and Picket 1982; Macmillan and Creelman 2005). Comparison stimuli with identical distances and opposite directions (e.g. 0.15 and -0.15) were collapsed for each prototype to obtain d' per distance and prototype. The visual data as measured by d' did not violate the assumption of a normal distribution, as indicated by the Kolmogorov-Smirnov test ($P > 0.2$ in all stimulus types). Data could therefore be tested with parametric tests. Statistical tests for the experimental groups and the control group consisted of planned comparisons t-tests per prototype, in which we were interested in the difference between visual discrimination before (pre-test) and after (post-test) motor training. To assess whether discrimination ability varied over different grades of two-thirds power law violation, and to assess response bias, a repeated measures analysis of variance (ANOVA) with factor prototype (3) and comparison stimulus distance (2) was conducted for the visual pre-test among all participants. Post-hoc t-tests examined differences between prototypes and were adjusted for multiple comparisons using Bonferroni correction.

Movement reproduction data. Effects of motor learning were examined on movement variability, geometry, velocity, and the curvature-velocity relationship. An example of movement data of one representative participant is shown in Fig. 3.

Movement variability was defined as the standard deviation (SD) of the 15 movement cycles within each reproduction block. Deviation from circular geometry was assessed by the averaged deviations (in %) from radius per time point taken per session. To obtain the dynamics of each movement, duration of movement data was first standardized on the duration of the movement produced by the motion device (3100 ms) by extrapolation[2]. Then, the two maxima and the minimum v (angular velocity) were sought, which had to occur at 780 ms and 2320 ms for the maxima and at 1560 ms for the minimum, according to the movement of the motion device (= ideal time points). A time window of + / - 200 ms around the ideal time points was applied to allow for some movement variance. The ratios were calculated with the following formula: $((min / max_1) + (min / max_2)) / 2$, where 'min' represents the minimum velocity of the velocity profile, and 'max' is the maximum velocity of the velocity profile. This formula therefore indicates how elliptic the velocity profile is. The more extreme the difference between minimum and maximum speed (i.e., the smaller the ratio), the more elliptic the velocity profile was. Note that this measure is used later on to express x-y ratio of the velocity profile (i.e., it describes the shape of the ellipse the velocity profile belongs to). This measure was used to determine whether the participant followed a biphasic, i.e. a vertically elliptic, velocity profile. In this case, the value had to be < 1 to verify that the value at the location of the expected minimum was smaller than the value at the location of the expected maxima.

To determine how well participants learned to reproduce the given velocity profile, we took the root mean squared error measure (RMSE) between the produced and the trained velocity profile curve. This was done by taking the root of the mean squared difference between these curves per time point: $\sqrt{\Sigma (C_t - C_p)^2}$ with C is the velocity value of the trained curve (C_t) and the velocity value of the produced curve (C_p). A smaller RMSE indicates a smaller error from the trained velocity curve. This is a common measure in the motor training literature to indicate motor learning (e.g. Hodges and Franks 2000, 2002; Siengsukon and Boyd 2009).

In order to investigate whether the curvature-velocity relationship deviated from the naturally occurring value, we calculated the logarithmic radius of curvature and the logarithmic tangential velocity for each trajectory per time point using Matlab 2007a. The slope between these parameters estimated by linear regression is the value β of the formula $V = KR^{\beta}$, which normally lies around $^1/_3$.

For all movement parameters, the mean over both movement reproduction blocks was taken to obtain a value for one motor training session (i.e. 2 times 15 movements). To test for learning effects over training sessions, a repeated measures ANOVA with factor session (4) was performed for all movement parameters. Statistical tests were 2-sided.
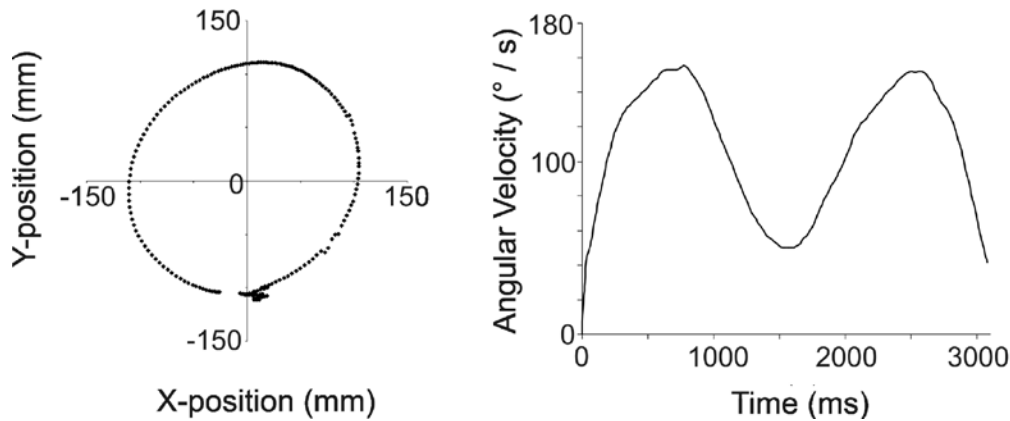
FIG. 3. Example data of one representative participant in the extreme elliptic condition during the third day. Data points reflect the means over one reproduction block (= 15 movements). Left: geometry of the movement trajectory (data are not time-standardized). Each dot represents the (x, y) coordinates (every 20ms). Mean deviation from radius here was 4.62 %. Right: Velocity over time of the movement trajectory (data are time-standardized). The ratio between minimum and maximum speed (x-y ratio simulated by the velocity profiles) here was 0.324 (i.e. dynamic eccentricity = -0.946).

Results

The aim of this study was to investigate how non-visual motor learning of a movement which violates the two-thirds power law, influences visual perception. First, we will show whether it is possible to learn such a movement. Second, we examine the results of the visual perception baseline (pre-test) to determine if discrimination ability varies over different grades of two-thirds power law violation. Finally, we compare the results of the visual discrimination task before and after motor training to test the effect of motor learning on visual perception. The statistics mean and standard deviations are reported separately for the movement parameters in Table 1 and 2, and the results of the visual discrimination task in Table 3 and 4.

Progress in motor learning

As shown in Fig. 4, participants in the extreme elliptic condition produced biphasic velocity profiles during movement reproduction sessions, which correspond to a vertical ellipse (Fig. 4*A*). In the weak elliptic condition, however, only 11 participants produced a biphasic elliptic velocity pattern ('learners') (Fig. 4*B*), while the other 8 showed a bell-shaped or tri-phasic velocity profile ('non-

learners') (Fig. 4*C*). Because learning of a vertical elliptic velocity profile was important to show effects of action on perception, the non-learners were analyzed as a separate group. Precisely, participants were classified as learners when they produced a mean velocity profile with a dynamic *x-y* ratio ≤ 1, which corresponds with an eccentricity of a vertical ellipse. Participants in the natural movement group produced a bell-shaped velocity profile (Fig. 4*D*). Due to stops between movement cycles and the constant geometric curvature, we expected this type of velocity profile which is normally seen in point-to-point reaching movements (Abend et al. 1982; Harris and Wolpert 1998). *X-y* ratios of non-learners lied around 1 and did not differ from the natural movement group [$F_{(1,12)} = 0.434$; $P = 0.523$]. In contrast, *x-y* ratios of learners were significantly smaller than 1 after the first motor training day and differed significantly from the natural movement group [$F_{(1,15)} = -14.421$, $P < 0.01$]. *X-*
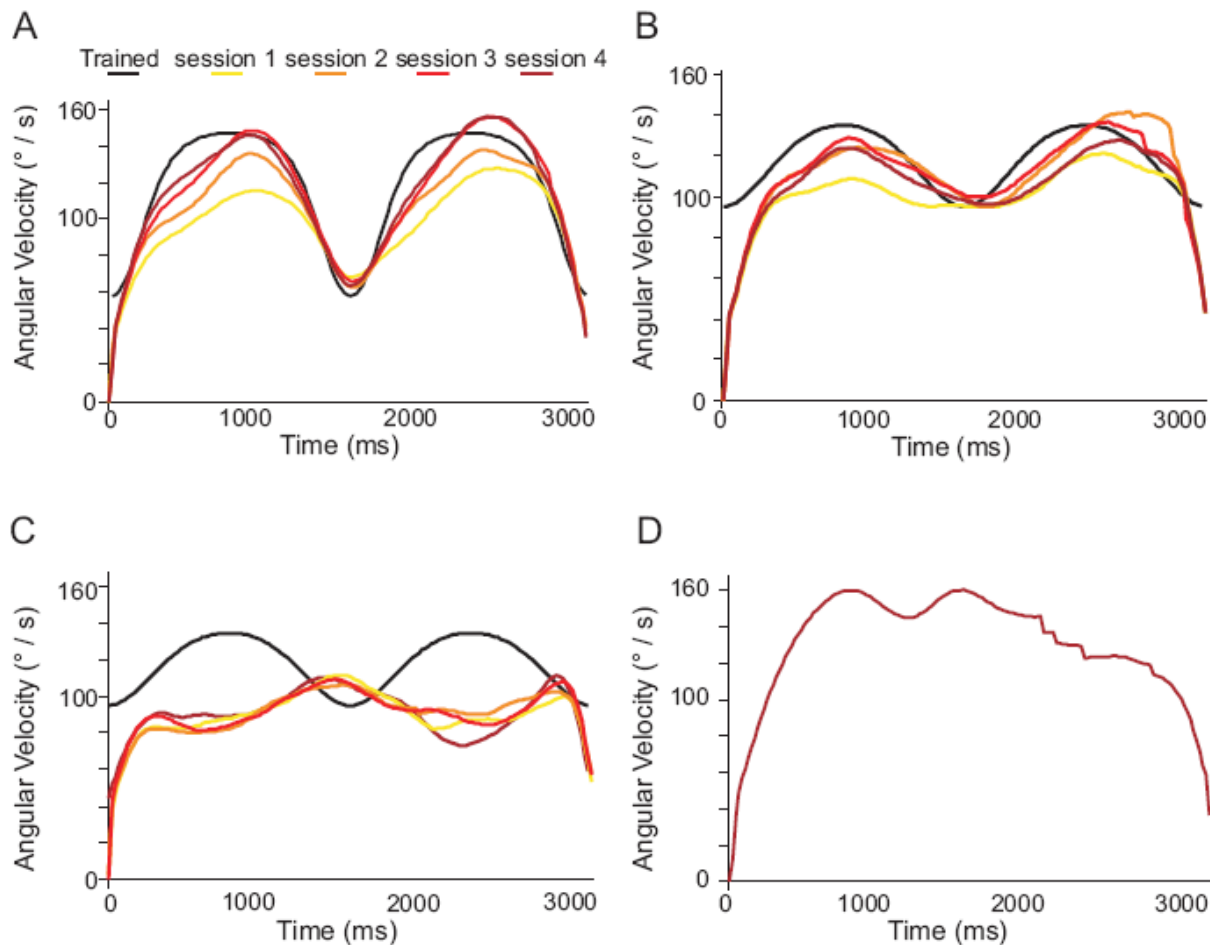

FIG. 4. Velocity profiles per condition per session. A: Extreme elliptic condition. B: Weak elliptic condition (learners). C: Weak elliptic condition (non-learners). D: Natural movement condition. Thick black line indicates the trained velocity profile; yellow to dark-red lines (see legend) indicate produced velocity profiles per session. Note that in the movement only condition, data for only one session exist.

y ratios also differed significantly between learners and non-learners [$F_{(1,17)}$ = 14.557, P < 0.01]. Trajectories of participants in the extreme elliptic condition also had x-y ratios significantly smaller than 1 and differed significantly from the natural movement group [$F_{(1,16)}$ = 72.224, P < 0.001] and from the learners in the weak elliptic condition [$F_{(1,21)}$ = 13.629; P < 0.01].

<Insert Table 1 about here>

Movement variability. Movement variability (Fig. 5*A*) significantly decreased over the motor training sessions in the extreme elliptic condition [$F_{(3,33)}$ = 6.374, P < 0.01]. In the weak elliptic condition, movement variability significantly decreased for learners [$F_{(3,30)}$ = 9.106, P < 0.001], but not for non-learners [$F_{(3,21)}$ = 2.015, P = 0.143].

Circular geometry. In both conditions, mean deviation of the radius of each movement from the circular trajectory (Fig. 5*B*) did not change significantly over sessions (extreme elliptic condition [$F_{(3,33)}$ = 0.823, P = 0.491]; weak elliptic condition - learners [$F_{(3,30)}$ = 0.376, P = 0.771]; weak elliptic condition - non-learners: [$F_{(3,21)}$ = 0.422, P = 0.739]), suggesting that the shape of trajectories remained circular. To test whether circular geometry deviated from the geometry observed during natural circle drawing, the produced geometry of the experimental conditions was tested against the natural-movement-group revealing no difference (extreme elliptic condition [$F_{(1,16)}$ = 1.221, P = 0.286]; weak elliptic condition – learners [$F_{(1,15)}$ = 0.460, P = 0.508]; weak elliptic condition – non-learners [$F_{(1,12)}$ = 0.419, P = 0.530]).
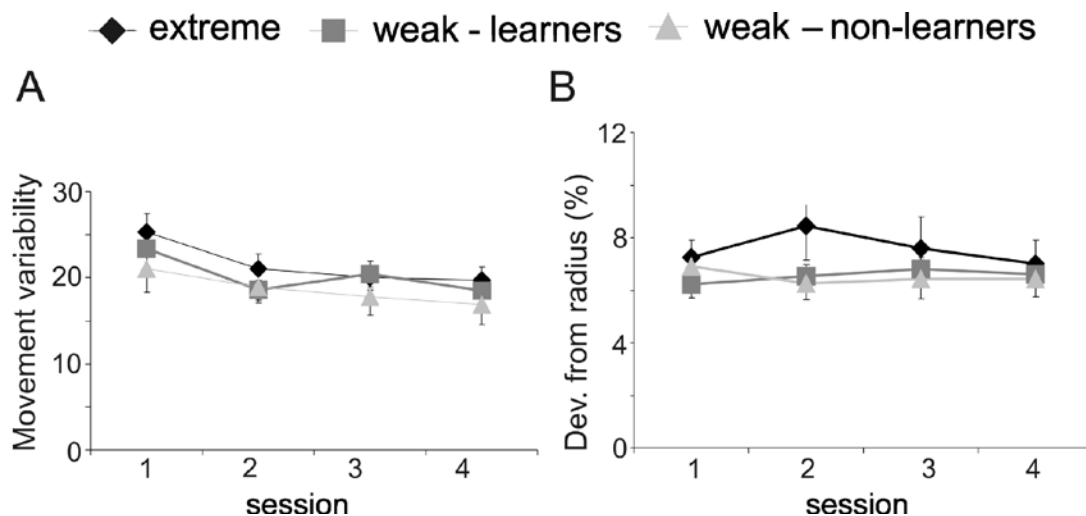

FIG. 5. Movement variability and geometry. A: Movement variability expressed in standard deviation (SD) between movements per active reproduction session. B: Geometry of trajectories expressed in per cent deviation from radius per session. See legend for each condition. Error bars represent standard error (SE).

Velocity. To assess how well participants learned the velocity distribution, the RMSE between the passively trained velocity profile curve and the actively produced velocity profile curve was calculated (see Fig. 4). A significant decline was observed in the extreme elliptic condition [$F_{(3,33)}$ = 3.426, $P < 0.05$], indicating a decreased error. In the weak elliptic condition (learners), no significant change was found [$F_{(3,30)} = 0.093$, $P = 0.857$].

Curvature-velocity relationship. To assess whether the curvature-velocity relationship was distorted by drawing circles with elliptic velocity profiles, a regression analysis was calculated between the logarithm of the radius of curvature and the logarithm of the tangential velocity. This yields the exponent β of the formula describing the two-thirds power law $V = KR^{\beta}$ in which β lies around $^1/_3$. The mean of exponent β was significantly smaller than $^1/_3$ in both experimental conditions (extreme elliptic condition: [$t_{(11)} = -3.730$, $P < 0.01$]; weak elliptic condition – learners: [$t_{(10)} = -3.826$; $P < 0.01$]). In the natural-movement-group, β did not differ from 1/3 [$t_{(5)} = -0.715$, $P = 0.507$] (see Table 2). To investigate whether the power-law relation emerged from greater variation in curvature around the stops between each movement cycle; each trajectory was split into quarters of which the exponent was calculated. In the natural movement group, the exponent did not differ from $^1/_3$ in any of the quarters. When the second and third quarter were collapsed and were compared with the collapsed first and last quarter (i.e., movement initiation and ending), the exponent lay closer to $^1/_3$ in the middle of the movement than in the beginning and the end of the movement [$t_{(5)} = 4.364$, $P < 0.01$], suggesting that the power law relation was stronger in segments where no stops occurred. In the experimental conditions, the exponent was significantly smaller than $^1/_3$ in the first three quarters of the trajectory. The middle and the beginning and end quarters did not differ [extreme elliptic condition: $t_{(11)} = 1.385$, $P = 0.194$; weak elliptic condition: $t_{(10)} = 0.248$, $P = 0.809$]. This suggests that the variation in curvature due to imperfections of drawing a circle was constant throughout the movement cycle and that the curvature-velocity relation was not influenced by stops between movement cycles.

R-squared, which is the explained variance of the cloud of dots in the logarithm of the radius of curvature against the logarithm of the tangential velocity, did not deviate from natural circle drawing in the extreme [$F_{(1,16)} = 1.850$, $P = 0.193$], nor in the weak elliptic [$F_{(1,15)} = 0.009$, $P = 0.927$] condition, suggesting that the reliability of the prediction of β by linear regression was similar to natural circle drawing. Data of two representative participants who participated in one experimental condition and in the natural-movement-condition are shown in Fig. 6. The figure shows different movement characteristics depending on the condition.
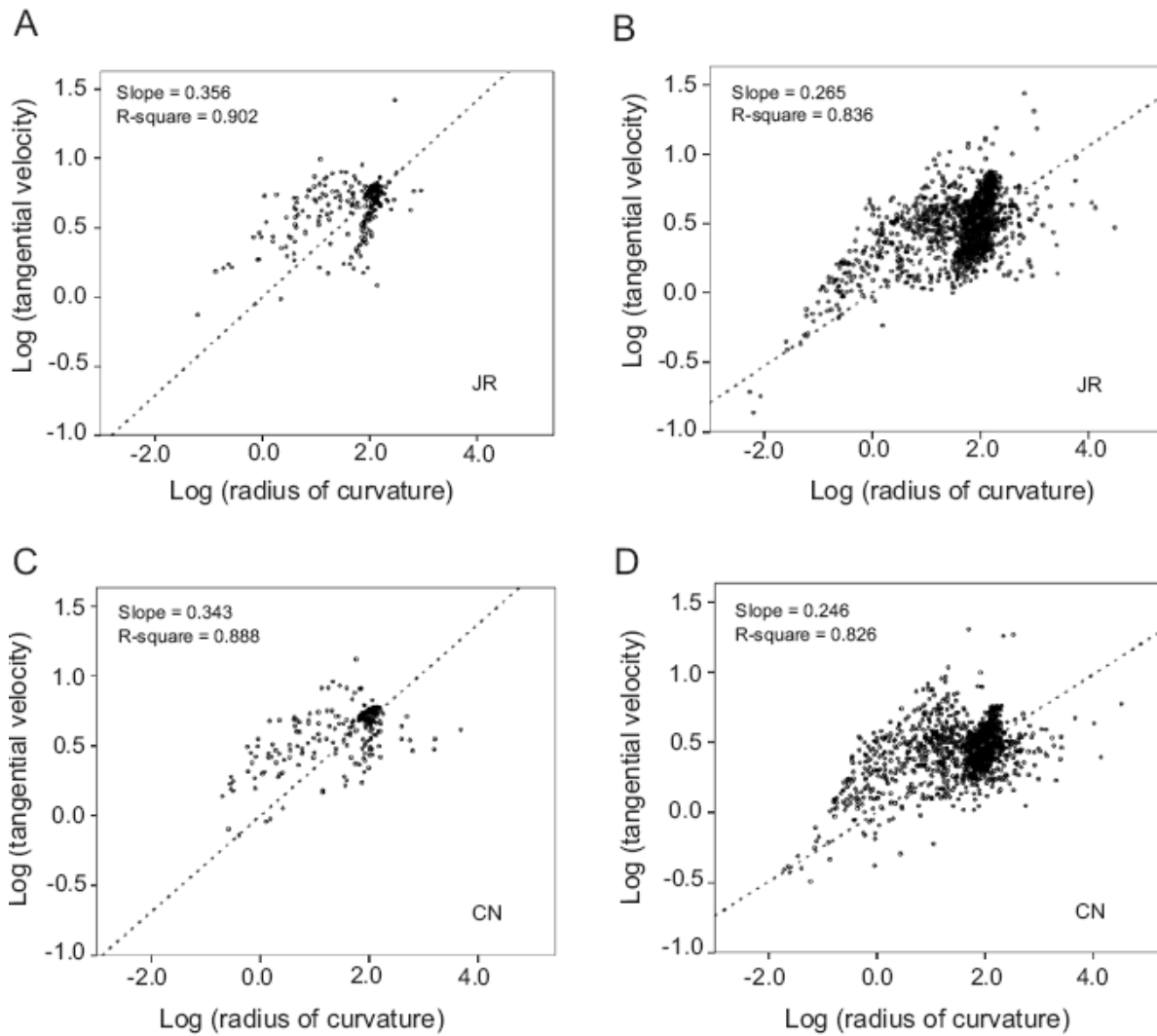
FIG. 6. Curvature-velocity relationship. A and B represent data of one participant (JR) who participated in the natural movement (A), and in the extreme elliptic condition (B). C and D represent data of a different participant (CN) who participated in the natural movement (C), and in the weak elliptic condition (D). On the x-axis the logarithm of the radius of curvature is plotted against the logarithm of the velocity (m/s) on the y-axis. The four sessions were taken together here for illustratory purposes (over which the slope was calculated). For data analyses, the slope (β) and R-square were only calculated per session.

<Insert Table 2 about here>

Visual discrimination performance

Baseline performance: Visual pre-test. We tested participants' ability to discriminate between differences in the velocity profiles when a dot moves along a circular trajectory with constant velocity

(circular prototype) which follows the two-thirds power law or with a velocity profile which violates the this movement constraint weakly or extremely (weak and extreme elliptic prototypes, respectively). Fig. 7*A* illustrates baseline level performance in visual discrimination ability (d') per prototype averaged across all participants. We observed a significant difference between the three prototypes [main effect prototype: $F_{(2,86)} = 23.261$, $P < 0.001$]. Post-hoc t-tests showed that the more elliptical the dynamic eccentricity of the prototype was, the better it was discriminated from nearby eccentricities [extreme > weak: $t_{(43)} = 4.414$, $P < 0.001$; extreme > circular: $t_{(43)} = 5.971$, $P < 0.001$; weak > circular: $t_{(43)} = 2.498$, $P < 0.05$]. We analyzed whether discrimination ability depended on the distance of the comparison stimuli from the prototype (near vs. far). As expected, performance on comparison stimuli lying far from the prototype and thus are most different were discriminated significantly better than comparison stimuli near to the prototype [$F_{(1,43)} = 294.475$, $P < 0.001$] (Fig. 7*B*).
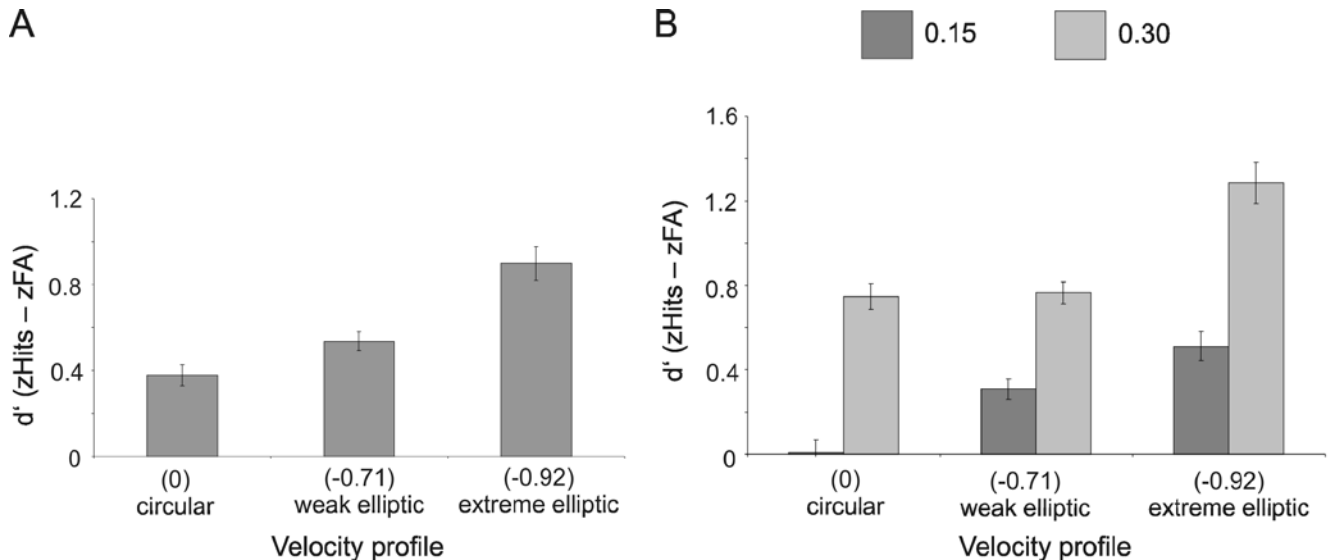

FIG. 7. Baseline visual discrimination ability (visual pre-test in all experimental conditions). A. D' per prototype on visual pre-test collapsed for all comparison stimuli. B. d' for all three prototypes for 'near' (0.15; dark grey) and 'far' (0.30; light grey) comparison stimuli from the concerning prototype. Error bars represent standard error.

Response bias. Due to our instruction that participants should press "different" only when they were sure that a difference was present, we expected participants to tend to answer more frequently with "same" (C > 0). Indeed, we found that the bias was significantly greater than zero [$t_{(44)} = 12.745$; $P < 0.001$]. The "same" responses occurred more often for difficult discriminations in which the comparison stimulus was lying near to the prototype [$F_{(1,43)} = 458.184$; $P < 0.001$], and less for

prototypes which had stronger dynamic eccentricities [$F_{(2,86)}$ = 17.613; $P < 0.001$]. These results thus suggest that the amount of "same" responses increases as the task difficulty increases. Between pre- and post test, we found an increase in response bias [$F_{(1,43)}$ = 14.007; $P < 0.01$]. However, there was no interaction between pre-post and condition [$F_{(3,40)}$ = 1.257; $P = 0.302$], suggesting that the change in criterion between visual pre- and post test did not differ between conditions.

Effects of motor learning on visual perception. Here we tested whether motor training of a circular trajectory with a varying velocity profile affects people's ability to visually discriminate between different velocity profiles of a moving dot. Fig. 8 depicts visual discrimination scores before and after motor training for participants of the experimental groups and the control group. Participants who were trained in the extreme elliptic condition showed a significant improvement in the visual post- compared to visual pre-test for the trained extreme elliptic prototype P-.92 [$t_{(11)}$ = 2.420, $P < 0.05$], marginally for the non-trained prototype P-.71 [$t_{(11)}$ = 2.046; $P = 0.065$] and not for P0 [$t_{(11)}$ = 0.847, $P = 0.415$] (Fig. 8*A*). Learners in the weak elliptic condition (Fig. 8*B*) significantly improved their visual discrimination ability for the trained prototype P-.71 [$t_{(10)}$ = 2.229, $P < 0.05$], and for P-.92 [$t_{(10)}$ = 3.225, $P < 0.01$], but not for P0 [$t_{(10)}$ = -0.163, $P = 0.873$]. In contrast, no changes in discrimination ability were observed for non-learners in the weak elliptic condition [P0: $t_{(7)}$ = 1.083, $P = 0.315$; P-.71: $t_{(7)}$ = 0.471, $P = 0.652$; P-.92: $t_{(7)}$ = -0.281, $P = 0.787$] (Fig. 8*C*). Consistently, participants in the control group, who underwent motor training on a non-related linear movement, did not show any changes on visual post- compared to pre-test [P0: $t_{(12)}$ = 0.206, $P = 0.840$; P-.71: $t_{(12)}$ = 0.776, $P = 0.453$; P-.92: $t_{(12)}$ = 0.343, $P = 0.738$] (Fig. 8*D*).

<Insert Table 3 about here>
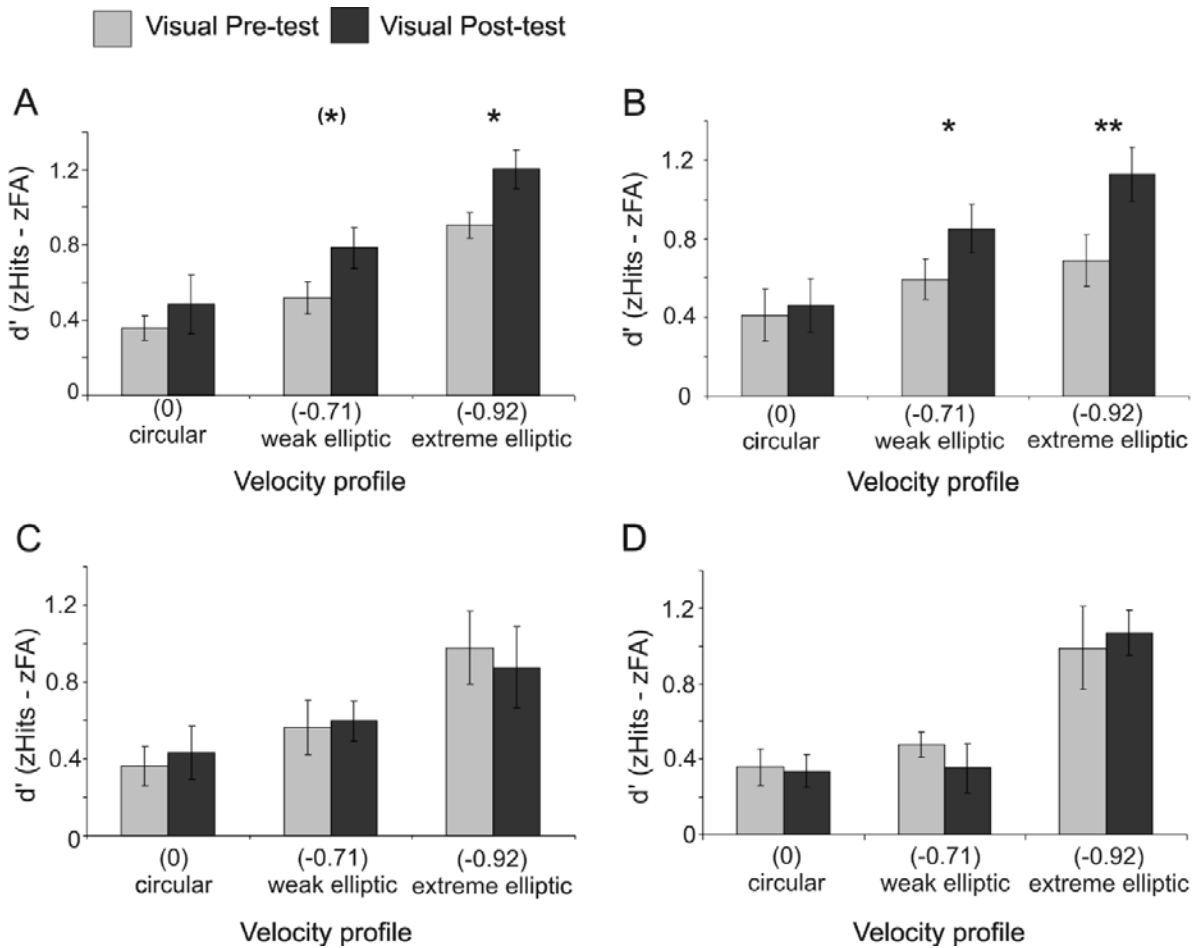
<Insert Table 4 about here>

FIG. 8. Visual discrimination ability before and after motor training. Light grey bars indicate discrimination ability (d') on visual pre-test; black bars indicate discrimination ability (d') on visual post-test. A. performance in extreme elliptic condition. B. performance in learners of the weak elliptic condition. C. performance in non-learners of the weak elliptic condition. D. performance in the visual control condition.. Error bars represent standard error; the asterisk indicates a significant difference with $P < 0.05$ between visual pre- and post-test.

Discussion

The aim of this study was to investigate the effect of action on perception by motor training of a movement without visual feedback that violates the two-thirds power law. First, we examine whether such an a-typical movement which is assumed not to be present in the motor repertoire, could be learned without visual feedback. Second, we test whether non-visual motor training could improve visual discrimination ability of the specific trained movement. We demonstrate that people are able to learn a-typical movements in which curvature and velocity do not match; exhibiting deviations from

the two-thirds power law. Successful motor learning of this novel movement improved visual perception of the trained movement and highly similar movements. However, action-to-perception transfer was not present if no motor learning occurred.

Progress in motor learning

We show that people generate circular hand movements with an elliptic velocity profile after passive motor training. Motor training led to significant changes in the velocity distribution toward the trained velocity profile of the produced movement without affecting the geometry. It thus seems to be possible to execute movements in which velocity and geometry do not match according to the two-thirds power law. This finding is in contrast with previous studies on manual tracking of predictable (Viviani and Mounoud 1990) and unpredictable two-dimensional movements (Viviani et al. 1987), and in a study in which participants had to reproduce a movement which was imposed on the right arm, with the left arm (Viviani et al. 1997). These studies demonstrated that it is nearly impossible to produce movements violating the two-thirds power law. In the Viviani and Mounoud (1990) and Viviani et al. (1987) studies, participants had to manually track a visual stimulus which followed the trajectory of an extremely elongated ellipse. In half of the trials, the velocity profile did not correspond to the trajectory (two-thirds power law violation). Additionally, the orientation of the ellipse and the speed of the trajectories were varied. This wide variation of the presented stimuli together with a short training time could have prevented participants from motor learning. The use of consistent stimuli over the experiment is very likely to be an important factor in motor learning of such an a-typical movement. It is therefore possible that our training which used one consistent violation of a movement constraint over a longer time period could yield participants to generate movements at variance with the two-thirds power law. Another contributing factor may be that we used passive training on the same hand which was used for reproduction; in contrast to Viviani et al. (1997). In this way, many consistent movement cycles could be learned in order to execute them later on with the same hand. Moreover, it has been found that the two-thirds power law does not hold for all movements, and that there can be significant deviations from the law when subjects perform movements at their chosen rate or when movements are simple and harmonic (Viviani and Flash 1995; Wann et al. 1988). Wann et al. (1988) suggested that conformity with and departures from the two-thirds power law can be better explained by their modification of the minimum-jerk model. Other findings have implied that the two-thirds power law seems to be a by-product of a movement system that favors smooth trajectories with

minimum variance rather than it is a primary movement-generating principle (e.g. Gribble and Ostry 1996; Harris and Wolpert 1998; Schaal and Sternad 2001; Todorov and Jordan 1998).

The exponent values in our data are in agreement with these latter studies (Viviani and Flash 1995; Wann et al. 1988) that found deviations of the two-thirds power law. Here, we find that strong elliptic velocity profiles could be produced without affecting the geometry of the movement, which implies a different relation between geometry and velocity as proposed by the two-thirds power law. As a consequence, the exponent describing the curvature-velocity relation was different from $^1/_3$, while this was not the case in natural circle drawing. In our experiment, the possibility to execute this movement at the own pace may have led to the finding that people are able to produce movements deviating from the two-thirds power law (Wann et al. 1988). However, to further substantiate this finding, a baseline measurement with which the movements after training could be compared is needed. In contrast to previous studies, movements were always interrupted by stops after each cycle. This procedure was employed to guarantee that stimuli used in the motor training and the visual discrimination test were presented in an equal manner. Although these stops did not seem to affect the two-third power law relation as observed by drawing natural circles (i.e., the exponent was 0.31 and did not significantly deviate from $^1/_3$), it might have affected movements which had circular geometry with an elliptic velocity profile.

While the kinesthetic presentation of movement stimuli led to the required biphasic velocity profile in the extreme elliptic condition in all cases, only a subset of participants in the weak elliptic condition was able to feel and reproduce this movement. This finding suggests that the stronger the movement violates the two-thirds power law the easier it is to identify and to acquire. According to the post-experimental interview, just over half of the participants in the weak elliptic condition were able to perceive a slight elliptic velocity profile. The others reported that the velocity profile appeared constant to them over the whole trajectory. In the extreme elliptic condition, however, all participants detected the given elliptic velocity distribution. Moreover, the velocity profiles produced in the extreme elliptic condition improved over sessions, while this improvement over sessions was not observed in participants who acquired the movement type in the weak elliptic condition. The reduced training success over sessions observed in the weak elliptic condition might be caused by a floor effect, i.e., there was less room for improvement in the weak than in the extreme elliptic condition due to the less pronounced differences between minimum and maximum velocity (i.e., more ambiguity).

In both conditions in which participants were trained to execute the extreme and the weak elliptic velocity profile, active movement reproduction variability decreased over training sessions.

This was not observed in a group which did not acquire the movement type. Decreases in movement variability demonstrate an increase in movement consistency reflecting greater motor control (Jordan et al. 2009). Based on the Haken-Kelso-Bunz (HKB)-model, increasing fluctuations, i.e. greater standard deviation, in relative phase between limbs is regarded as a loss of stability in intra-limb coordination (Haken et al. 1985).

In summary, a-typical combinations of curvature and velocity may be learned in the same way as learning unusual phase shifts in bimanual coordination (Zanone and Kelso 1992, 1997).

Visual perception baseline

We found that participants were more accurate at discriminating moving dots whose motion violated the two-thirds power law. Visual discrimination was even superior for strongly compared to weakly violated movement constraints despite the use of comparison stimuli which deviated from the visual prototype in discrete *x-y* ratio steps. The two-thirds power law has also been explained to be an effect of constant affine velocity (Pollick and Sapiro 1997). The constant velocity which is perceived in movements complying with the two-thirds power law can thus be explained by the constant affine velocity that these movements feature. Any other functions which are not affine invariant are thus perceived as non-uniform (Pollick and Sapiro 1997). The degree of non-uniformity (or non-smoothness) may have been used as a marker to discriminate these types of motion in our study.

Effects of motor learning on visual perception

In line with previous studies which found an effect of action on visual (Brown et al. 2007; Hecht et al. 2001) and auditory (Repp and Knoblich 2007) perception, visual perception significantly improved by motor training. Since we aimed to double-dissociate the effects of learning a-typical movements on visual perception (in contrast to other studies) we tested participants on two different movements. Consistent with previous studies (Casile and Giese 2006; Reithler et al. 2007), we find a significant improvement in visual perception of the trained movement, but in addition, we find that training can transfer to highly similar movement types. Although training of both movement types led to improved visual discrimination ability of the trained movement type, this effect seemed to transfer to the non-trained, elliptic prototype, but not to the unrelated, circular prototype. This suggests that the

information of one movement type may have been used to discriminate highly related movement types as well. The transfer effect seemed to be stronger in the group which was trained on the weak elliptic velocity profile, which may be due to a higher level of fine-tuning to the movement caused by the ambiguity of the stimulus. It remains an issue for future research to further determine how action-to-perception transfer generalizes across different types of action.

The present study extends previous findings demonstrating action-to-perception transfer for different a-typical movements applying a highly standardized motor learning procedure. We trained participants on a movement which violates a common motor constraint, the two-thirds power law, instead of using pre-defined movement trajectories (e.g., Engel et al. 2008; Hecht et al. 2001; Reithler et al. 2007). Thus, we could assure that participants had no visual experience of the applied movement and that motor learning led to an acquisition of a motor representation (defined by geometry and dynamics) rather than a mere use of memorizing trajectories. In contrast to the previous study which also trained on a-typical movements violating a motor constraint (Casile and Giese 2006), we used passive motor training. Thereby, we could ensure that participants acquired the novel movement in a highly standardized manner and could achieve training success in most of our participants. Taken together, this study provides reliable evidence that motor learning affects visual perception.

We show that successful motor learning is a necessary requirement for action-to-perception transfer. Participants who were not able to actively execute the trained movement did not improve in the visual discrimination task. This suggests that even when low-level sensory experience of the novel movement was present, improvements in visual perception depended upon successful motor learning of the specific movement. Moreover, learning of movements unrelated to the visually perceived stimuli did not lead to perceptual improvements either. Thus, our findings support the tight link between action and perception (e.g. Prinz 1997; Schütz-Bosbach and Prinz 2007) especially in the case of action-to-perception (Hecht et al. 2001).

A possibility which cannot be fully excluded by the present data is that improvement in visual perception may have been affected by increased attention for the trained movement during the visual discrimination task. Motion processes are supposed to be 'low-level' and stimulus driven (Werkhoven et al. 1993, 1994). Evidence is accumulating, however, that it is mediated by attention (Cavanagh 1992) and that motion capture may be better conceived as a 'high-level' process involving active attention (Culham and Cavanagh 1994; Wohlschläger 2000). Our motor training may thus have led to increased attention paid to the learned stimulus, rather than that the increased visual discrimination performance was due to mnemonic effects.

Conclusion

Our results reliably demonstrate that non-visual motor learning of a novel movement improves visual perception of the trained movement and highly related movements. Moreover, action-to-perception transfer seems to be dependent on the successful acquisition of the trained movement. In line with some previous studies, the typical curvature-velocity relation as predicted by the two-thirds power law seems to be susceptible to changes after motor training.

Acknowledgements

References

Abend W, Bizzi E and Morasso P. Human arm trajectory formation. *Brain* 105: 331-348, 1982.

Bidet-Ildei C, Orliaguet JP, Sokolov AN and Pavlova M. Perception of elliptic biological motion. *Perception* 35*:* 1137-1147, 2006.

Brown LE, Wilson ET, Goodale MA and Gribble PL. Motor force field learning influences visual processing of target motion. *J Neurosci* 27: 9975-9983, 2007.

Calvo-Merino B, Glaser DE, Grezes J, Passingham RE and Haggard P. Action observation and acquired motor skills: an FMRI study with expert dancers. *Cereb Cortex* 15: 1243-1249, 2005.

Calvo-Merino B, Grezes J, Glaser DE, Passingham RE and Haggard P. Seeing or doing? Influence of visual and motor familiarity in action observation. *Curr Biol* 16: 1905-1910, 2006.

Casile A, Dayan E, Caggiano V, Hendler T, Flash T and Giese MA. Neuronal encoding of human kinematic invariants during action observation. *Cereb Cortex, 20:* 1647-1655, 2010.

Casile A and Giese MA. Nonvisual motor training influences biological motion perception. *Curr Biol* 16: 69-74, 2006.

Cavanagh P. Attention-based motion perception. *Science* 257: 1563-1565, 1992.

Culham JC and Cavanagh P. Motion capture of luminance stimuli by equiluminous color gratings and by attentive tracking. *Vision Res* 34: 2701-2706, 1994.

Dayan E, Casile A, Levit-Binnun N, Giese MA, Hendler T and Flash T. Neural representations of kinematic laws of motion: evidence for action-perception coupling. *Proc Natl Acad Sci U S A* 104: 20582-20587, 2007.

de'Sperati C and Viviani P. The relationship between curvature and velocity in two-dimensional smooth pursuit eye movements. *J Neurosci* 17: 3932-3945, 1997.

di Pellegrino G, Fadiga L, Fogassi L, Gallese V and Rizzolatti G. Understanding motor events: a neurophysiological study. *Exp Brain Res* 91: 176-180, 1992.

Engel A, Burke M, Fiehler K, Bien S and Rösler F. Motor learning affects visual movement perception. *Eur J Neurosci* 27: 2294-2302, 2008.

Flach R, Knoblich G and Prinz W. The two-thirds power law in motion perception: when do motor anticipations come into play? *Visual Cognition* 11: 461-481, 2004.

Gallese V, Fadiga L, Fogassi L and Rizzolatti G. Action recognition in the premotor cortex. *Brain* 119 (Pt 2): 593-609, 1996.

Giese MA and Poggio T. Neural mechanisms for the recognition of biological movements. *Nat Rev Neurosci* 4: 179-12, 2003.

Gribble PL and Ostry DJ. Origins of the power law relation between movement velocity and curvature: modeling the effects of muscle mechanics and limb dynamics. *J Neurophysiol* 76: 2853-2860, 1996.

Haken H, Kelso JA and Bunz HA. theoretical model of phase transitions in human hand movements. *Biol Cybern* 51: 347-356, 1985.

Harris CM and Wolpert DM. Signal-dependent noise determines motor planning. *Nature* 394: 780-784, 1998.

Hecht H, Vogt S and Prinz W. Motor learning enhances perceptual judgment: a case for action-perception transfer. *Psychol Res* 65: 3-14, 2001.

Hodges NJ and Franks IM. Attention focusing instructions and coordination bias: Implications for learning a novel bimanual task. *Hum Mov Sci* 19: 843-867, 2000.

Hodges NJ and Franks IM. Learning as a function of coordination bias: building upon pre-practice behaviours. *Hum Mov Sci* 21: 231-258, 2002.

Hommel B, Müsseler J, Aschersleben G and Prinz W. The Theory of Event Coding (TEC): a framework for perception and action planning. *Behav Brain Sci* 24: 849-878; discussion 878-937, 2001.

Jeannerod M. The representing brain: Neural correlates of motor intention and imagery. *Behav Brain Sci* 17: 187-245, 1994.

Jeannerod M. Neural simulation of action: a unifying mechanism for motor cognition. *Neuroimage* 14: S103-109, 2001.

Jordan K, Challis JH, Cusumano JP and Newell KM. Stability and the time-dependent structure of gait variability in walking and running. *Hum Mov Sci* 28: 113-128, 2009.

Lacquaniti F, Terzuolo C and Viviani P. The law relating the kinematic and figural aspects of drawing movements. *Acta Psychol* (Amst) 54: 115-130, 1983.

Macmillan N and Creelman C. Detection Theory: A user's Guide. *Lawrence Erlbaum Associates*, 2nd edition. Mahwah, New Jersey, 2005.

McCullagh P, Weiss MR and Ross D. Modeling considerations in motor skill acquisition and performance: an integrated approach. *Exerc Sport Sci Rev* 17: 475-513, 1989.

Pollick FE and Sapiro G. Constant affine velocity predicts the 1/3 power law of planar motion perception and generation. *Vision Res* 37: 347-353, 1997.

Prinz W. Perception and action planning. *European journal of cognitive psychology* 9: 129-154, 1997.

Reithler J, van Mier HI, Peters JC and Goebel R. Nonvisual motor learning influences abstract action observation. *Curr Biol* 17: 1201-1207, 2007.

Repp BH and Knoblich G. Action can affect auditory perception. *Psychol Sci* 18: 6-7, 2007.

Rizzolatti G, Fogassi L and Gallese V. Neurophysiological mechanisms underlying the understanding and imitation of action. *Nat Rev Neurosci* 2: 661-670, 2001.

Schaal S and Sternad D. Origins and violations of the 2/3 power law in rhythmic three-dimensional arm movements. *Exp Brain Res* 136: 60-72, 2001.

Schütz-Bosbach S and Prinz W. Perceptual resonance: action-induced modulation of perception. *Trends Cogn Sci* 11: 349-355, 2007.

Siengsukon CF and Boyd LA. Does sleep promote motor learning? Implications for physical rehabilitation. *Phys Ther* 89: 370-383, 2009.

Swets JA and Pickett RM. Evaluation of diagnostic systems. Methods from signal detection theory. *Academic Press: Series in cognition and perception.* New York, 1982.

Tanner WP and Swets JA. A decision-making theory of visual detection. *Psychol Rev* 61: 401-409, 1954.

Todorov E and Jordan MI. Smoothness maximization along a predefined path accurately predicts the speed profiles of complex arm movements. *J Neurophysiol* 80: 696-714, 1998.

Viviani P. Common mechanisms in perception and action. Attention and Performance XIX. *Oxford university Press.* New York, 2002.

Viviani P, Baud-Bovy G and Redolfi M. Perceiving and tracking kinesthetic stimuli: further evidence of motor-perceptual interactions. *J Exp Psychol Hum Percept Perform* 23: 1232-1252, 1997.

Viviani P, Campadelli P and Mounoud P. Visuo-manual pursuit tracking of human two-dimensional two-dimensional

movements. *J Exp Psychol Hum Percept Perform* 13: 62-78, 1987.

Viviani P and Flash T. Minimum-jerk, two-thirds power law, and isochrony: converging approaches to movement planning. *J Exp Psychol Hum Percept Perform* 21: 32-53, 1995.

Viviani P and McCollum G. The relation between linear extent and velocity in drawing movements. *Neuroscience* 10: 211-218, 1983.

Viviani P and Mounoud P. Perceptuomotor compatibility in pursuit tracking of two-dimensional movements. *J Mot Behav* 22: 407-443, 1990.

Viviani P and Schneider R. A developmental study of the relationship between geometry and kinematics in drawing movements. *J Exp Psychol Hum Percept Perform* 17: 198-218, 1991.

Viviani P and Stucchi N. Biological movements look uniform: evidence of motor-perceptual interactions. *J Exp Psychol Hum Percept Perform* 18: 603-623, 1992.

Viviani P and Stucchi N. The effect of movement velocity on form perception: geometric illusions in dynamic displays. *Percept Psychophys* 46: 266-274, 1989.

Wann J, Nimmo-Smith I and Wing AM. Relation between velocity and curvature in movement: equivalence and divergence between a power law and a minimum-jerk model. *J Exp Psychol Hum Percept Perform* 14: 622-637, 1988.

Werkhoven P, Sperling G and Chubb C. The dimensionality of texture-defined motion: a single channel theory. *Vision Res* 33: 463-485, 1993.

Werkhoven P, Sperling G and Chubb C. Perception of apparent motion between dissimilar gratings: spatiotemporal properties. *Vision Res* 34: 2741-2759, 1994.

Winter DA. Biomechanics and motor control of human movement. *Wiley-Interscience*, 2nd edition. Waterloo Canada, 1990.

Wohlschläger A. Visual motion priming by invisible actions. *Vision Res* 40: 925-930, 2000.

Wolpert DM and Ghahramani Z. Computational principles of movement neuroscience. *Nat Neurosci* 3 Suppl: 1212-1217, 2000.

Wolpert DM, Ghahramani Z and Jordan MI. Are arm trajectories planned in kinematic or dynamic coordinates? An adaptation study. *Exp Brain Res* 103: 460-470, 1995.

Zanone PG and Kelso JA. Evolution of behavioral attractors with learning: nonequilibrium phase transitions. *J Exp Psychol Hum Percept Perform* 18: 403-421, 1992.

Zanone PG and Kelso JA. Coordination dynamics of learning and transfer: collective and component levels. J *Exp Psychol Hum Percept Perform* 23: 1454-1480, 1997.

Footnotes

[1.] The *x-y* ratio of an ellipse represents the minor divided by the major axis of an ellipse. Comparison stimuli were calibrated at *x-y* ratio distances (cf. de'Sperati and Viviani 1997). The expression of elliptic eccentricity has a non-linear relation to *x-y* ratios. At greater elliptic eccentricities, the *x-y* ratios decrease disproportionally. *X-y* ratios were thus used to ensure that dynamic elliptic eccentricities would differ according to what their geometric ellipse would look like. The stimuli for the other two prototypes had the following *x-y* ratios: the circular prototype "0": *x-y* ratio = 1; its comparison stimuli: 0.85, 0.70 (horizontal and vertical); the weak elliptic prototype "-.71": *x-y* ratio = 0.7; its comparison stimuli: 0.4, 0.55, 0.85, 1; the extreme elliptic prototype "-.92": *x-y* ratio = 4; its comparison stimuli: 0.1, 0.25, 0.55, 0.7.

[2.] The reason we did not time-standardize data for movement variance calculations was that variations in movement duration / timing also play a role in this parameter and should thus be included. As time standardization does not influence calculations on movement geometry (deviation from radius), it is preferable to use the original data. Time-standardization in the Java program took place just before smoothing data.

Table 1. *Movement parameter values over training sessions.*

Training Condition	Movement variability	Geometry	Dynamics (*x-y* ratio)	Velocity (RMSE)	Session
Extreme elliptic condition	25.32 ± 7.73	7.26 ± 2.15	0.51 ± 0.20	32.75 ± 11.76	1
	21.05 ± 6.26	8.33 ± 4.49	0.44 ± 0.20	27.59 ± 11.27	2
	20.01 ± 5.04	7.59 ± 4.15	0.40± 0.16	24.97 ± 8.76	3
	19.73 ± 5.51	7.01 ± 3.03	0.38 ± 0.15	28.49 ± 9.25	4
Weak elliptic condition – learners	23.43 ± 3.51	6.23 ± 1.75	0.75 ± 0.30	31.74 ± 6.25	1
	18.58 ± 4.81	6.54 ± 1.44	0.67 ± 0.18	30.78 ± 7.73	2
	20.44 ± 4.71	6.80 ± 1.53	0.67 ± 0.21	30.16 ± 11.30	3
	18.49 ± 3.09	6.61 ± 1.74	0.71 ± 0.24	31.20 ± 8.84	4
Weak elliptic condition – non-learners	21.09 ± 7.90	7.02 ± 1.22	1.05 ± 0.13	-	1
	18.87 ± 5.16	6.38 ± 1.55	1.01 ± 0.15	-	2
	17.78 ± 5.95	6.53 ± 1.95	1.02 ± 0.21	-	3
	16.86 ± 6.47	6.42 ± 1.92	1.00 ± 0.26	-	4
Natural movement group	-	6.01 ± 2.1	1.07 ± 0.16	-	1

Values are Mean ± SD. 'Movement variability' is the standard deviation (SD) between movement trajectories in millimetres. The geometry is expressed in deviation from radius in per cent. The velocity profile is expressed in dynamic *x-y* ratio (minimum / maximum velocity). Velocity (RMSE) is the root of the mean squared deviation between the trained velocity profile curve and the reproduced velocity profile curves. Note that the control group only produced 2 times 15 movements, so data exist only for session 1.

Table 2. *Curvature-velocity relationship.*

Training Condition	Exponent β	R-squared	Session
Extreme elliptic condition	0.26 ± 0.06	0.83 ± 0.10	1
	0.28 ± 0.06	0.85 ± 0.06	2
	0.29 ± 0.05	0.85 ± 0.04	3
	0.29 ± 0.05	0.83 ± 0.09	4
Weak elliptic condition – learners	0.27 ± 0.06	0.85 ± 0.08	1
	0.28 ± 0.06	0.89 ± 0.04	2
	0.28 ± 0.05	0.88 ± 0.05	3
	0.27 ± 0.05	0.88 ± 0.04	4
Natural movement group	0.31 ± 0.07	0.88 ± 0.04	1

Exponent β of the formula $V = KR^{\beta}$, as indicated by the slope between the logarithm of the radius of curvature and the logarithm of the tangential velocity, and R-squared of the cloud of dots. Values are Mean ± SD.

Table 3. *Visual discrimination ability (d') on visual pre- and post-test per prototype and comparison stimuli (CS).*

Training Condition	Visual Pre-test			Visual Post-test			CS
	P 0	P-.71	P-.92	P 0	P -.71	P-.92	
Baseline all	0.40 ± 0.30	0.59 ± 0.32	0.87 ± 0.34	x	x	x	Mean
participants	0.05 ± 0.32	0.36 ± 0.35	0.47 ± 0.34	x	x	x	.15
	0.75 ± 0.34	0.81 ± 0.35	1.27 ± 0.46	x	x	x	.30
Extreme elliptic	0.36 ± 0.24	0.52 ± 0.30	0.91 ± 0.24	0.48 ± 0.54	0.78 ± 0.37	**1.20 ± 0.36***	Mean
condition	0.00 ± 0.18	0.26 ± 0.34	0.48 ± 0.25	0.07 ± 0.88	0.50 ± 0.44	0.74 ± 0.46	.15
	0.71 ± 0.36	0.78 ± 0.33	1.33 ± 0.34	0.90 ± 0.37	1.07 ± 0.44	**1.67 ± 0.30****	.30
Weak elliptic	0.43 ± 0.43	0.60 ± 0.32	0.72 ± 0.41	0.46 ± 0.39	**0.87 ± 0.48***	**1.14 ± 0.41****	Mean
condition – learners	0.02 ± 0.53	0.40 ± 0.30	0.39 ± 0.33	0.07 ± 0.41	0.66 ± 0.53	0.71 ± 0.36	.15
	0.84 ± 0.39	0.81 ± 0.39	1.05 ± 0.55	0.86 ± 0.49	**1.08 ± 0.51***	**1.57 ± 0.57****	.30
Weak elliptic	0.38 ± 0.28	0.61 ± 0.35	0.85 ± 0.59	0.59 ± 0.52	0.67 ± 0.21	0.81 ± 0.65	Mean
condition – non-	0.05 ± 0.26	0.29 ± 0.42	0.57 ± 0.52	0.05 ± 0.36	0.38 ± 0.34	0.51 ± 0.49	.15
learners	0.67 ± 0.32	0.84 ± 0.38	1.38 ± 0.56	0.82 ± 0.42	0.80 ± 0.26	1.24 ± 0.71	.30
Visual Control	0.36 ± 0.34	0.48 ± 0.23	0.99 ± 0.78	0.34 ± 0.30	0.35 ± 0.45	1.07 ± 0.41	Mean
group	-0.03 ± 0.51	0.29 ± 0.31	0.60 ± 0.65	-0.01 ± 0.26	-0.01 ± 0.52	0.67 ± 0.34	.15
	0.75 ± 0.54	0.67 ± 0.32	1.38 ± 0.95	0.68 ± 0.41	0.71 ± 0.46	1.47 ± 0.59	.30

Values (d') are Mean ± SD. 'Mean' in the CS column is mean d' over both comparison stimuli. Significant increases in d' on post-test are marked in bold. One asterisk indicates $P < 0.05$; two asterisks indicate $P < 0.01$.

Table 4. *Criterion (bias) of visual pre- and post-test per prototype and comparison stimuli (CS).*

Training Condition	Visual Pre-test			Visual Post-test			CS
	P 0	P -.71	P -.92	P 0	P -.71	P -.92	
Baseline all	0.67 ± 0.42	0.38 ± 0.29	0.44 ± 0.37	x	x	x	Mean
participants	0.85 ± 0.47	0.49 ± 0.30	0.63 ± 0.40	x	x	x	.15
	0.48 ± 0.40	0.27 ± 0.30	0.24 ± 0.36	x	x	x	.30
Extreme elliptic	0.78 ± 0.47	0.46 ± 0.28	0.66 ± 0.32	0.96 ± 0.56	0.58 ± 0.36	0.71 ± 0.45	Mean
condition	0.96 ± 0.51	0.59 ± 0.30	0.88 ± 0.37	1.17 ± 0.67	0.71 ± 0.41	0.94 ± 0.42	.15
	0.60 ± 0.44	0.33 ± 0.28	0.45 ± 0.28	0.75 ± 0.50	0.45 ± 0.35	0.48 ± 0.50	.30
Weak elliptic	0.61 ± 0.28	0.44 ± 0.25	0.46 ± 0.32	0.97 ± 0.46	0.76 ± 0.44	0.67 ± 0.38	Mean
condition – learners	0.81 ± 0.25	0.54 ± 0.26	0.63 ± 0.36	1.17 ± 0.44	0.87 ± 0.49	0.89 ± 0.39	.15
	0.40 ± 0.33	0.34 ± 0.26	0.29 ± 0.30	0.77 ± 0.50	0.66 ± 0.42	0.46 ± 0.41	.30
Weak elliptic	0.83 ± 0.23	0.42 ± 0.22	0.42 ± 0.44	1.14 ± 0.63	0.70 ± 0.37	0.65 ± 0.45	Mean
condition – non-	0.98 ± 0.27	0.56 ± 0.19	0.62 ± 0.52	1.34 ± 0.72	0.80 ± 0.38	0.83 ± 0.49	.15
learners	0.68 ± 0.19	0.28 ± 0.26	0.21 ± 0.40	0.95 ± 0.54	0.60 ± 0.38	0.47 ± 0.41	.30
Visual Control	0.52 ± 0.53	0.23 ± 0.34	0.22 ± 0.31	0.61 ± 0.55	0.39 ± 0.47	0.23 ± 0.28	Mean
group	0.71 ± 0.65	0.32 ± 0.34	0.41 ± 0.29	0.78 ± 0.52	0.57 ± 0.49	0.43 ± 0.31	.15
	0.32 ± 0.46	0.13 ± 0.37	0.02 ± 0.36	0.43 ± 0.58	0.21 ± 0.47	0.03 ± 0.30	.30

Values are Mean criterion $((z_{hits} + z_{false\ alarms}) / 2) \pm SD$. 'Mean' in the CS column is mean criterion over both comparison stimuli.

Study II

Beets I.A.M., 't Hart B.M., Rösler F., Henriques D.Y.P., Einhäuser W. and Fiehler K. (under review). **Online action-to-perception transfer: only percept-dependent action affects perception.** *Vision Research*

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

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Abstract

Perception self-evidently affects action, but under which conditions does action in turn influence perception? Observers view an ambiguous stimulus that is perceived rotating either clockwise or counterclockwise. When observers report their perceived direction by rotating a manipulandum, opposing directions between report and percept ("incongruent report") destabilize the percept as compared to same-direction ("congruent") report. In contrast, when observers report their percept by key presses while performing a predefined movement, we find no difference between congruent, incongruent and unrelated movements. Consequently, action has a direct influence on perceptual experience if and only if it is related to the perception itself.

Introduction

The integration between action and perception makes up one of the most important facets of everyday life. The common coding theory (Prinz, 1997) and the theory of event coding (Hommel, Müsseler, Ascherleben and Prinz, 2001) posit that the final stages of perception and the initial stages of motor control share a common representational domain, where planned actions are represented in the same format as perceived events. Many studies support the idea that perception affects action (Hecht, Vogt

and Prinz, 2001; McCullagh, Weiss and Ross, 1989). In addition, visual stimuli tend to dominate over perception in other modalities, even when the visual modality has no task-relevant information (e.g., Colavita, 1974; Posner, 1980; Posner, Nissen and Klein, 1976; Sinnett, Spence and Soto-Faraco, 2007). On the other hand, if perception and action share the same representation, changes due to action should lead to corresponding changes in perception (Hecht et al., 2001; Prinz, 1997; Schütz-Bosbach & Prinz, 2007 for review).

Some studies demonstrated an influence of action on perception. In the case of motor learning, several studies report the effects of intensively learned movements on visual perception (e.g. Beets, Rösler and Fiehler, under review; Calvo-Merino, Glaser, Grèzes, Passingham and Haggard, 2005; Casile & Giese, 2006; Engel, Burke, Fiehler, Bien and Rösler, 2008; Hecht et al., 2001; Reithler, van Mier, Peters and Goebel, 2007). Beyond the realm of motor learning, the motor system also interacts on-line with visual perception (for review, Müsseler, 1999; Schütz-Bosbach & Prinz, 2007). When reaching to grasp a bar with a certain orientation, the mere motor preparation suffices to facilitate responses to a congruent visual stimulus (Craighero, Fadiga, Rizzolatti and Umiltà, 1999). The *direct* and *online* influence of action on the corresponding perceptual representations, however, remains to be tested.

So-called rivalry allows us to test action-to-perception transfer without learning or changing the stimulus. In rivalry, the perceptual interpretation of an ambiguous stimulus changes over time, while at any given time one interpretation dominates (Blake & Logothetis, 2002; Leopold & Logothetis, 1999; Wohlschläger, 2000). Besides vision, rivalry has been observed in other modalities such as touch (Carter, Konkle, Wang, Hayward and Moore, 2008), audition (van Noorden, 1975), and olfaction (Zhou & Chen, 2009). Thus, rivalry seems to be a ubiquitous phenomenon covering many modalities and cross-modal interactions. For instance, the direction of a tactilely presented stimulus biases the observed direction of an ambiguous visual stimulus (Blake, Sobel and James, 2004). Yet, research on how the motor system affects the perception of visual ambiguity is sparse. Since in rivalry the stimulus remains unchanged, action or action planning cannot operate on the stimulus itself but rather directly on its perceptual representation. Hence, such ambiguous stimuli are ideal to test the direct effects of action on motion perception.

In one of the few studies on the effect of action on rivalry perception, Maruya, Yang and Blake (2007) used a binocular rivalry paradigm. Observers were trained to make sinusoidal mouse movements when the percept of either a rotating sphere or an unrelated stimulus was dominant. The self-produced movements (which determined the speed of the stimulus motion) led to prolonged

durations in the perception of the same movement and shorter stimulus suppression rates. It is possible that this visuo-motor coupling and / or intensive training may have affected these results. Furthermore, it is unknown whether these findings generalize to perceptual rivalry, which shares most but not all the characteristics of binocular rivalry (van Ee, 2009).

Wohlschläger (2000) investigated the effect of action on perceptual rivalry and showed that hand movements influenced the perceptual judgement of an ambiguous visual stimulus in the direction of performed and planned movements. This pioneering study however, has left unresolved the extent to which the action needs to be coupled to the perception to exert an effect on perception. The present study directly addresses this question by asking whether concurrent action influences the visual perception of a constant (ambiguous) stimulus and to what degree the motor output needs to be related to the perception in order to trigger action-to-perception transfer. Specifically, we ask whether a mere generation of actions in a pre-defined direction will shape perception, or whether the action needs to be functionally coupled with the current percept. We present a structure-from-motion cylinder which may be perceived as rotating either clockwise (CW) or counterclockwise (CCW). We carefully distinguish conditions in which action, the rotation of a manipulandum, is used to report the current perceptual experience from conditions in which observers perform the same movements, but unrelated to their current perceptual state. By this experimental manipulation we assess whether action must depend on perception to exert an influence on the perceptual experience.

Materials and Methods

Observers

Fourteen naïve observers between the ages of 19 and 26 years (mean age: 22.8; SD: 2.7 years; 6 male / 8 female) participated in this study. Three additional observers were excluded from analysis: one observer aborted the experiment; in another, the movement data were not usable due to a technical problem; and another failed to comply with task instructions. All observers had normal or corrected-to-normal vision, were right-handed as assessed by a German translation of the Edinburgh Handedness Inventory (mean ± standard deviation: 84.6 ± 15.2) (Oldfield, 1971), and had no history of psychiatric or neurological disorders. All observers were recruited from the Philipps-University Marburg, and were compensated with course-credits or money (€6 per hour) for their participation. Written informed consent was obtained, and the procedure was in accordance with the ethical standard laid down in the

II. Experimental part_____

Declaration of Helsinki (2000) as well as with departmental guidelines.

Stimuli

Four-hundred white dots of 4*4 pixels (~0.065° * ~0.065°) were presented on a 1024*768 pixels, 16"
black screen (refresh rate 75Hz) to perceptually induce the shape of a rotating cylinder (structure-from-
motion) of 175*400 pixels (~2.86° * ~6.53°) (fig. 1a). The cylinder made one full revolution every
3.6s. Dot life-time was set at 0.3s. This ambiguous structure-from-motion stimulus produced a percept
of a cylinder, switching between CW and CCW rotation.

For some conditions, we created an unambiguous version of the stimulus. A red bar of 10*500
pixels (~0.16° * ~8.16°) was drawn over the cylinder. When moving along the 'back' of the cylinder,
the bar was partially occluded. To enhance disambiguation, the dots at the back were fully occluded by
a black plane in the center of the perceived cylinder.

Apparatus

Stimuli were viewed through a black cardboard tunnel with a length of 110 cm to prevent interference
from other visual input (fig. 1b). A black cloth covered the back of the head and part of the tunnel to
prevent observers from watching their own movements. Observers were instructed to direct their gaze
toward the center of the stimulus and to try seeing the stimulus as a whole. A manipulandum with a
turntable on the horizontal plane was used to perform actions during perception of the ambiguous
cylinder (fig. 1b). The turntable was rotated by using the attached vertical handle with an effective
radius of 5 cm. In the motor conditions (see procedure), observers sat facing the screen and grasped
the vertical handle of the manipulandum with a precision grip using their thumb, index and middle
finger of the right hand (fig 1b). The perception of the direction of motion of the visual stimulus was
indicated by either moving the manipulandum or by pressing one of two arrow keys (left arrow key for
CW; right arrow key for CCW) with the left hand (see procedure). A chinrest was used to keep a stable
head position throughout the experiment. The chair and chinrest were adjusted individually to assure a
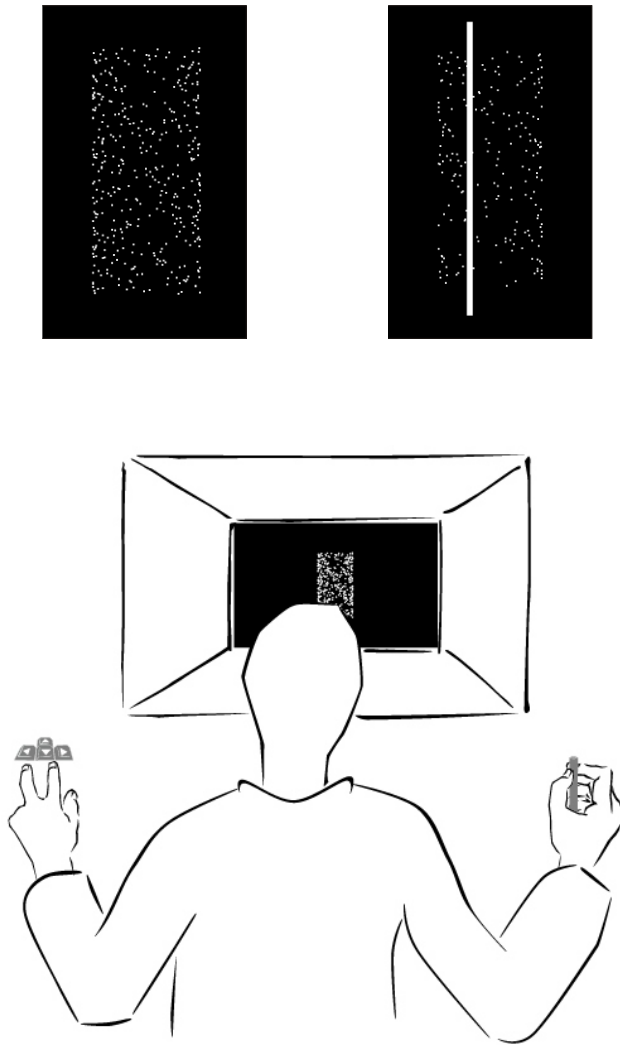comfortable position.

Fig. 1. Experimental Design. (A) Visual structure-from-motion stimuli which observers viewed through the tunnel. Left: The ambiguous stimulus could be interpreted as a cylinder rotating CCW or CW; Right: The unambiguous stimulus over which a red bar was drawn (here illustrated in white). (B) Setup. Observers sat in front of a tunnel through which the visual stimuli were presented. A black cloth covered the head and part of the tunnel, to ensure that the self-produced movements were not seen. Observers pressed one of the arrow keys with the index and ring finger of the left hand. The right hand was used for rotating the turntable, or to make movements along the vertical plane of the right side of the tunnel (not shown).

Movement trajectories were recorded with an ultrasound motion recording device (ZEBRIS CMS20, Zebris Medical GmbH, Isny im Allgäu, Germany). To measure related rotational hand movements, a sensor was attached to the top of the vertical handle of the turntable. For the unrelated movement condition (see procedure), the signal was recorded from a sensor placed on the top of a

freely movable stylus used to execute straight vertical trajectories. The stylus was moved between an upper and a lower stopper mounted on the right side of the tunnel. The data were sampled with 100 Hz and analysed offline.

Procedure

Ambiguous and unambiguous stimuli (fig. 1a) were used for different kinds of blocks. There were two kinds of report modes: a key press and the rotation of the manipulandum. In the case of key presses, observers kept the key pressed during the percept, until it switched. Three instruction modes were employed: (i) no movement of the manipulandum, (ii) moving the manipulandum either congruently or incongruently with the perceived stimulus, (iii) moving the manipulandum in a pre-defined direction (CW, CCW, or vertical in the unrelated movement condition). This resulted in eight conditions under which the task was performed (table 1). In the unambiguous catch blocks, a red bar was tracked by rotating the turntable either congruently or incongruently (fig. 1a, right). These blocks were used as a baseline measure to test the ability to switch quickly and to track the direction and speed of the cylinder accurately. The rotating direction of the red bar and the dots switched within each block. The durations per rotation direction were determined by the observers' own shuffled dominance durations from the preceding "no movement" block. In the no movement blocks, observers indicated by key presses in which direction the ambiguous stimulus rotated. In the motor instruction blocks, observers had to continuously move the manipulandum in a specified direction (CW, CCW) or move a stick vertically ("unrelated") throughout the block, trying to match velocity with that of the cylinder. Simultaneously, key presses were used to indicate rotation direction of the ambiguous stimulus. In all blocks that used keyboard report, observers were instructed to press no key when they were not sure about the direction. 2.8% of time either no key or two keys were pressed and these periods were discarded from analysis. In the motor report blocks, observers reported the rotation direction of the ambiguous stimulus by moving the manipulandum congruently or incongruently relative to the perceived stimulus (table 1).

<Insert Table 1 about here>

Before starting the experiment, observers were familiarized with the procedure and the stimulus by performing each of the eight different conditions for one minute. As explained above, these consisted of no movement, the unambiguous catch blocks (moving congruently / incongruently), motor instruction (moving CW, CCW, vertical), and motor report (reporting percept congruently or

incongruently). The experiment consisted of 19 blocks lasting 5 minutes each. In between blocks, there was an opportunity to take a break. The order of the unambiguous catch blocks (congruent / incongruent) was counterbalanced. The order of all types of motor report and motor instruction blocks was randomized between observers (table 1, right column).

Movement data pre-processing

Data pre-processing was done in Python (Version 2.6.5) using Numpy (Oliphant, 2007) and SciPy (Jones et al., 2001). Observers' trajectories were constrained by the manipulandum to produce a circular movement with a constant radius (i.e., a one-dimensional movement given by the angle as a function of time). We discarded data points whose Euclidian distance to the previous point deviated more than 3 standard deviations from the mean. Cubic splines were used to interpolate these data points. A circle was fitted to the samples after which all samples were converted to their angle on/in this circle. An angular velocity signal was based on that, which was smoothed using a 5-sample median filter before extracting the direction of movement.

Data analyses

Dominance durations for CW and CCW percepts were extracted from the keyboard data in the no movement and motor instruction blocks. The dominance duration was the period of time that exactly one key was held down. Periods in which no key or two keys were simultaneously pressed were discarded. When one direction was interrupted by a short period in which both keys were pressed, the percept was separated and thus resulted in two dominance durations (plus the short period of discarded data). Dominance durations were extracted from the manipulandum movement data for the unambiguous catch blocks and the motor report blocks. Velocities below a threshold of 1°/s were counted as no movement. From the no-movement condition, we defined for each observer a threshold as the first percentile of dominance durations; we discarded values below this threshold to remove jitter in the motor report conditions. Due to these unavoidable differences in treating key press and manipulandum data, we refrain from any direct comparisons between key-press report and manipulandum-report data.

Statistical tests. Since dominance durations in rivalry typically follow leptokurtic (heavy-tailed) distributions (e.g., Logothetis, 1998), we use medians (rather than means) to characterize the

distribution of dominance durations per observer and block. Across observers, however, these values can safely be assumed to follow a Gaussian distribution such that for group comparisons paired t-tests (for testing differences between conditions) and repeated measures ANOVA (for testing effects over blocks) are the appropriate measures. All statistics were computed using R (Version 2.10.1; R Development Core Team, 2009).

Results

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

Unambiguous stimuli

To test whether observers veridically reported their percepts, we used disambiguated versions of the rotating cylinder. Using the manipulandum, observers reported the direction of motion correctly 93.4% of the time when report was congruent with the perception, and 90.2% of time when the report was incongruent. These proportions did not differ significantly from each other ($t(13) = -1.067$; $p = 0.305$). Speed accuracy as measured by RMSE from the goal angular velocity was 74.6°/s in the congruent and 73.5°/s in the incongruent tracking condition which did not differ significantly ($t(13) = -0.185$; $p = 0.856$). Hence, we are confident that observers performed the task correctly and reported movement directions equally well for congruent and incongruent movements.

Ambiguous stimuli

No movement condition. The median dominance duration was 6.49 s $\pm$ 6.50 s (mean±sd over observers). In line with earlier findings (Nawrot & Blake, 1991; Blake et al., 2004), none of the observers showed a significant bias toward CW (49.1 % $\pm$ 5.9 %) or CCW (48.1 % $\pm$ 5.2 %) percepts (<3% discarded for non-unique key presses). We found no significant bias for either percept in any observer with the longer median dominance duration not different from the shorter per individual ($p = 0.140$, Wilcoxon test). Dominance durations were stable across repetitions ($F(2, 26) = 0.649$; $p = $

0.531). This allows us to pool dominance durations from both percepts and across repetitions for all further analysis.

Motor instruction condition. In conditions when observers rotated the manipulandum irrespective of the perceived motion, they reported their percept by key presses. We separated the data according to times when manipulandum movement and perceived motion were in the same ("congruent motor instruction") or in the opposite ("incongruent motor instruction") direction (fig 2a). Dominance durations did not differ significantly between incongruent and congruent movements ($t(13) = 1.048$, $p = 0.314$; table 2). These percept durations also did not differ from a condition in which observers performed an unrelated movement perpendicular to the table (comparison to congruent movements: $t(13) = 0.809$, $p = 0.433$; comparison to incongruent movements: $t(13) = 1.433$, $p = 0.175$). Nor did these instructed movement conditions differ from a condition in which no movement was required (congruent vs. no movement: $t(13) = -1.089$, $p = 0.296$; incongruent vs. no movement: $t(13) = 0.212$, $p = 0.836$). Finally, pre-defined movements (CCW, CW, unrelated) did not differ from the no movement condition (all $p > 0.296$). Consequently, movements that were conducted irrespective of the current perceptual state did not exert an influence on the percept duration.

Motor report condition. In all the aforementioned conditions, percept durations were reported by key presses, while the critical movement (none, congruent, incongruent, unrelated) was conducted independently of the perceptual state. In contrast, in motor-report conditions, observers were instead asked to *report* their percept with the movement of the manipulandum. In one condition observers were instructed to move the manipulandum in the same direction as their percept ("congruent motor report"), in another condition in the opposite direction ("incongruent motor report"). In these conditions, a vastly distinct result emerged (fig. 2b): percept durations were significantly shorter for incongruent movements than for congruent movements ($t(13) = 2.914$, $p = 0.012$). This shows that only percept-related action affects the perceived direction of ambiguous stimuli.
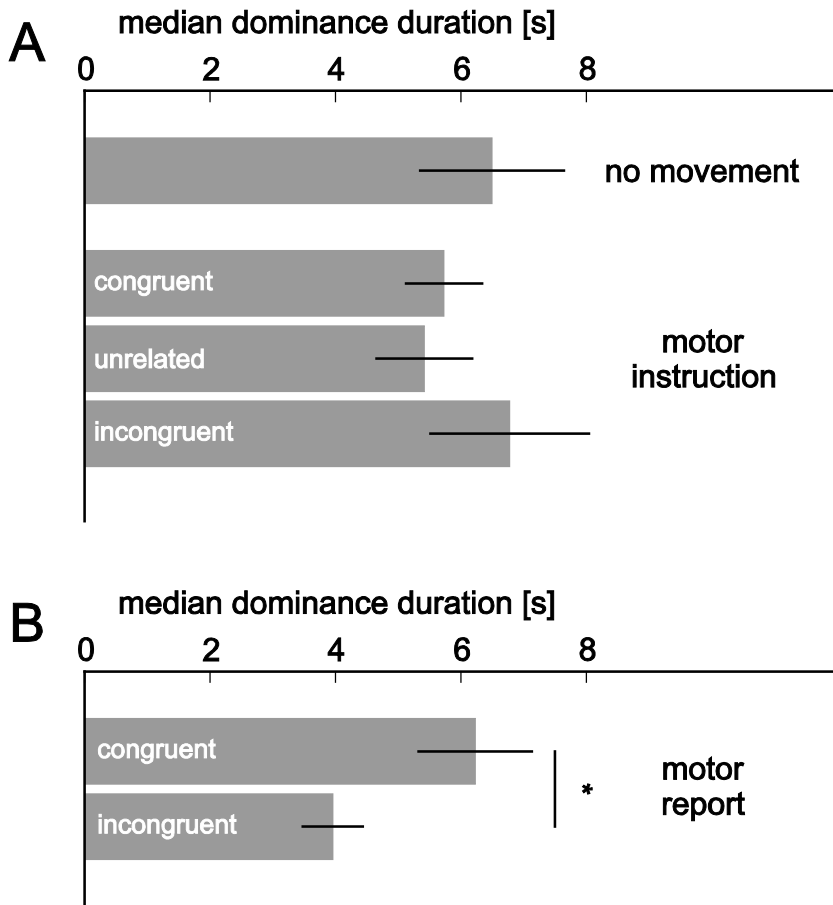
<Insert Table 2 about here>

Fig. 2. Dominance durations per condition in seconds. (A) Mean dominance durations for keyboard responses. (B) Mean dominance durations for movement manipulandum responses. The error bars represent standard errors of the mean.

Direction transitions in motor report conditions

To verify whether transitions were similar for reporting percept by congruent and for reporting percept by incongruent movements, we investigated the change in direction of the movement data in the motor-report conditions. When aligning all movement traces to the time of transition between the two rotation directions (fig. 3), we found that transition slopes (i.e., acceleration) did not differ between congruent and incongruent motor report conditions ($F(1,48) = 1.492$, $p = 0.229$), nor between transition types (i.e., from CW to CCW and from CCW to CW) ($F(1,48) = 0.172$, $p = 0.680$), nor was there an interaction between transition type and condition ($F(1,48) = 0.057$, $p = 0.812$). Hence, our findings that dominance durations were shorter in the incongruent motor report condition than in the congruent one

cannot be explained by a difference in motor performance in the two conditions.
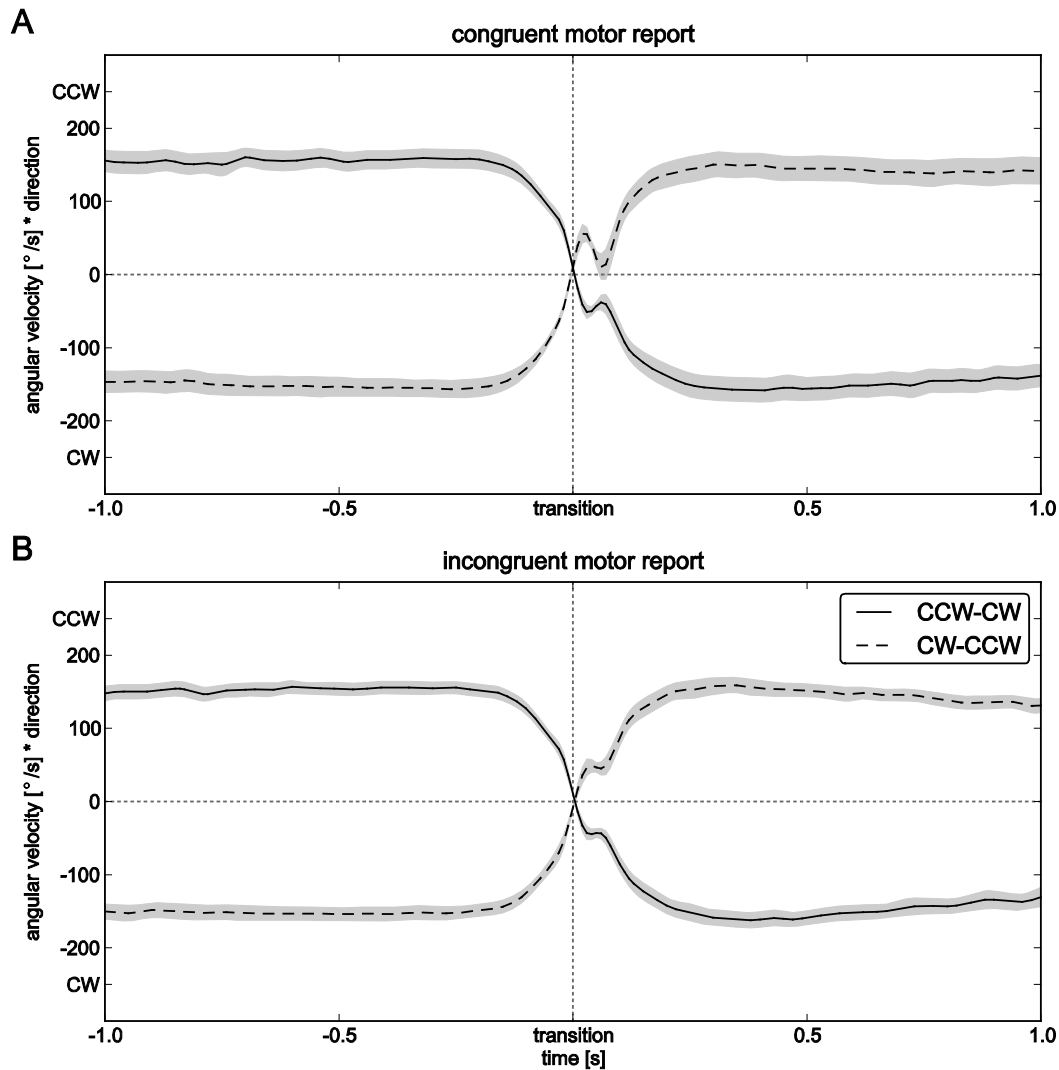

Fig. 3. Movement transitions. Movement trajectories were aligned to time of perceptual transitions (defined as zero-crossings of the angular velocity) in motor-report conditions; positive values denote CCW movement, negative CW movement; solid lines denote mean velocities across observers for switches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

Discussion

Our results show that action shapes perception, but only when the action is coupled with the current

perceptual state; when observers use rotational movements to indicate their percept of an ambiguous stimulus, percept durations change significantly. In contrast, rotating in a pre-defined direction does not lead to changes in percept durations in the same visual stimuli.

In previous studies (Maruya et al., 2007; Wohlschläger, 2000), it has been shown that pre-defined movements influence the visual interpretation of ambiguous stimuli. In these experiments, however, the start of the stimulus movement was directly coupled to the observers' movement initiation. Furthermore, in Maruya et al. (2007), observers were trained to make movements in order to drive the speed of the visual stimulus. Thus in these studies action had a direct effect on the perceptual outcome of the stimulus which may have led to a tight interplay of action and perception through stimulus manipulation, rather than a direct effect of action on perceptual representations. Here, in contrast, tasks were performed in which perception and action were closely linked next to tasks in which perception and action were independent from each other, minimizing the potential confound of learning a specific perception-action relation. It seems conceivable that a detailed investigation of the effects of learning specific action-stimulus congruencies resolves the seeming conflict between these studies and the present findings. If there is no effect of action on the stimulus at any time, however, our data clearly show that a direct effect of action on perception requires the action to be percept-related.

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

Recent studies have demonstrated that rivalry elicited in one sensory modality can be altered by other sensory modalities, i.e., the perception of the ambiguous stimulus is biased towards the percept consistent with the non-ambiguous modality (Blake et al., 2004; van Ee, van Boxtel, Parker and Alais,

2009). Here we show that visual rivalry can be influenced by concurrent movements as well (see also, Maruya et al., 2007, Wohlschläger et al., 2007). It is conceivable that the interaction of perception and action relies on similar underlying mechanisms as has been proposed for multisensory integration. This could provide a promising link between common coding theory (Prinz, 1997) or the theory of event coding (Hommel et al., 2001) and research on multisensory processes (e.g., Alais & Burr, 2004; Ichikawa & Masakura, 2006; Repp & Knoblich, 2007; Sekuler, Sekuler and Lau, 1997; Shimojo & Shams, 2001; Witten & Knudsen, 2005).

In the case of rivalry, we find that only incongruent actions influence perception by shortening percept durations; congruent actions do not prolong percept durations. While there has been little research on the effect of hand movements on rivalry, many studies have addressed the relationship between *eye* movements and rivalry. Over 175 years after Necker's (1832) original proposal that perceptual switches of his eponymous cube were a consequence of "the adjustment of the eye for obtaining distinct vision", a wide consensus on a coupling between eye movements and perceptual dominance seems to exist (e.g., Brouwer & van Ee, 2006; Laubrock, Engbert and Kliegl, 2008; Toppino, 2003; van Dam & van Ee, 2005), although the direction of causality is still in debate (Ellis & Stark, 1978; Eure, Hamilton and Pheiffer, 1956; Kawabata, Yamagami and Noaki, 1978; Zimmer, 1913) and is likely to be bi-directional (Einhäuser, Martin and König, 2004). In the context of (visual) rivalry, oculomotor behavior brings two additional challenges: first, any eye movement has a direct impact on the retinal stimulus; second, eye movements are coupled to shifts in focal attention, which itself influences switch rates (Paffen, Alais and Verstraten, 2006). Despite all the advantages of the oculomotor system acting as the interface between input and output (i.e., between perception and action) to test how action influences perceptual representations while minimizing other factors (stimulus, focal attention), manual movements, as used here, circumvent these potential confounds.

Since attention speeds up rivalry (Paffen et al., 2006) and this increase in speed is not restricted to one modality (Alais, van Boxtel, Parker and van Ee, 2010), we have to ask whether our results can be explained by attention alone. One may argue that reporting by incongruent tracking is more difficult and thus requires more attentional resources which would consequently speed up switching between percepts. We consider this explanation unlikely for several reasons. First, one can also argue for the opposite with equal justification: incongruent action requires more attention, thus less attention is available for perception and thus rivalry should slow down, contrary to our findings. Second, we failed to find any differences in dominance durations between no movement and unrelated movements on the one hand, and between dominance durations in pre-defined incongruent or congruent movements (i.e.,

percept unrelated) on the other hand. This implies that movement *per se* is not an attentionally challenging task. Third, for unambiguous stimuli, movement characteristics and errors between congruent and incongruent tracking were very similar, again arguing against a different attentional effect on both. However, it is undisputable that attention plays a key role in rivalry. We argue, however, that there is no differential effect of attention on incongruent and congruent movements, and consequently, our main finding cannot be explained solely by differences in attentional demand. As binding diverse representations is a main function of attention in the sensory domain (Wolfe & Bennett, 1997), it seems conceivable that attention is a key ingredient to bind sensory and motor representations. This implies that in certain cases, the common coding framework is not generic, but rather needs additional attention on bodily movements in order to function properly. Beyond a potential impact of attentional processes, our findings provide support for the common coding concept and refine this model by demonstrating that action-to-perception transfer requires the action to be directly coupled to motion perception.

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References

Alais, D., & Burr, D. (2004). The ventriloquist effect results from near-optimal bimodal integration. *Current Biology, 14*, 257-262.

Alais, D., van Boxtel, J. J., Parker, A., & van Ee, R. (2010). Attending to auditory signals slows visual alternations in binocular rivalry. *Vision Research, 50*, 929-935.

Beets, I. A. M., Rösler, F., & Fiehler, K. (under review). Non-visual motor training affects visual motion perception: Evidence from violating the two-thirds power law.

Blake, R., & Logothetis, N. K. (2002). Visual competition. *Nature Reviews Neuroscience, 3*, 13-21.

Blake, R., Sobel, K. V., & James, T. W. (2004). Neural synergy between kinetic vision and touch. *Psychological Science, 15*,

397-402.

Brouwer, G. J., & van Ee, R. (2006). Endogenous influences on perceptual bistability depend on exogenous stimulus characteristics. *Vision Research, 46*, 3393-3402.

Calvo-Merino, B., Glaser, D. E., Grezes, J., Passingham, R. E., & Haggard, P. (2005). Action observation and acquired motor skills: an FMRI study with expert dancers. *Cerebral Cortex, 15*, 1243-1249.

Carter, O., Konkle, T., Wang, Q., Hayward, V., & Moore, C. (2008). Tactile rivalry demonstrated with an ambiguous apparent-motion quartet. *Current Biology, 18*, 1050-1054.

Casile, A., & Giese, M. A. (2006). Nonvisual motor training influences biological motion perception. *Current Biology, 16*, 69-74.

Colavita, F. B. (1974). Human sensory dominance. *Perception & Psychophysics, 16*, 409-412.

Craighero, L., Fadiga, L., Rizzolatti, G., & Umiltà, C. (1999). Action for perception: a motor-visual attentional effect. *Journal of Experimental Psychology: Human Perception and Performance, 25*, 1673-1692.

Einhäuser, W., Martin, K. A., & König, P. (2004). Are switches in perception of the Necker cube related to eye position? *European Journal of Neuroscience, 20*, 2811-2818.

Ellis, S. R., & Stark, L. (1978). Eye movements during the viewing of Necker cubes. *Perception, 7*, 575-581.

Engel, A., Burke, M., Fiehler, K., Bien, S., & Rösler, F. (2008). Motor learning affects visual movement perception. *European Journal of Neuroscience, 27*, 2294-2302.

Eure, S. P., Hamilton, C. B., & Pheiffer, C. H. (1956). Reversible figures and eye-movements. *American Journal of Psychology, 69*, 452-5.

Hecht, H., Vogt, S., & Prinz, W. (2001). Motor learning enhances perceptual judgment: a case for action-perception transfer. *Psychological Research, 65*, 3-14.

Hommel, B. (2004). Event files: feature binding in and across perception and action. *Trends in Cognitive Sciences, 8*, 494-500.

Hommel, B., Müsseler, J., Aschersleben, G., & Prinz, W. (2001). The Theory of Event Coding (TEC): a framework for perception and action planning. *Behavioral and Brain Sciences, 24*, 849-878; discussion 878-937.

Ichikawa, M., & Masakura, Y. (2006). Auditory stimulation affects apparent motion. *Japanese Psychological Research, 48*, 91-101.

Jones, E., Oliphant, T., Peterson, P., et al. (2001). SciPy: open source scientific tools for python. Available at: http://www.scipy.org

Kawabata, N., Yamagami, K., & Noaki, M. (1978). Visual fixation points and depth perception. *Vision Research, 18*, 853-854.

Laubrock, J., Engbert, R., & Kliegl, R. (2008). Fixational eye movements predict the perceived direction of ambiguous

apparent motion. *Journal of Vision, 8*, 13.1-13.17

Leopold, D. A., & Logothetis, N. K. (1999). Multistable phenomena: changing views in perception. *Trends in Cognitive Sciences, 3*, 254-264.

Logothetis, N. K. (1998). Single units and conscious vision. *Philosophical Transactions of the Royal Society B, 353*, 1801-1818.

Maruya, K., Yang, E., & Blake, R. (2007). Voluntary action influences visual competition. *Psychological Science, 18*, 1090-1098.

McCullagh, P., Weiss, M. R., & Ross, D. (1989). Modeling considerations in motor skill acquisition and performance: an integrated approach. *Exercise and Sport Sciences Reviews, 17*, 475-513.

Müsseler, J. (1999). How independent from action control is perception? An event-coding account for more equally-ranked crosstalks. In G. Ascherleben, T.Bachman & J. Müsseler (Eds.), *Cognitive contributions to the perception of spatial and temporal events* (pp. 121-147). Amsterdam: Elsevier.

Nawrot, M., & Blake, R. (1991). The interplay between stereopsis and structure from motion. *Perception and Psychophysics, 49*, 230-244.

Necker, L. (1832). Observations on some remarkable optical phenomena seen in Switzerland, and on an optical phenomenon which occurs on viewing a figure of a crystal or geometrical solid. *London Edinburgh Philosophical Magazine and Journal of Science, 1*, 329-337.

Oldfield, R. C. (1971). The assessment & analysis of handedness: the Edinburgh inventory. *Neuropsychologia, 9*, 97-113.

Oliphant, T. E. (2007). Python for Scientific Computing. *Computing in Science and Engineering, 9*, 10-20.

Paffen, C. L., Alais, D., & Verstraten, F. A. (2006). Attention speeds binocular rivalry. *Psychological Science, 17*, 752-756.

Posner, M. I. (1980). Orienting of attention. *Quarterly Journal of Experimental Psychology, 32*, 3-25.

Posner, M. I., Nissen, M. J., & Klein, R. M. (1976). Visual dominance: an information-processing account of its origins and significance. *Psychological Review, 83*, 157-171.

Prinz W. (1997). Perception & action planning. *European journal of cognitive psychology, 9*, 129-154.

R Development Core Team (2009). R: A language and environment for statistical computing. Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org.

Reithler, J., van Mier, H. I., Peters, J. C., & Goebel, R. (2007). Nonvisual motor learning influences abstract action observation. *Current Biology, 17*, 1201-1207.

Repp, B. H., & Knoblich, G. (2007). Action can affect auditory perception. *Psychological Science, 18*, 6-7.

Schütz-Bosbach, S., & Prinz, W. (2007). Perceptual resonance: action-induced modulation of perception. *Trends in Cognitive Sciences, 11*, 349-355.

Sekuler, R., Sekuler, A. B., & Lau, R. (1997). Sound alters visual motion perception. *Nature, 385*, 308.

Shimojo, S., & Shams, L. (2001). Sensory modalities are not separate modalities: plasticity and interactions. *Current Opinions in Neurobiology, 11*, 505-509.

Sinnett, S., Spence, C., & Soto-Faraco, S. (2007). Visual dominance and attention: the Colavita effect revisited. *Perception & Psychophysics, 69*, 673-686.

Toppino, T. C. (2003). Reversible-figure perception: mechanisms of intentional control. *Perception and Psychophysics, 65*, 1285-1295.

van Dam, L. C., & van Ee, R. (2005). The role of (micro)saccades and blinks in perceptual bi-stability from slant rivalry. *Vision Research, 45*, 2417-2435.

van Ee, R. (2009). Stochastic variations in sensory awareness are driven by noisy neuronal adaptation: evidence from serial correlations in perceptual bistability. *Journal of the Optical Society of America A, 26*, 2612-2622.

van Ee, R., van Boxtel, J. J., Parker, A. L., & Alais, D. (2009). Multisensory congruency as a mechanism for attentional control over perceptual selection. *Journal of Neuroscience, 29*, 11641-11649.

van Noorden, L. (1975). *Temporal coherence in the perception of tone sequences.* Eindhoven, The Netherlands: Unpublished doctoral dissertation, Eindhoven University of Technology.

Witten, I. B., & Knudsen, E. I. (2005). Why seeing is believing: merging auditory and visual worlds. *Neuron, 48*, 489-496.

Wohlschläger, A. (2000). Visual motion priming by invisible actions. *Vision Research, 40*, 925-930.

Wolfe, J. M., & Bennett, S. C. (1997). Preattentive object files: shapeless bundles of basic features. *Vision Research, 37*, 25-43.

Zhou, W., & Chen, D. (2009). Binaral rivalry between the nostrils and in the cortex. *Current Biology, 19*, 1561-1565.

Zimmer, A. (1913). Die Ursachen der Inversionen mehrdeutiger stereomatrischer Konturenzeichnungen. *Zeitschrift für Sinnespysiologie, 47*, 106–158.

Table 1. Experimental conditions and their order.

condition		stimulus	report	serial order
	No movement	ambiguous	keys	1,9,17
Catch blocks	Congruent	unambiguous	turntable	2/3, 10/11, 18/19
	Incongruent	unambiguous	turntable	
Motor instruction	Clockwise	ambiguous	keys	4/5/6/7/8, 12/13/14/15/16
	Counterclockwise	ambiguous	keys	
	Unrelated	ambiguous	keys	
Motor report	Congruent	ambiguous	turntable	
	Incongruent	ambiguous	turntable	

Table 2. Dominance durations per observer.

Ob-server	No movement	Motor instruction			Motor report	
		Congruent	Unrelated movement	incongruent	congruent	incongruent
1	4.92 ± 8.07	5.98 ± 8.07	6.97 ± 5.41	6.09 ± 6.81	3.58 ± 6.03	6.26 ± 6.22
2	4.22 ± 7.08	4.36 ± 7.64	4.56 ± 5.53	5.08 ± 5.86	7.34 ± 13.97	3.00 ± 4.64
3	14.31 ± 33.61	8.04± 26.63	5.20 ± 11.99	6.12 ± 12.87	14.90 ± 16.16	7.23 ± 12.21
4	7.46 ± 7.19	6.38 ± 8.63	7.14 ± 3.76	6.93 ± 9.20	7.41 ± 8.06	4.79 ± 6.20
5	0.92 ± 16.38	2.26± 18.22	1.91 ± 15.72	3.85 ± 19.42	2.61 ± 10.84	1.53 ± 7.87
6	10.08 ± 12.40	8.40± 15.07	6.25 ± 7.10	10.28 ± 11.44	7.97 ± 18.81	6.27 ± 18.02
7	4.22 ± 15.92	6.35 ± 9.55	5.25 ± 21.20	5.15 ± 9.65	2.72 ± 3.67	2.83 ± 5.26
8	2.01 ± 2.76	1.67 ± 4.54	1.76 ± 2.71	1.55 ± 2.07	2.01 ± 5.68	2.04 ± 1.92
9	16.93 ± 18.74	9.88± 16.36	12.61 ± 16.52	9.91 ± 14.77	9.06 ± 10.36	2.54 ± 5.24
10	7.85 ± 31.71	8.17± 35.23	9.30 ± 20.40	21.74 ± 18.30	6.31 ± 10.25	2.82 ± 6.17
11	4.01 ± 5.02	4.53 ± 4.31	3.83 ± 3.73	4.50 ± 3.86	4.50 ± 5.39	2.92 ± 3.45
12	3.97 ± 6.23	4.59 ± 4.26	4.01 ± 4.67	4.03 ± 4.68	5.48 ± 5.78	3.49 ± 3.60
13	5.18 ± 8.94	3.84 ± 4.43	2.57 ± 2.59	3.31 ± 3.46	4.62 ± 4.91	4.70 ± 4.24
14	5.52 ± 4.86	5.71 ± 8.77	4.32 ± 4.06	6.42 ± 4.10	5.68 ± 5.79	4.04 ± 4.17

Values are median dominance duration in seconds. ± SD gives the standard deviation within each observer.

Study III

Beets I.A.M., Rösler F. and Fiehler K. (submitted for publication). **Acquisition of a bimanual coordination skill after active and passively guided motor training.** *Experimental Brain Research*

Acquisition of a bimanual coordination skill after active and passively guided motor training

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Abstract

Although there have been many investigations about the function of passive movements, little is known about how passively guided movements can influence motor learning. On the one hand, passively induced movements have been found to lead to inferior performance and reduced neural changes after intervention compared to active movements. On the other hand, a recent study indicated that passive guidance could lead to successful motor learning. Here, the role of passively guided motor training in the acquisition of a new bimanual coordination skill is directly compared with active motor training. The findings indicate that passively guided training leads to successful acquisition of a bimanual coordination skill but at a later stage than active training. Performance during the final session was comparable to active training and significantly better than a group which did not receive training. Although the consolidation processes seem to be slower, passively guided motor training can provide a valuable means of training which has implications for motor rehabilitation.

Keywords: bimanual coordination, hand movement, motor control, motor learning

Introduction

When we move our limbs freely, we naturally produce symmetrical or asymmetrical movements. They thus feature a stable phase difference of either 0° (in-phase) or 180° (out-of-phase), respectively (e.g. Kelso 1984; Zanone and Kelso 1992, 1997). Moving one limb ahead of another by e.g. a quarter of a cycle, (i.e., 90° out-of-phase) is not intrinsic to the motor system and requires extensive motor training before it can be executed (Debaere et al. 2004; Swinnen et al. 1997; Zanone and Kelso 1992, 1997). In

one of the classic studies (Zanone and Kelso 1997), participants were trained to execute a 90° out-of-phase pattern or its symmetry partner, 270°. Training was done actively by which participants had to follow a visual metronome indicating the required phase relation with their left and right index fingers, without imposing any movement constraints. The results demonstrated a continuous reduction in absolute error and variability of the trained relative phase over the first training day and a more rapid improvement on the second training day.

Typically, training of such a new coordination skill has been done actively. A direct comparison between passive and active training in acquiring a new motor skill is still lacking. On behavioral measures such as pointing accuracy, active movements have been found to lead to better performance compared to passively trained movements (e.g. Féry et al. 2004; Lotze et al. 2003). On the other hand, it has been shown that pointing to passively presented kinesthetic targets was as accurate as pointing to actively presented kinesthetic targets, whereas variable errors of the movement path were smaller in the active than in the passive condition. Also, when an arm of a subject was passively moved and the supporting device was removed, subjects could actively maintain their arm position (Darling and Miller 1993). Moreover, in one of our recent studies passively guided motor training led to successful learning of a new hand movement over a course of 4 days (Beets et al. in press). Directly comparing active with passively guided training in the acquisition of a new motor skill can provide insight into the learning mechanisms of active versus passive movements.

Previous neurophysiological research suggests that active movements result in superior encoding compared to passively guided movements as revealed by neurophysiological studies (Kaelin-Lang et al. 2005; Lotze et al. 2003; Mima et al. 1999; Nakata et al. 2003). Kaelin-Lang and colleagues (2005) for example, found that active training led to changes in corticomotor excitability whereas passive training did not. However, passively elicited movements are associated with increased blood flow in the same brain regions engaged in executing voluntary movements (Weiller et al. 1996) suggesting similar underlying cortical mechanisms. Moreover, even training consisting of mere motor imagination in the absence of actual movements, results in improved motor performance (Denis 1985) and in brain-activity as observed by executed movements (Gerardin et al. 2000; Jeannerod and Decety 1995).

This study aims to investigate the effects of passively guided versus active training in the acquisition of a new bimanual coordination skill. Based upon our previous study (Beets et al. in press), we hypothesize that passively guided training can lead to successful bimanual skill coordination. However, the active production of a constrained movement may lead to a more accurate internal model

as the muscle activations can be used to anticipate the requirements of the task (Shadmehr and Holcomb 1997). This may lead to a superior performance and a faster consolidation process than passively guided training. Passively guided training may thus lead to learning effects towards latter stages of motor skill acquisition compared to active training.

Materials and Methods

Participants

Forty-five participants between the ages of 17 and 26 years (mean age, standard deviation: 21.0, ± 1.9 years) performed the experiment over four consecutive days. The sample consisted of female participants only to avoid gender effects which have been observed in several spatial tasks (Voyer et al. 1995). All participants had normal or corrected-to-normal vision and were right-handed according to a German translation of the Edinburgh Handedness Inventory (mean, standard deviation: 80.6, ± 14.8) (Oldfield 1971). Naïve participants were recruited from the Philipps-University Marburg, and were compensated with course-credits for their participation. The experiment was performed in accordance with the ethical standard laid down in the Declaration of Helsinki (2000).

Apparatus

We used a programmable movement device consisting of two turntables on the horizontal plane to implement active and passively guided motor training, and movement reproduction (Fig. 1a). The turntables had a diameter of 120 mm and were rotated clockwise by using the attached vertical handles. Their effective radius was 5 cm. The distance between the centers of both turntables was 450 mm. During active and passively guided motor training, the turntables were mechanically coupled with each other, i.e., the relative phase shift between both turntables was fixed at 90°. Both training types thus took place under similar circumstances. During passively guided training, the turntables were driven by a servo-motor, controlled by LabVIEW (http://www.ni.com/labview). Participants were blindfolded, sat facing the workspace and grasped the vertical handles of the motion device with a precision grip using their thumb and index and middle fingers. The chair was adjusted individually to assure a comfortable position during motor training sessions. No support for the arms was provided during passively guided motor training.

Movement reproduction subsequent to each active and passively guided training session was done by actively rotating the same turntables, which were then decoupled to allow free rotation. Movement trajectories were recorded with an ultrasound motion recording device (ZEBRIS CMS20, Zebris Medical GmbH, Isny im Allgäu, Germany) which registers the position of the sensors attached to the top of the vertical handles. The data were sampled with 100 Hz and analyzed offline.
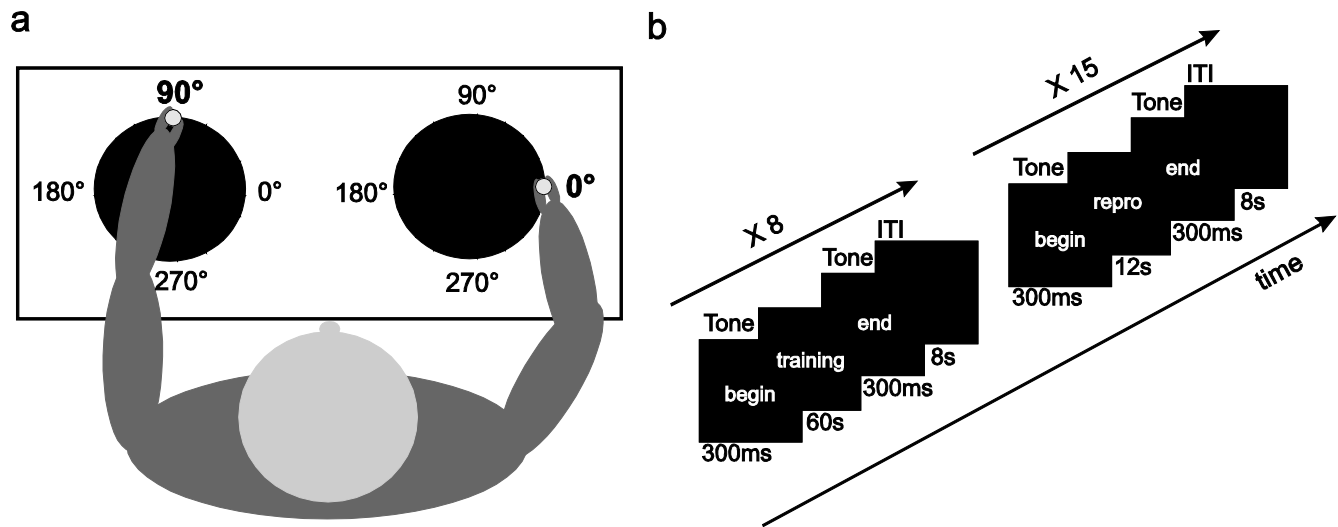

Fig. 1 Experimental setup. **a** Movement device by which participants were trained to move both hands with a relative phase shift of 90°. Each turntable was turned clockwise by a precision grip on both handles. Both turntables could be coupled so that a relative phase shift of 90° could be maintained during training; or decoupled in which turntables could be freely rotated. A motor could be coupled to both turntables for clockwise rotation in passively guided training. **b** Training procedure illustrated for one training session (1 day). Each training block lasted 60s and started and ended with a tone. After 8 training blocks, turntables were decoupled in order to actively reproduce the movement ('repro') in 15 trials lasting 12s each. A metronome (not illustrated here) paced at 1.25 Hz indicated tempo during all phases of the experiment

Procedure

Participants were blindfolded during all phases of the experiment. Before the experiment started, the movement device and the task were explained to participants. The left hand always started at 90°; the right hand at 0° (to provide a reference). Before the first training session, participants were asked to rotate the decoupled turntables clockwise using both hands with a relative phase shift of 90° to obtain a baseline measurement. Baseline measurement consisted of only two trials lasting 12 seconds each to minimize the amount of pre-training motor experience. The tempo was metronome paced at 1.25 Hz,

as well as during both types of training and during movement reproduction. Participants were randomly assigned to two experimental groups (N = 15 each) or a no training group (N = 15) which did not undergo training. Both experimental groups were trained to rotate both hands clockwise with a relative phase shift of 90°. One group was passively guided during training in which the turntables were rotated by the servo-motor; the other group actively rotated the turntables while they were coupled. The instruction in both groups was to feel the movement as well as possible so that they could accurately reproduce it later. During training, the turntables were fixed at a relative phase shift of 90°. Training was divided into eight blocks lasting one minute each, resulting in 600 training cycles per training session. Directly following training, participants actively reproduced the learned movement pattern as well as possible with freely rotating turntable (Fig. 1b). The reproduction session was divided into 15 trials lasting 12 seconds each, using the same metronome frequency; resulting in 225 movement cycles per session. A tone indicated start and end of each trial which were interleaved with an eight seconds break. In the no training group, the same procedure was maintained except that no training phase was present. The requirement was to actively produce the 90° phase shift as well as possible. Their experimental protocol consisted only of the baseline measurement and the 'reproduction' phase where the movement was actively produced. Feedback was not provided in any of the groups.

Movement data pre-processing

Movement data pre-processing was executed in Java (Eclipse 3.3.2). Movement trajectories acquired during active movement reproduction were smoothed using a weighted moving average filter that weighted data point x_i with 0.3; $x_{i\ +/-\ 1}$ with 0.25; and $x_{i\ +/-\ 2}$ with 0.1, to minimize amplitude and phase distortion (Winter 1990). From x and y coordinates, the position angle for both hands per time point was calculated. The relative phase between both hands was calculated by subtracting the angular position of the left hand from the right hand. The pre-processed data had a spatial resolution of 1 mm^2 and a temporal resolution of 10 ms.

Relative phase measures

All movement data were calculated using the last 10.4 seconds of the movement per trial to allow participants to adopt a more stable performance (i.e., the first 2 movement cycles were discarded). To

avoid any misrepresentations due to the circular nature of relative phase (i.e., 0° is equal to 360°); the relative phase difference was converted so that the target relative phase (i.e., 90°) was coded as 0° (cf. Maslovat et al. 2009). The values around 90° were coded in so that they ranged between plus and minus 180° from the target relative phase. A relative phase of 91° would thus be coded as +1°. Performance accuracy was determined by root mean squared error (RMSE) of goal relative phase (RP), reflecting the absolute deviation from the required RP. Within trial standard deviation (SD) of mean RP was taken as a measure of movement precision or stability (e.g., Haken et al. 1985).

Both RMSE and SD during baseline measurement were corrected for the number of executed cycles during baseline, as participants were not always able to keep up with the metronome. To this end, the number of produced cycles was divided by the number of cycles which ought to be produced (i.e., 15). RMSE and SD were then divided by this ratio (i.e., less than 15 reproduced movement cycles led to a ratio < 1, leading to a higher RMSE and SD). We checked whether baseline performance was equal between all groups. The number of movement cycles during reproduction after each training session was as high as required (mean ± SD: 224 ± 14 and did not differ from the required 225; $t_{(44)} = 0.641$, $p = 0.525$), therefore a correction in the reproduction phase was not necessary.

Statistical analyses

R (version 2.10.0; R Development Core Team, 2009) was used to test our circular data. The data yielded a significant Watson's test for circular uniformity and Kuiper's test of uniformity, indicating that data were not equally wrapped around the circular distribution. The high test statistics (7.0292 and 8.5996, respectively) indicated that values lied tightly around the mean (μ). When the data become concentrated around the mean, the results become consistent with linear data (Otieno and Anderson-Cook 2006). Therefore, regular repeated measures ANOVA was used to test for learning effects over sessions and between training groups using SPSS. Tests were 2-sided and the critical level of significance was set at 0.05.

Results

We investigated the role of passively guided compared to active motor training in learning a new bimanual coordination skill. To control for training effects caused by merely being tested over four

consecutive days, performance of a no training group was compared with the experimental groups. To indicate how well participants learned the new movement skill, we report the deviation measure RMSE from the goal relative phase shift RP (i.e., 90°) and the movement variability as indicated by SD of RP.

Progress in motor learning

Movement frequency. As reported above, movement frequency was as high as required (i.e., >99%). Furthermore, there was no overall difference in mean movement frequency between groups ($F_{(2,42)}$ = 2.187, p = 0.125). Therefore, speed cannot account for any further differences on movement accuracy or stability. However, group interacted with session ($F_{(6,126)}$ = 2.666, $p < 0.05$), which is driven by increases from session 1 to 2 in both the passive and the no training groups.

    Root mean squared error (RMSE). **Baseline:** Baseline RMSE of goal RP did not differ between groups ($F_{(2,42)}$ = 0.145, p = 0.865), which indicates comparable pre-training accuracy. **Training effects:** Overall RMSE (fig. 2a) differed between groups ($F_{(2,42)}$ = 8.875, $p < 0.001$), but did not interact with session ($F_{(6,126)}$ = 1.368, p = 0.233). The passively guided group exhibited higher overall RMSE than the active group ($F_{(1,28)}$ = 9.363, $p < 0.01$) and RMSE was significantly higher in the no training group compared to the active group ($F_{(1,28)}$ = 17.625, $p < 0.001$) but did not differ between the passively guided and the no training group ($F_{(1,28)}$ = 1.159, p = 0.291).

    In a second step, we tested our a-priori hypothesis that passively guided training leads to successful motor learning and that such motor learning should occur in latter stages of motor skill acquisition. We first examined the time course of motor learning accuracy within each training group. RMSE significantly decreased over sessions in the passively guided group ($F_{(3,42)}$ = 3.686, $p < 0.05$, partial eta squared = 0.208), but not in the active group ($F_{(3,42)}$ = 0.760, p = 0.523, partial eta squared = 0.052), nor in the no training group ($F_{(3,42)}$ = 1.180, p = 0.329, partial eta squared = 0.078). Second, motor learning accuracy was compared between training groups per session. In session 1 the effect of group was significant ($F_{(2,42)}$ = 7.391, $p < 0.01$). Both the passively guided and the no training group exhibited comparable RMSE ($F_{(1,28)}$ = 0.222, p = 0.641) which were significantly higher than the RMSE of the active group ($F_{(1,28)}$ = 12.102, $p < 0.01$; $F_{(1,28)}$ = 11.585, $p < 0.01$, respectively). No effect of group was found in session 2 ($F_{(2,42)}$ = 2.452, p = 0.1). In session 3, there was a significant group effect ($F_{(2,42)}$ = 4.420, $p < 0.05$). The passively guided and the no training group exhibited higher RMSE than the active group ($F_{(1,28)}$ = 6.002, $p < 0.05$; $F_{(1,28)}$ = 7.243, $p < 0.05$, respectively). The

passively guided group did not differ from the no training group ($F_{(1,28)} = 0.137$, $p = 0.714$). In session 4, a clear group effect was present ($F_{(2,42)} = 10.419$, $p < 0.001$). The passively guided training group exhibited a smaller RMSE than the no training group ($F_{(1,28)} = 6.887$, $p < 0.05$), and did not significantly differ from the active group ($F_{(1,28)} = 3.647$, $p = 0.07$). RMSE was significantly lower in the active compared to the no training group ($F_{(1,28)} = 20.882$, $p < 0.001$). Thus, both active and passively guided training resulted in a superior performance compared to the group which was not trained, while passively guided training resulted in an outcome comparable with active training.

Movement variability. **Baseline:** Baseline within trial SD of RP did not differ between groups ($F_{(2,42)} = 0.437$, $p = 0.649$), which indicates comparable pre-training movement stability. **Training effects:** Overall SD (fig. 2b) did not differ between groups ($F_{(2,42)} = 2.695$, $p = 0.08$) and did not vary as a function of session ($F_{(6,126)} = 0.655$, $p = 0.686$).

To test our a-priori hypothesis that passively guided motor training could lead to successful motor learning, and to directly test between the types of training, we calculated effects separately per training group. SD decreased significantly over sessions in the passively guided group ($F_{(3,42)} = 10.995$, $p < 0.001$, partial eta squared = 0.440), as well as in the active group ($F_{(3,42)} = 10.623$, $p < 0.001$, partial eta squared = 0.575), but also in the no training group ($F_{(3,42)} = 2.875$, $p < 0.05$, partial eta squared = 0.170). Importantly, variability decreased to a clearly smaller extent in the no training group than the active and passive groups as reflected by the effect sizes given by partial eta squared. To test our hypothesis that passively guided training leads to learning in latter stages of motor skill acquisition, the effect of group was calculated per session. However, in none of the sessions, a significant group effect was present (all $p > 0.06$).
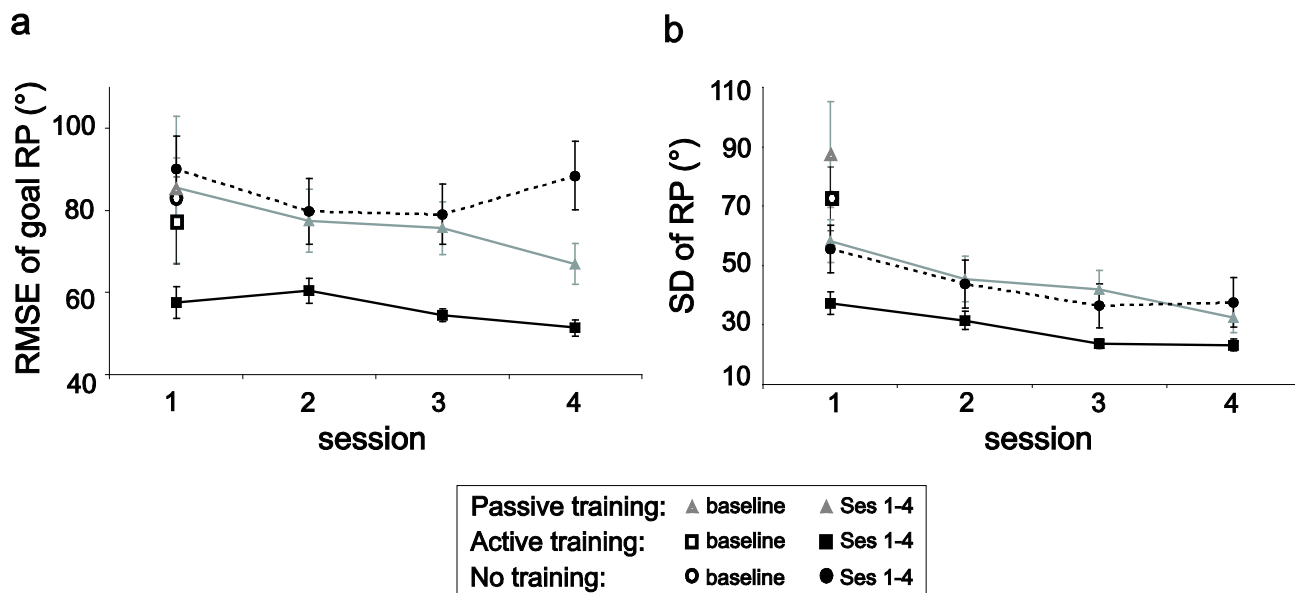
Fig. 2 Movement accuracy (a) and precision (b) over sessions. **a** Root mean squared error (RMSE) of goal relative phase (RP) between hands in degrees. **b** Movement variability (within-trial SD) of relative phase. Error bars represent standard error (SE)

Discussion

The aim of this study was to investigate the role of passively guided compared to active motor training in learning a new bimanual coordination skill. We find a more accurate overall movement reproduction performance of the active than the passive group. The passively guided training group, however, improves in accuracy and ends with similar accuracy as the active group during the final stage of training. Overall movement stability and its improvement are equal for both active and passively guided training groups. Active movement reproduction without training does not affect movement reproduction accuracy, but results in an improvement in stability; however, this effect is substantially smaller than in both training groups.

Progress in motor learning - accuracy

First, active training results in a higher overall accuracy compared to passively guided training and no training in executing a new bimanual coordination skill, which is in line with previous findings (Féry et al. 2004; Kaelin-Lang et al. 2005; Paillard and Brouchon 1968, 1974). Active training thus seems to

lead to superior encoding compared to passively guided training of a new movement. Second, consistent with studies in which a relative phase shift of 90° between both hands was actively trained (e.g. Hodges and Franks 2000, 2002; Maslovat et al. 2009; Rémy et al. 2008; Swinnen et al. 1997; Zanone and Kelso 1992, 1997), we find that passively guided training leads to an increase in accuracy over sessions. In our study, active training, however, does not produce an increasing accuracy, probably because of a ceiling effect due to the relatively high accuracy brought about by the first training session. Third, while passively guided training results in a continuous improvement in accuracy over sessions, this is not the case in the no training group. Although overall accuracy in the passively guided training group does not differ from the no training group, when performance is assessed per session, the passively guided group improves to such an extent that performance during the last session is significantly better compared to the no training group and even does not differ from the active group. This confirms our hypothesis that passively guided training may lead to improvements especially during latter stages of motor skill acquisition due to a flattened learning curve. Consolidation in motor memory is thought to consist of two separate processes; fast learning where improvements occur within one training session, and slow learning over the course of several sessions of practice (Nudo et al. 1996; Karni et al. 1998; Ungerleider et al. 2002). Since passively guided training requires less engagement of brain areas involved in motor control (e.g., Kaelin-Lang et al. 2005; Mima et al. 1999), cortical reorganization may occur at a slower rate, leading to a slower consolidation process. Together with previous findings, movement accuracy seems to improve at very early stages in active training but seems to be delayed in passively guided training suggesting a slower consolidation process. When no training is undergone, accuracy of the bimanual movement does not improve and is worse than both active and passively guided motor training.

Progress in motor learning - variability

First, movement variability was not affected by the type of training, suggesting that movement production over days per se led to the same movement stability. In all groups, movement stability increased, even in the group which did not receive training. However, the effect size in the group without training was substantially smaller than in the active or passive training groups suggesting a smaller improvement in movement stability. Considering the results of movement accuracy, no training increases the stability of the wrong movement pattern as accuracy does not change. The procedure in the no training group which required the production of the target relative phase shift

might have led to motor experience resulting in a more stable movement execution over the course of training. A further issue to note is that the relatively high overall error and variability we found compared to other studies was probably due to lack of visual feedback, blindfolding of participants, and the isodirectional coordination pattern which is associated with less accurate and stable performance than mirror-symmetric coordination patterns (Li et al. 2004). In conclusion, the movement reproduction over days itself seems to bring about improvements in movement stability. However, this improvement is much stronger for the active and the passively guided group. The effect sizes in improvement in stability are nearly equal in the active and passive group suggesting that the effectiveness of obtaining improved movement stability is comparable between both types of training.

Implications

Our finding that passively guided training leads to improvements in accuracy, supports the idea that brain activations during motor tasks are largely related to the processing of afferent information (Weiller et al. 1996). Another finding speaking for the strength of afferent information is that vibration of the biceps tendon could distort position sense by as much as $8°$ (Goodwin et al. 1972). Even though active movements are probably more effective, the afferent information induced by passive movements may have been used by higher cognitive functions as well, e.g. by building an internal model (Klaiman and Karniel 2006; Shadmehr and Holcomb 1997; Wolpert et al. 1995). The increased movement accuracy acquired during latter stages in the passively guided condition suggests an increased reliance on this internal model, which may be mediated by longer-term consolidation.

We cannot exclude the possibility that efferent electromyographic (EMG) activity may have played a role in the passive condition because participants had to actively hold their arms while following the movement of the handle. However, the fact that a clear overall difference between the active and passive groups was present implies that these effects may be small. In a study in which EMG was controlled when executing similar passive and active movements, Craske and Crawshaw (1975) only found small between group differences in pointing accuracy. Moreover, the passive and active movement of the target hand do not affect target location estimation by the other hand (Jones et al. in press), and a superior precision (absolute errors) has been found in passive movements (Chokron et al. 2004). Even the mere passive movement of the eye is sufficient to reduce perceived motion smear during a saccade, just as well as active eye movements (Tong et al. 2008).

Our findings suggest that bimanual motor skill learning on the basis of passively guided and

active motor training may be grounded on similar neural mechanisms. This hypothesis has been supported by previous neurophysiological findings. Passively elicited movements are associated with increased blood flow in regions similar to those activated during active performance of voluntary movements (Weiller et al. 1996). In addition, brain activity elicited by mere motor imagination, overlaps to a great extent with areas associated with the execution of the same action (Gerardin et al. 2000; Jeannerod and Decety 1995). These findings suggest that passive movements are able to evoke a neuronal representation comparable to active movements.

In summary, active and passively guided training lead to improved performance on a new bimanual coordination skill reflected by an increased accuracy and precision over time. The consolidation process in passively guided training, however, appears to be slower than in active training. The results obtained during the last training session indicate that passively guided training can lead to an accuracy level comparable to active training. While the amount of increase in movement stability is similar for active and passively guided training groups, it is much smaller when no training is undergone. The learning success under passive motor training can be of great value for motor rehabilitation of neurologically impaired patients (cf., Hesse et al. 2003; Nelles et al. 1999).

Acknowledgements

References

Beets IAM, Rösler F, Fiehler K (in press) Non-visual motor training affects visual motion perception: Evidence from violating the two-thirds power law. J Neurophysiol

Chokron S, Colliot P, Atzeni T, Bartolomeo P, Ohlmann T (2004) Active versus passive proprioceptive straight-ahead pointing in normal subjects. Brain Cogn 55: 290-294

Craske B, Crawshaw M (1975) Shifts in kinesthesis through time and after active and passive movement. Percept Mot Skills 40: 755-761

Darling WG, Miller GF (1993) Transformations between visual and kinesthetic coordinate systems in reaches to remembered object locations and orientations. Exp Brain Res 93: 534-547

Debaere F, Wenderoth N, Sunaert S, Van Hecke P, Swinnen SP (2004) Changes in brain activation during the acquisition of a new bimanual coodination task. Neuropsychologia 42: 855-867

Denis M (1985) Visual imagery and the use of mental practice in the development of motor skills. Can J Appl Sport Sci 10: 4S-16S

Féry YA, Magnac R, Israel I (2004) Commanding the direction of passive whole-body rotations facilitates egocentric spatial updating. Cognition 91: B1-10

Gerardin E, Sirigu A, Lehericy S, Poline JB, Gaymard B, Marsault C, Agid Y, Le Bihan D (2000) Partially overlapping neural networks for real and imagined hand movements. Cereb Cortex 10: 1093-1104

Goodwin GM, McCloskey DI, Matthews PB (1972) The contribution of muscle afferents to kinaesthesia shown by vibration induced illusions of movement and by the effects of paralysing joint afferents. Brain 95: 705-748

Haken H, Kelso JA, Bunz H (1985) A theoretical model of phase transitions in human hand movements. Biol Cybern 51: 347-356

Hesse S, Schulte-Tigges G, Konrad M, Bardeleben A, Werner C (2003) Robot-assisted arm trainer for the passive and active practice of bilateral forearm and wrist movements in hemiparetic subjects. Arch Phys Med Rehabil 84: 915-920

Hodges NJ, Franks IM (2000) Attention focusing instructions and coordination bias: Implications for learning a novel bimanual task. Hum Mov Sci 19: 843-867

Hodges NJ, Franks IM (2002) Learning as a function of coordination bias: building upon pre-practice behaviours. Hum Mov Sci 21: 231-258

Jeannerod M, Decety J (1995) Mental motor imagery: a window into the representational stages of action. Curr Opin Neurobiol 5: 727-732

Jones AH, Cressman EK, Henriques DYP (in press). Proprioceptive localization of the left and right hands. Experimental Brain Research.

Kaelin-Lang A, Sawaki L, Cohen LG (2005) Role of voluntary drive in encoding an elementary motor memory. J Neurophysiol 93: 1099-1103

Karni A, Meyer G, Rey-Hipolito C, Jezzard P, Adams MM, Turner R, Ungerleider LG (1998) The acquisition of skilled motor performance: fast and slow experience-driven changes in primary motor cortex. Proc Natl Acad Sci U S A 95: 861-868

Kelso JA (1984) Phase transitions and critical behavior in human bimanual coordination . Am J Physiol 246: R1000-R1004

Klaiman E, Karniel A (2006) Bimanual adaptation: internal representations of bimanual rhythmic movements. Exp Brain

Res 171: 204-214

Li Y, Levin O, Carson RG, Swinnen SP (2004) Bimanual coordination: constraints imposed by the relative timing of homologous muscle activation. Exp Brain Res 156: 27-38

Lotze M, Braun C, Birbaumer N, Anders S, Cohen LG (2003) Motor learning elicited by voluntary drive. Brain 126: 866-872

Maslovat D, Lam MY, Brunke KM, Chua R, Franks IM (2009) Anchoring in a novel bimanual coordination pattern. Hum Mov Sci 28: 28-47

Mima T, Sadato N, Yazawa S, Hanakawa T, Fukuyama H, Yonekura Y, Shibasaki H (1999) Brain structures related to active and passive finger movements in man. Brain 122 (Pt 10): 1989-1997

Nakata H, Inui K, Wasaka T, Nishihira Y, Kakigi R (2003) Mechanisms of differences in gating effects on short-and long-latency somatosensory evoked potentials relating to movement. Brain Topogr 15: 211-222

Nelles G, Spiekermann G, Jueptner M, Leonhardt G, Muller S, Gerhard H, Diener HC (1999) Reorganization of sensory and motor systems in hemiplegic stroke patients. A positron emission tomography study. Stroke 30: 1510-1516

Nudo RJ, Milliken GW, Jenkins WM, Merzenich MM (1996) Use-dependent alterations of movement representations in primary motor cortex of adult squirrel monkeys. J Neurosci 16: 785-807

Oldfield RC (1971) The assessment and analysis of handedness: the Edinburgh inventory. Neuropsychologia 9: 97-113

Otieno BS, Anderson-Cook CM (2006) Measures of preferred direction for environmental and ecological circular data. Environ Ecol Stat 13: 311-324

Paillard J, Brouchon M (1968) Active and passive movements in the calibration of position sense. S.J. Freedman (ed), pp 37-55

Paillard J, Brouchon M (1974) A proprioceptive contribution to the spatial encoding of position cues for ballistic movements. Brain Research 71: 273-284

R Development Core Team (2009). R: A language and environment for statistical computing. Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org.

Rémy F, Wenderoth N, Lipkens K, Swinnen SP (2008) Acquisition of a new bimanual coordination pattern modulates the cerebral activations elicited by an intrinsic pattern: an fMRI study. Cortex 44: 482-493

Shadmehr R, Holcomb HH (1997) Neural correlates of motor memory consolidation. Science 277: 821-825

Swinnen SP, Lee TD, Verschueren S, Serrien DJ, Bogaerds H (1997) Interlimb coordination: Learning and transfer under different feedback conditions. Hum Mov Sci 16: 749-785

Tong J, Stevenson SB, Bedell HE (2008) Signals of eye-muscle proprioception modulate perceived motion smear. J Vis 8: 7.1-6

Ungerleider LG, Doyon J, Karni A (2002) Imaging brain plasticity during motor skill learning. Neurobiol Learn Mem 78:

553-564

Voyer D, Voyer S, Bryden MP (1995) Magnitude of sex differences in spatial abilities: a meta-analysis and consideration of critical variables. Psychol Bull 117: 250-270

Weiller C, Juptner M, Fellows S, Rijntjes M, Leonhardt G, Kiebel S, Muller S, Diener HC , Thilmann AF (1996) Brain representation of active and passive movements. Neuroimage 4: 105-110

Winter D.A. (1990) Biomechanics and motor control of human movement. Wiley-Interscience, Waterloo, Canada

Wolpert DM, Ghahramani Z, Jordan MI (1995) An internal model for sensorimotor integration. Science 269: 1880-1882

Zanone PG, Kelso JA (1997) Coordination dynamics of learning and transfer: collective and component levels. J Exp Psychol Hum Percept Perform 23: 1454-1480

Zanone PG, Kelso JA (1992) Evolution of behavioral attractors with learning: nonequilibrium phase transitions. J Exp Psychol Hum Percept Perform 18: 403-421

III. Zusammenfassung

Der Gedanke, dass Wahrnehmung und Handlung stark miteinander verknüpft sind, existiert schon seit über einem Jahrhundert. Schon Lotze (1852) und James (1890) beschrieben, dass bei jeder Handlung, die man wahrnimmt, die eigenen motorischen Repräsentationen aktiviert werden. Diese These ist die Grundlage von modernen Theorien (Hommel et al. 2001; Prinz 1997) über Handlung und Wahrnehmung. Das vor kurzem entdeckte Spiegelneuronensystem bestätigt, dass das motorische System an der Wahrnehmung von Handlungen beteiligt ist. Dieses System könnte zum Wiedererkennen und Verstehen der Handlungen und Intentionen anderer dienen (Rizzolatti & Craighero 2004). Während der Effekt von Wahrnehmung auf Handlung intensiv erforscht wurde, gibt es nur wenige Studien, die umgekehrt einen direkten Einfluss von Handlung auf die Wahrnehmung nachweisen konnten. Um Letzteres zu untersuchen, sollte jede bereits existierende visuelle oder motorische Erfahrung mit einer Handlung und jede Art visuelle Rückmeldung während der Bewegungsausführung ausgeschlossen werden. Daher bieten sich solche Bewegungen an, die für das menschliche motorische System neuartig und nicht ohne Training ausführbar sind. Bisher existiert lediglich eine Studie, in der eine atypische Bewegung trainiert und der Effekt dieses Trainings auf die visuelle Wahrnehmung der gleichen Bewegung untersucht wurde (Casile & Giese 2006). Das Training bestand aus einer zyklischen Armbewegung, bei der die Bewegung beider Arme um 270° gegeneinander verschoben war. Bei natürlichen Bewegungen oszillieren Gliedmaßen nur in Phasenunterschieden von 0° (z.B. beim Rudern) oder 180° (z.B. beim Gehen). Andere Verhältnisse der Gliedmaßen zueinander sind erst nach intensivem Training erlernbar (z.B. Zanone & Kelso 1992, 1997). Vor und nach dem Training absolvierten die Probanden in der Untersuchung von Casile & Giese (2006) einen visuellen Test, bei dem verschiedene Bewegungen voneinander unterschieden werden mussten. Probanden, die das 270° Phasenmuster trainiert hatten, konnten die trainierte Bewegung im visuellen Nachtest besser von abweichenden Bewegungen unterscheiden. Ein Nachteil dieser Studie bestand jedoch darin, dass nur zwei Probanden die Bewegung gelernt hatten. Zudem wurde im visuellen Test nur die Anzahl der Hits betrachtet, sodass nicht ausgeschlossen werden kann, dass diese Verbesserung nur durch eine Verschiebung des Entscheidungskriteriums zustande kam (MacMillan & Creelman 2005; Swets & Picket 1982).

In Studie I wurde der Effekt des Erlernens einer untypischen Bewegung auf die visuelle Wahrnehmung der gleichen und verwandten Bewegungen untersucht. Hierzu wurden zwei Gruppen

von Probanden in standardisierter Weise über vier Tage trainiert. Die erlernte Bewegung war immer kreisförmig, aber das Geschwindigkeitsmuster war entweder schwach oder stark elliptisch. Hiermit wurde die natürliche Beziehung zwischen Krümmung und Geschwindigkeit, und somit ein wichtiges Gesetz der Bewegungsausführung, das „two-thirds power law", verletzt. Die Bewegungen der Probanden, die ein extrem elliptisches Geschwindigkeitsprofil trainierten, wurden von Tag zu Tag besser ausgeführt, im Gegensatz zu Probanden, die das schwache elliptische Muster trainiert hatten. Dies kann dadurch erklärt werden, dass die Verbesserungsmöglichkeiten kleiner waren als in der extremen Bedingung und dass es schwieriger war, die genauen Verhältnisse zwischen schnellen und langsamen Abschnitten zu erkennen. D-Strich (oder d') wurde als abhängiges Maß im visuellen Test benutzt, um die Anzahl der Hits um die Anzahl falscher Alarme zu korrigieren. Im visuellen Nachtest wurde die erlernte Bewegung besser von ähnlichen Bewegungen diskriminiert als im visuellen Vortest. Dieser Effekt war aber auch nachweisbar bei nicht erlernten, elliptischen Geschwindigkeitsmustern. Das heißt, dass die erlernte Bewegung bei der Diskrimination von ähnlichen Bewegungen auch von Nutzen gewesen sein kann.

In Studie II wurde der Echtzeit-Effekt von der Handlung auf die Wahrnehmung untersucht. Stimuli, die bei gleicher physikalischer Gegebenheit unterschiedliche Wahrnehmungen zulassen sind hierfür gut geeignet. Zwei Studien untersuchten bereits, ob die Handlung die Wahrnehmung binokularer (Maruya et al. 2007) oder mehrdeutiger (Wohlschläger 2000) Stimuli beeinflussen kann. Der Stimulus wurde in diesen Studien immer in Abhängigkeit von der Handlung präsentiert und die Geschwindigkeit des bewegenden visuellen Stimulus in der binokularen Aufgabe wurde sogar von der Geschwindigkeit der Handlung bestimmt. Somit war die Handlung mit der Wahrnehmung der Bewegung konfundiert, was ein methodisches Problem darstellt.

In Studie II wurde immer ein mehrdeutiger Stimulus unabhängig von der ausgeführten Handlung dargeboten. Der Stimulus bestand aus 400 bewegten Punkten in Form eines vertikal orientierten Zylinders, der sich um seine vertikale Achse bewegte und sich aus Sicht des Wahrnehmenden im oder gegen den Uhrzeigersinn drehte. Während der Proband den Stimulus beobachtete, wurden von dem Probanden entweder keine aktiven Bewegungen ausgeführt; oder er führte Bewegungen ohne visuelle Rückmeldung (mit verdeckter Hand) aus. Wenn eine Bewegung ausgeführt wurde, war sie entweder vertikal (nicht verwandt mit dem visuellen Stimulus) oder rotierend (verwandt mit dem Stimulus) im Uhrzeigersinn oder gegen den Uhrzeigersinn, die abhängig oder unabhängig von der Wahrnehmung sein konnte. Wenn die Handbewegung abhängig war von der Wahrnehmung, konnte die Bewegung entweder kongruent (in die gleiche Richtung)

oder inkongruent (in die entgegengesetzte Richtung) sein. Der Median der Zeitdauer, in denen keine veränderte Bewegungsrichtung wahrgenommen wurde, war gleich lang, in den Bedingungen in denen keine aktive Bewegung ausgeführt wurde bzw. in denen eine vorgegebene Bewegung ausgeführt wurde, die nicht verwandt oder verwandt war mit dem Stimulus, und unabhängig von der Wahrnehmung des Reizes. Bewegung an sich hatte also keinen Effekt auf die Wahrnehmung, selbst wenn die Achsen der Bewegung übereinstimmten. Wenn aber die wahrgenommene Rotation des Reizes mit einer Bewegung angegeben wurde, dann war der Medianschnitt der Zeitdauer kürzer, wenn die Bewegung entgegen der Wahrnehmung ausgeführt wurde, im Vergleich zu Bewegungen die kongruent (mit) der Wahrnehmung ausgeführt wurden. Die Wahrnehmung ist also instabiler, wenn inkongruente Handlungen ausgeführt werden. Das deutet darauf hin, dass die Wahrnehmungstendenz in die Richtung der ausgeführten Bewegung geht. Dies gilt jedoch nur, wenn die Handlung mit der Wahrnehmung direkt verknüpft ist. Handlung beeinflusst die Wahrnehmung somit nur, wenn sie intentional ist und somit relevant für den Wahrnehmungskontext.

Studie I zeigte, dass passives Training zu erfolgreichem Lernen einer Bewegung führen kann. Daraus ergibt sich die Frage, inwieweit sich das passive vom aktiven Training unterscheidet. Einerseits gibt es Studien, die berichten, dass aktive Bewegungen im Bezug auf Zeigeaufgaben zu besserer Leistung führen (Féry et al. 2004; Kaelin-Lang et al. 2005; Paillard & Brouchon 1968, 1974). Andererseits fand man heraus, dass passive Bewegungen zu ähnlichen neuronalen Veränderungen führen (Gerardin et al. 2000; Weiller et al. 1996) wie aktive Bewegungen, und dass sogar passiv geführte Augenbewegungen zu gleichen Effekten führen wie aktiv ausgeführte Augenbewegungen (Tong et al. 2008). Passiv geführte Bewegungen sind insbesondere wichtig für Rehabilitationspatienten (Hesse et al. 2003; Nelles et al. 1999). Bisher gibt es keine Studien, die Effekte von aktiven und passiven Bewegungen beim Erlernen einer neuen Bewegung verglichen haben. Dieser Vergleich ist allerdings wichtig, um genauer feststellen zu können, wie sich passive Bewegungen von aktiven Bewegungen unterscheiden. Hierzu wurde für Studie III ein Gerät gebaut, mit welchem unter gleichen Bedingungen ein neues bimanuales Bewegungsmuster entweder aktiv oder passiv trainiert werden konnte. Dazu konnten beide Hände mit einer Phasendifferenz von 90° entweder passiv oder aktiv bewegt werden. Je eine Gruppe mit aktiver bzw. einer passiven Bewegung wurden über vier Tage trainiert und die Performanz (absoluter Fehler und Stabilität) wurde nach jedem Trainingstag gemessen. Während des Trainings und des Tests waren die Augen verbunden, sodass es keine visuelle Rückmeldung über die Bewegungsausführung gab. Die Leistung verbesserte sich in beiden Gruppen über die Tage. Die aktiv trainierte Gruppe zeigte

allerdings eine bessere Leistung. Am letzten Tag war die Leistung in beiden Gruppen gleich. Zudem war der Zunahme in Bewegungsstabilität gleich groß in beiden Gruppen, während diese viel kleiner war in einer Kontrollgruppe, die nicht trainiert wurde (und nur aktiv versuchte, die Bewegung auszuführen). Zusammenfassend ergab sich, dass Konsolidierungsprozesse in motorischem Lernen durch passives Training langsamer sind als durch aktives Training und dass beide Trainingstypen erfolgreiches Lernen hervorbringen können.

Diese Arbeit hat gezeigt, dass Handlung einen Effekt auf Wahrnehmung hat, und dass es möglich ist, untypische Bewegungsarten zu lernen, selbst mit passiv geführten Bewegungen während des Trainings. Außerdem kann das Lernen einer neuen Bewegung zu besseren Diskriminationsleistungen der gleichen und ähnlichen visuell wahrgenommenen Bewegungen führen. Handlungen können die Wahrnehmung allerdings nur beeinflussen, wenn sie aufgrund der Aufgabenstellung miteinander verknüpft werden müssen.

Literatur

Sehe Kapitel I.

IV. Samenvatting

Het idee dat perceptie en actie sterk met elkaar verbonden zijn bestaat al langer dan een eeuw. Lotze (1852) en James (1890) beschreven al dat elke waargenomen actie representaties in ons eigen motorische systeem oproept. Dit idee is later in andere theorieën, zoals 'common coding' (Prinz 1997) en de 'theory of event coding' (TEC) (Hommel et al. 2001) belangrijk geweest. Het recentelijk ontdekte spiegelneuronensysteem bevestigt dat het motorische systeem betrokken is bij de waarneming van actie. Het spiegelneuronensystem speelt waarschijnlijk een rol in het begrijpen en inschatten van andermans acties en intenties (Rizzolatti & Craighero 2004). Hoewel aan de ene kant het effect van perceptie op actie grondig onderzocht is, bestaan er maar weinig publicaties die het omgekeerde; het effect van actie op perceptie onderzoeken. Om zo'n effect te onderzoeken zou de visuele feedback tijdens het experiment uitgesloten moeten worden alsook elke bestaande visuele of motorische ervaring met de beweging. Idealiter onderzoekt men dus bewegingen die nieuw zijn en niet intrinsiek aan ons motorische systeem, waarbij de eigen bewegingen tijdens het experiment niet gezien worden. Tot nu toe is er één publicatie waarin zo'n atypische beweging getraind is om het effect van deze nieuwe motorische representatie op perceptie te onderzoeken (Casile & Giese 2006). Er werd in dit geval een beweging getraind waarbij beide handen een coordinatiepatroon van 270° volgden; de ene hand lag ongeveer een kwart beweging voor op de andere. In natuurlijke bewegingen oscilleren ledematen alleen in fasenverschillen van 0° (bv. tijdens het roeien) en 180° (bv. tijdens het lopen). Andere patronen zijn meestal niet intrinsiek maar wel aan te leren door ze intensief te trainen (bv. Zanone & Kelso 1992, 1997). Voor en na de training werd een visuele test afgenomen waarin bewegingen van elkaar onderscheiden moesten worden. Proefpersonen die getraind waren om hun armen met een faseverschil van 270° te bewegen, konden de getrainde beweging ook beter herkennen in de visuele natest. Een nadeel van deze studie was dat slechts twee proefpersonen de getrainde beweging ook werkelijk konden uitvoeren, en dat alleen het aantal hits gerapporteerd werd in de visuele test, zodat niet kan worden uitgesloten dat deze verbetering tot stand is gekomen door een verschuiving in het criterium (bias) (MacMillan & Creelman 2005; Swets & Picket 1982).

In studie I is het effect van het leren van een atypische beweging op visuele perceptie van dezelfde en gerelateerde bewegingen onderzocht. Er werden twee groepen van proefpersonen vier dagen lang op een gestandardiseerde manier getraind. De beweging die getraind werd was

cirkelvormig maar het snelheidsprofiel kon licht of sterk elliptisch zijn. Hierbij was de snelheid relatief snel aan de zijkanten van de circel en relatief langzaam aan de boven- en onderkant van de circel. Hierdoor werd de natuurlijke verhouding tussen kromming en snelheid verstoord, waardoor er afgeweken werd van den een belangrijke wet: de „two-thirds power law". De bewegingen van de groep die het sterk elliptische snelheidsprofiel getraind hadden verbeterden met de tijd, terwijl dat niet het geval was in de groep die het licht elliptische snelheidsprofiel trainde. Reden daarvoor was waarschijnlijk dat er minder ruimte voor verbetering was en dat het waarschijnlijk moeilijker was de precieze verhoudingen tussen maximum en minimum snelheid in te schatten doordat het verschil hiervan kleiner was. D-prime (d') is als afhankelijke maat voor visuele discriminatie gebruikt, om het aantal hits voor het aantal false alarms te corrigeren. De getrainde beweging werd in de visuele natest beter gediscrimineerd van licht afwijkende bewegingen dan voor de training. Dit effect werd echter ook overgedragen aan de niet getrainde, visuele stimuli met elliptische snelheidsprofielen maar niet aan stimuli met niet-elliptische snelheidsprofielen. De geleerde beweging is waarschijnlijk nuttig geweest bij het inschatten van bewegingen met dezelfde kwalitatieve kenmerken.

In studie II werd het online effect van actie op perceptie getest. Stimuli waarbij de visuele input altijd constant is, terwijl de peceptie tussen twee interpretaties kan wisselen zijn hier goed inzetbaar. Tot nu toe hebben twee studies onderzocht of actie de waarneming van binoculaire (Maruya et al. 2007) en van meerduidige (Wohlschläger 2000) stimuli kan beïnvloeden. De stimuluspresentatie was hier afhankelijk van de actie die uitgevoerd werd. De stimulus begon bijvoorbeeld pas te bewegen in zodra de beweging gestart was en de snelheid van de stimulus werd in de binoculaire taak door de snelheid van de uitgevoerde actie bepaald. Doordat actie hier al een effect uitoefent op de stimulus, kan niet meer vastgesteld worden dat de effecten door deze manipulatie of door de actie zelf onstaan zijn.

In studie II werd altijd een meerduidige stimulus gepresenteerd die onafhankelijk was van de uitgevoerde actie. De stimulus was een verticale cylinder die bestond uit 400 bewegende punten De draaiing van de cylinder om de verticale as kon waargenomen worden als met de klok mee of tegen de klok in. Omdat de twee interpretaties even plausibel zijn, kan de waargenomene richting steeds wisselen. De duur dat een bepaalde richting waargenomen wordt, wordt als afhankelijke maat genomen om de stabiliteit van de waarneming te meten. Tijdens de waarneming van de cylinder voerden de proefpersonen of geen bewegingen uitgevoerd of bewegingen die niet door de proefpersoon zelf gezien konden worden. Deze bewegingen waren of niet gerelateerd aan de

stimulus (verticaal); of ze waren gerelateerd aan de stimulus (met de klok mee of tegen de klok in) maar niet aan de waarneming; of ze waren gekoppeld met de perceptuele bewegingsrichting van dat moment. Wanneer de handbeweging gekoppeld was aan de stimulus kon deze beweging in dezelfde richting zijn als de waargenomen beweging (congruent) of in de andere richting (incongruent). De tijdsduur dat een beweging werd waargenomen was even lang voor condities waarin geen beweging werd uitgevoerd als voor condities waarin bewegingen in een voorgedefinieerde richting werden uitgevoerd, ook als deze gerelateerd waren aan de stimulus. Wanneer de waargenomene bewegingsrichting echter aangegeven werd door de draairichting van de actie, duurden de perceptuele interpretaties veel korter in gevallen waar incongruent gedraaid werd. De waarneming kon dus gedestabiliseerd worden wanneer incongruente acties uitgevoerd werden. Actie kan echter alleen een invloed hebben op perceptie als actie en perceptie aan elkaar gekoppeld zijn.

Doordat studie I gevonden heeft dat bewegingen geleerd kunnen worden door training met passieve bewegingen, is het de vraag in hoeverre passief trainen zich onderscheidt van actief trainen. Aan de ene kant is er in aanwijsopgaves gevonden dat actieve bewegingen tot betere prestaties leiden (Féry et al. 2004; Kaelin-Lang et al. 2005; Paillard & Brouchon 1968, 1974). Aan de andere kant leiden passieve bewegingen tot vergelijkbare neuronale veranderingen in motorische hersengebieden als actieve bewegingen (Gerardin et al. 2000; Weiller et al. 1996) en zelfs passief gedreven oogbewegingen leiden tot dezelfde effecten als actieve oogbewegingen (Tong et al. 2008). Passieve bewegingen zijn erg belangrijk voor revalidatie (Hesse et al. 2003; Nelles et al. 1999). Tot nu toe is er nog geen directe vergelijking geweest tussen actieve en passieve bewegingen in het aanleren van een nieuwe beweging. Zo'n vergelijking is belangrijk om preciezere uitspraken te kunnen doen over de vergelijking tussen actieve en passieve bewegingen. Om deze vraag te kunnen beantwoorden is voor Studie III er een apparaat gebouwd waarop onder dezelfde omstandigheden passief of actief een nieuw bewegingspatroon getraind kon worden, waarin beide handen met een faseverschil van 90° bewogen. Allebei de groepen werden vier dagen lang getraind waarop de prestaties elke dag onderzocht werden (gekeken werd naar absolute fout en stabiliteit van het faseverschil). Proefpersonen werden geblinddoekt, zodat er geen visuele informatie kon interfereren met de pure motorische ervaring. De prestaties verbeterden in beide groepen over de dagen, maar de accuratesse was beter in de groep die actief getraind werd. De accuratesse was echter vergelijkbaar tussen beide groepen op de laatste trainingsdag. Ook was de toename in bewegingsstabiliteit even sterk in beide groepen, terwijl deze veel kleiner was dan in een groep die niet getraind werd (en de beweging alleen actief probeerde uit te voeren). De consolidering van de nieuwe beweging verliep

dus sneller in de actief getrainde groep dan in de passieve groep en beide traintypes kunnen leiden tot een succesvolle verwerving van een nieuwe, atypische beweging.

In dit proefschrift is bewijs geleverd dat actie een effect op perceptie heeft, en dat het mogelijk is nieuwe, atypische bewegingen te leren, zelfs als de training bestaat uit passieve bewegingen. Het leren van een nieuwe beweging leidt tot een beter visueel onderscheidingsvermogen van de geleerde beweging en van bewegingen met dezelfde karakteristieken. Als acties tegelijk met perceptie worden uitgevoerd, kan actie perceptie alleen beïnvloeden als deze voor de taak met elkaar gekoppeld moeten worden.

Literatuur

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Eingeladene Vorträge

5.5.2009: Von Dr. Mathias Reisser & Prof. Dr. Jörn Munzert, Justus-Liebig-Universität Gießen, Fachbereich Sportpsychologie und Bewegungswissenschaft. Vortrag im AG-Kolloquium: „Der Einfluss von motorischem Lernen auf visuelle Wahrnehmung".

12.3.2010: Von Prof. Dr. Stephan Swinnen, Universität Leuven, Biomedical Kinesiology / Movement Control and Neuroplasticity. Vortrag im AG-Kolloquium: "Motor learning and motor-perceptual interactions".

Publikationen

Slagter H.A., Johnstone T., **Beets** I.A.M. and Davidson R.J (2010). Neural competition for conscious representation across time: An fMRI study. *PLoS ONE 5*(5): e10556. doi:10.1371/journal.pone.0010556.

Beets I.A.M., Rösler F. and Fiehler K. (accepted for publication). Non-visual motor learning improves visual motion perception: Evidence from violating the two-thirds power law. *Journal of Neurophysiology*

Beets I.A.M.*, 't Hart B.M.*, Rösler F., Henriques D.Y.P., Einhäuser W. and Fiehler K. (under review). Online action-to-perception transfer: only percept-dependent action affects perception. *IAMB & BmtH contributed equally. *Vision Research*

Beets I.A.M., Rösler F. and Fiehler K. (submitted for publication). Acquisition of a bimanual coordination skill after active and passively guided motor training. *Experimental Brain Research*

Peer-reviewed Abstracts

Slagter, H.A., Johnstone, T., **Beets**, I.A.M., & Davidson, R.J. (2008). Conscious perception in the attentional blink, an fMRI study. Society for Neuroscience, Washington, USA (Poster).

Beets, I.A.M., Slagter, H.A., Johnstone, T., Kelly, B, and Davidson, R.J. (2008). Effects of threat-evoked anxiety on attention and conscious perception. Tagung experimentell arbeitender Psychologen, Marburg, Germany (Poster).

Beets, I.A.M., Fiehler, K., Rösler, F. (2008). Effects of motor learning on visual elliptic speed-pattern

perception. Neurowissenschaftliche Nachwuchskonferenz, Ellwangen, Germany (Poster).

Beets, I.A.M., Rösler, F., & Fiehler, K. (2009). Non-visual motor learning enhances visual motion perception: Evidence from violating the two-thirds power law. Progress in Motor Control, Marseille, France (Poster).

Beets, I.A.M., Rösler, F., & Fiehler, K. (2009). Non-visual motor learning enhances visual motion perception: Evidence from violating the two-thirds power law. Symposium University of Potsdam and Beijing Normal University, Beijing, China (Poster).

Beets, I.A.M., Rösler, F., & Fiehler, K. (2009). Passive and active training of a new bimanual coordination skill. Society for Neuroscience, Chicago, USA (Poster).

Fiehler, K., 't Hart, B.M., **Beets**, I.A.M., Henriques, D.Y.P., & Einhäuser, W. (2010). The impact of action on perception: Evidence from ambiguous visual stimuli. 33rd European Conference on Visual Perception (ECVP), Lausanne, Switzerland (Poster).

Erklärung

Ich versichere, dass ich meine Dissertation

„On the effects of action on visual perception & How new movement types are learned"

selbständig und ohne unerlaubte Hilfe angefertigt und mich dabei keiner anderen als der von mir ausdrücklich bezeichneten Quellen und Hilfen bedient habe.

Diese Dissertation wurde in der jetzigen oder einer ähnlichen Form noch bei keiner anderen Hochschule eingereicht und hat noch keinen sonstigen Prüfungszwecken gedient.

Marburg, 07.07.2010

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(Ort/Datum) (Unterschrift mit Vor- und Zuname)