Shaping motor behavior on multiple levels by modifying perceptual settings

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1   Introduction

Peak performance in sport is achieved on the motor and the perceptual-cognitive level. The success of long range and lay off passes depends on the spatial accuracy of the passes themselves as well as on the temporal alignment of the own movement with the predicted movement of the team-mate. It is hypothesized that the own movements as well as the prediction of movements are based on internal representations (Knoblich, Seigerschmidt, Flach & Prinz, 2002; Schack, Schütz, Krause & Seegelke, 2016). Those representations can adapt: quickly, when players have to adjust their paths; slowly during exposure to altered environmental conditions, in the context of motor and cognitive development as well as by goal-directed exercise and training.

It is the aim of the science of motor behavior in sport, one sub-discipline of sport science, to understand and enhance such performance. To the major research topics belong the internal control of movements as well as the learning, refinement and recovery of motor skills. Research predominantly focuses on sport-related contexts and sport practice is the intended field of application (Hossner, Müller & Voelcker-Rehage, 2013). However, sport science is a cross-sectional science and thus it is closely connected to other disciplines. Its methods and findings can be applied in a variety of contexts, and the knowledge gained in other disciplines can be transferred to the field of sport science (Krüger & Emrich, 2013). Accordingly, the methods and principles derived from sport scientific research can not only be applied to enhance sport performance, but also to address general competences and skills in a variety of fields such as rehabilitation, activities of daily living, work and school.

The complexity in sport situations meaning a large number of influencing factors is challenging: A pass in handball requires the coordination of the eyes, one hand, one arm and the upper body. Furthermore, as exemplified, different types of representations seem to be at work. Therefore, to understand motor behavior in sports, it is deemed necessary to investigate motor behavior on different levels. In this regard, hierarchical models on cognitive-motor control, which have been developed in the fields of psychology (Chein & Schneider, 2012), computational neuroscience (Haruno, Wolpert & Kawato, 2003) as well as movement science (Schack & Ritter, 2009), provide starting points. According to theory, different hierarchies can be accessed by varying movement types and tasks.

The present thesis follows a similar approach. It subsumes basic and applied research activities which were performed to understand and support movements of different complexity (Figure 1). The most distinctive feature of the approach is the implementation of two methods that allow to vary and shape perceptual scenes and thus motor behavior: Visuomotor methods are applied to adapt movement precision by designing visual information about single movement features. The sonification method is applied to address

movement representations of higher complexity by transforming two to four movement parameters to sound. It will be shown that these methods allow addressing and enhancing a broad spectrum of different movement types.
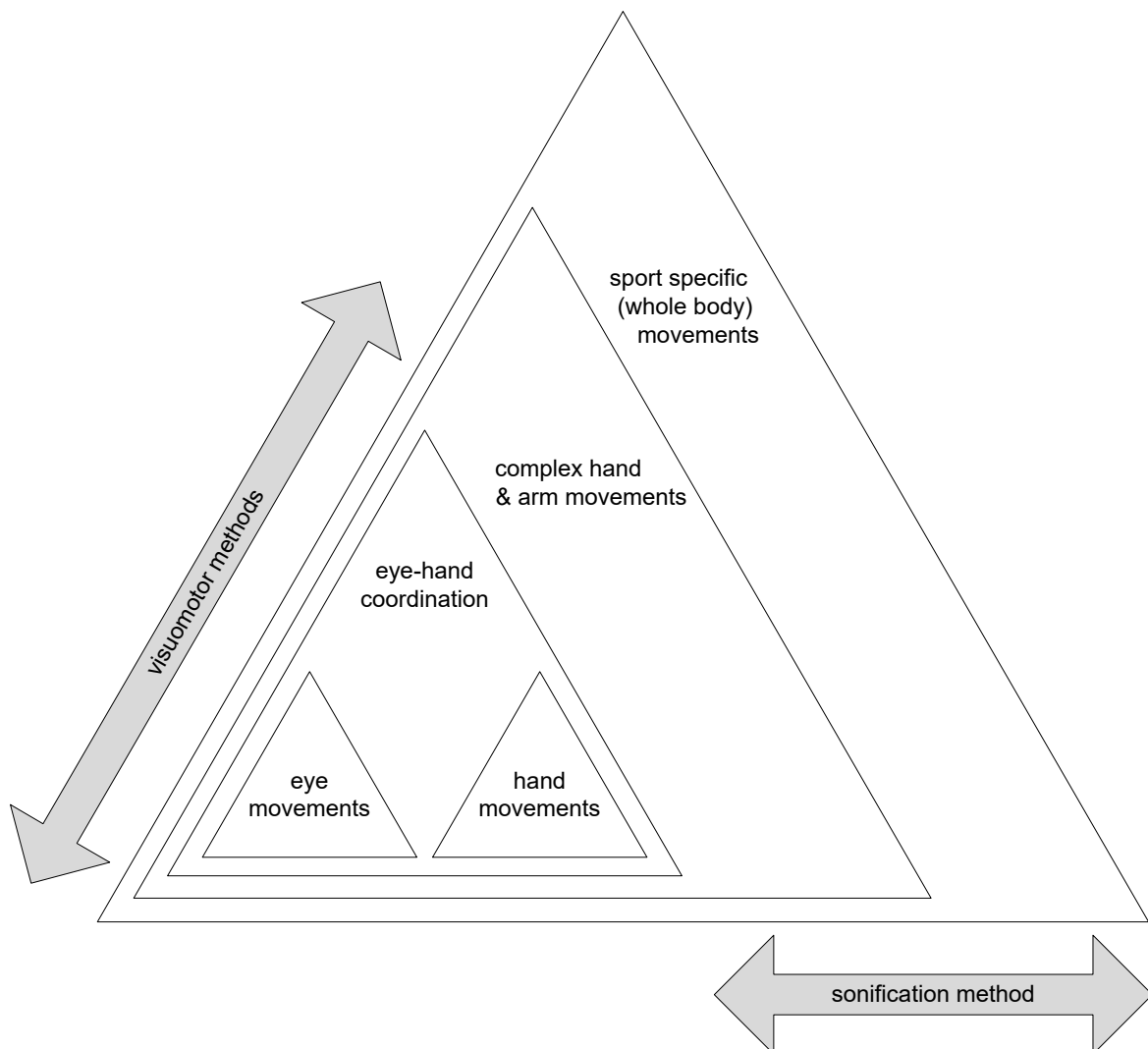
Figure 1: Scheme of the methodological approach. Triangles represent movement types. Movement types in small triangles are considered to be an essential part of more complex movement types in larger triangles. Arrows indicate which type of movements was investigated by which method.

1.1   Sensorimotor representations

Motion is a key feature of life. Organisms need motion to survive and act, which is a fundamental principle reflected at almost all levels of the human organism. For example, at a molecular level, random molecular motion supports the cellular metabolism based on diffusion. At a more complex level, motion builds the basis for sensory perception. One example is auditory perception, which is based on the sensing of motion as the tympanic membrane (eardrum) senses air oscillations induced by motion. Accordingly, kinetic events

in the environment determine sound events (Effenberg, 2005). How closely perceptual and movement functions are linked is illustrated by visually-induced eye movements. An object appearing in the periphery of the visual field attracts attention and drives the motor system to perform a rapid eye movement (saccade), which brings the object into the point of central and sharp vision, the fovea. These basic eye functions typically occur as automatized motor reactions in response to sensory signals. Nevertheless, eye movements are finely tuned and can represent goal-directed motor behavior in response to sensory stimuli (Purves et al., 2001).

A variety of terms and concepts have been developed to describe rule-based relations bet-ween sensory, perceptual and motor functions. The most prominent are the terms of senso-rimotor transformation rules, sensorimotor or internal representations, internal models and sensorimotor contingencies (Bastian, 2008; Battaglia-Meyer, Caminiti, Lacquaniti & Zago, 2003; O'Reagan & Noe, 2011; Wolpert, Ghahramani & Jordan, 1995). Here, the neutral term of internal representations will be used.

Experimental findings indicate that internal representations govern simple movements as well as complex actions, whereby hand and arm movements can serve as an example (Battaglia-Meyer et al., 2003; Land, Volchenkov, Bläsing & Schack, 2013). Goal-directed reaches are already characterized by remarkably complexity due to the numerous degrees of freedom of the hand and arm joints. It is hypothesized that the brain reduces the complexity by building synergies (Bizzi & Cheung, 2013; Santello, Baud-Bovy & Jörntell, 2013), which allow the emergence of straight-line movement vectors of reaches (Kuppuswamy & Harris, 2014), and by representing the hand as the endpoint within a variety of spatial reference frames (Graziano, 2001). The coding and control of movement vectors in body-centered and allocentric reference frames reflect a fundamental principle in kinematic hand motor control (Shadmehr & Wise, 2005; Thier, 2006).

Closely associated with the concepts on muscle synergies is the concept of modularity, which refers to the organizational structure of motor control. According to this view, motor commands are based on the composition of multiple single units (here defined as modules), each of which is responsible for a single sub-process. For example, Lacquaniti, Guigon, Bianchi, Ferraina and Carniniti (1995) have shown that direction, amplitude and elevation of three-dimensional arm movement trajectories are coded in parallel, but by independent neuronal populations. The concept of modularity is also discussed with respect to cognition (Barrett & Kurzban, 2006) and multimodal perception (Tagliabue & McIntyre, 2014) and it is utilized to describe the architecture of the brain as well as functions of the central and peripheral nervous system (Bertolero, Yeo & D'Esposito, 2015; Bizzi & Cheung, 2013;

d'Avella, Giese, Ivanenko, Schack & Flash, 2015). Therefore, it seems to be reasonable to focus on modular functions when investigating motor functions.

1.2   Mechanisms of change

The majority of all sensorimotor, perceptual and motor functions are controlled by the brain. Hollmann and Strüder (2009) describe the brain as a perfect control system. However, in their view, the brain has no a stable state, since internal and external situations constantly change (ibidem, p. 21). It is difficult to imagine stability of motor behavior based on instable brain states: Flint, Scheid, Wright, Solla and Slutzky (2016) recorded neuronal activity of a set of neurons in monkeys over a period of three years. They "found that the brain appears capable of maintaining stable movement representations for extremely long periods of time" (ibidem, p. 3623). Due to monkeys' life in the laboratory, the environments might have been quite stable over time, providing the monkeys with relative constant stimulation, whereby there not might have been the need to update representations. However, if environments and stimulation change, representations become inaccurate and they have to adapt or novel representations have to be established.

The brain has mechanisms for short- and long-term changes of behavior. On a cognitive level, the so-called executive functions guide short-term changes of behavior by supporting self-regulation and shifting between response sets (Anderson, Jacobs & Anderson, 2008). Similar mechanisms exist at the sensorimotor level. They are represented by fast-acting adaptation mechanisms, which induce immediate changes without persistence (Smith, Ghazizadeh & Shadmehr, 2006). These mechanisms share in common the fact that they maintain the capacity to act and allow flexible behavior. The short-term nature of induced changes might have the function to first test new behavior before it becomes part of the behavioral repertoire. Further (slow-acting) mechanisms induce long-term effects and changes that are resistant against interference. As cognitive flexibility and sensorimotor adaptation seem to be interconnected (Bock & Girgenrath, 2006), as well as short-term adaptation and long-term learning (Bastian, 2008), it seems to be necessary to develop common frameworks that incorporate these aspects and describe the linkages between perceptual, cognitive and motor representations and the mechanisms of change.

A respective approach has recently been developed by Chein and Schneider (2012). Based on behavioral and neuroscientific findings, they describe a general learn and control architecture characterized by three hierarchies: 1. metacognition, 2. the cognitive control network and 3. the representation system.

The representation system is considered the basic learn and control system. At this level, knowledge develops slowly by integrating sensory, perceptual, motor and multimodal associations, probably based on Hebbian learning. The cognitive control network represents the second hierarchy. It is related to the representation system, although the learned associations are more general, represent routines and rather have a variable-binding property, which means that the input-output associations are not rigid. This allows the generalization of learning. The cognitive control network further regulates complex and goal-directed actions through attention control, the sequencing, adaptation and improvement of actions as well as the control of information processing; for example, through the inhibition of task-irrelevant information. The third hierarchy is the metacognitive system, which serves the monitoring of behavior during the acquisition of new routines and modifies the setting of cognitive control network routines. The three hierarchies learn in different time scales. Learning only supported by the representation system would take thousands of trials. The metacognitive system and the cognitive control network accelerate learning and enable adapted and flexible behavior in new situations by overcoming overlearned behavioral routines. "With this triarchic learning-and-control architecture, humans can learn to perform a new task in just a few trials and to perform that task more or less automatically after a few hundred" (Chein & Schneider, 2012, p. 83).

It holds sport scientific interest and general scientific interest to understand the nature of internal representations, the mechanisms of change and how both can be addressed. The understanding of mechanisms provides the basis for developing methods that specifically activate or establish representations to improve the learning of new skills, the re-learning of everyday actions when motor functions have been impaired, as well as the adaptation of motor control when environmental or bodily changes have occurred. The present thesis deals with these aspects. The first line of research investigates mechanisms for hand and eye movement control and sensorimotor adaptation with methods for visuomotor adaptation. The second line of research investigates features of sport-related perceptuo-motor representations and how they can be addressed with audiomotor methods. Finally, three articles describe the development of new methods for supporting the re-learning of everyday arm movements after stroke and the character acquisition in children. The model of Chein and Schneider (2012) will be taken as a reference to assign research findings to different learning and control hierarchies, highlight their interconnectedness and provide a coherent view on the control of motor behavior.

2   Adapting sensorimotor control

2.1   Sensorimotor adaptation

Adaptation paradigms belong to the fundamental approaches to investigate motor control (Haar, Donchin & Dinstein, 2015). Sensorimotor adaptation can be described as a function or ability that restores motor capabilities when environmental or bodily changes occur. Although literature reflects this idea is rather implicitly than explicitly, mechanisms of adaptation seem to be closely linked to sensorimotor as well as other types of internal representations: adaptation paradigms typically start and end with the assessment of motor control abilities, and several authors speak of true adaptation or sensorimotor recalibration only, if the adaptive intervention alters motor control persistently (Bock, 2005; Weiner et al., 1983). Linkages to other types of representations are reflected by reports on the impact of adaptation on the perception of space (Bedford, 2007; Girardi, McInstosh, Michel, Vallar & Rossetti, 2004; Simani, McGuire & Sabes, 2007) and correlations between cognitive representations of space and sensorimotor adaptation performance (Lex, Weigelt, Knoblauch & Schack, 2012, 2014).

Some authors regard sensorimotor adaptation as a specific part of motor learning. Shadmehr and Wise (2005) decompose motor learning into evolution, adaptation and skill acquisition; however, such a distinction is not trivial. Well-established tool-use skills, such as the skill to efficiently move a computer mouse to guide a cursor on the screen, are based on the ability of the sensorimotor system to establish and store new rules for the transformation of visual input to motor output. Based on the available literature, a sharp distinction between sensorimotor representations, sensorimotor adaptation and sensorimotor learning cannot be made in that case: When describing tool-use, authors typically refer to internal models (forward and inverse models). Imamizu and Kawato (2009) speak of learning a new internal model, when participants learn a new relationship between mouse and cursor movement. Bastian (2008) speaks of sensorimotor adaptation of an existing internal representation and denotes the development of the ability to switch efficiently (i.e. without cost) between alternative representations as motor learning. It becomes more complex when it is considered that even simple sensorimotor discordances such as a rotation of the relationship between cursor and mouse movements already address multiple adaptation or learning mechanisms with different time scales (Lee & Schweighofer, 2009). Recently, one group of authors argued that fast processes of adaptation might reflect the acquisition or the adaptation of a forward model, whereas slow adaptive processes might reflect the acquisition or the adaptation of an inverse model (Yavari, Towhidkhah & Ahmadi-Pajouh, 2013).

In the present thesis, adaptation will be understood as specific type of motor learning, which alters parameters of a previously established representation, while the movement remains what is was before. By contrast, new combinations of many different sub-motions or modules, which create a completely new representation or movement, will be regarded as skill acquisition, which is another form of motor learning (Bastian, 2008; Shadmehr & Wise, 2005).

2.2   Eye-hand coordination

Manual interactions with the world in sports or during daily activities require goal-directed reaching. Goal-directed reaches call for the coordination of eye and hand movements. The sensorimotor system has become very efficiently in the coordination of the hand and the oculomotor system, despite the fact that these effectors have largely different anatomical and physiological properties. Moving the eyes and a hand together has become a behavioral routine (Horstmann & Hoffmann, 2005) and seems to be the default setting to simplify movement coordination (Gorbet & Sergio, 2009). Accordingly, it is assumed that the brain has established representations to control the coordinated motion of the eyes and the hand. Indications for such representations are the increase of saccade velocities, when a hand movement is performed concurrently (Epelboin et al., 1997) and the yoking of eyes and hand during the pointing to a target, which manifests in the inability to direct the eyes willingly away from a target to which a quick hand movement is currently performed (Neggers & Bekkering, 2002). However, it is the exception rather than the rule that one points and reaches to a target or passes a ball to a team member without looking at the goal. Performing a goal-directed movement into a direction to which we do not look significantly changes the kinematics of the arm movement (including latencies and velocities), confirming that the decoupling is computationally demanding, perhaps because it happens with recourse to a different, and in the case of eye-hand-coupling, less often used neuronal circuit (Gorbet & Sergio, 2016). The answer to the question, whether eye and hand movements use common or independent representations and adaptation mechanisms is relevant for the training in sports. It decides on the optimal training regime for situations, in which body movements are directed to a place to where the eyes do not look; for example, when one's own intention shall be hidden from opponents or during feints. Moreover, this issue is relevant for other fields of application, such as the rehabilitation of stroke patients who show the phenomenon of 'magnetic misreaching'. In that case, they are only able to guide their hand to places to where the eyes look (Jackson, Newport, Mort & Husain, 2005).

The first two studies of the present thesis investigate features of the oculomotor and the hand motor system with the method of sensorimotor adaptation. In particular, it is scrutinized whether they use the same, similar or different sensorimotor representations and mechanisms for the adaptation of movement directions.

2.3   Mechanisms of eye and hand movement adaptation to double steps (Schmitz et al., 2010)

Sensorimotor adaptation can be induced by different methods. Adaptation of hand movements is usually induced with prism glasses or the method of feedback rotation, which both introduce a sensory or sensorimotor discordance. Such discordances mean a discrepancy between intended and actually performed movement or a conflict at the level of perception; for example, when vision and proprioception provide diverging information about the location of a limb in space (Henrique & Cressmann, 2012). In contrast to hand movements, saccades cannot be adapted with real-time feedback-based methods, because they are performed too quickly to be corrected online. Therefore, McLaughlin (1967) developed the double-step method: immediately before the onset or during a saccade the target is displaced, whereby the saccade misses the target and a second – corrective – saccade occurs. Repeated exposure to double steps lets saccades adapt and their metrics change persistently. Since the double steps method has also been successfully applied to induce adaptation of hand movements (Bock, Schmitz & Grigorova, 2008; Magescas & Prablanc, 2006), it was the method of choice for the studies on hand and eye movement adaptation.

The article 'Adaptation of eye and hand movements to target displacements of different size' from Schmitz Bock, Grigorova and Ilieva (2010) compares the mechanisms for the adaptation of eye and hand movements. It was investigated how eye and hand movements adapt to target displacements of various sizes and whether adaptation to a small double step facilitates adaptation to larger double steps. The results showed that participants adapt with the eyes as well as with the hand well to 10 degree (deg) and 30 deg double steps, but worse to 60 deg double steps. The relative magnitude of hand and eye movement adaptation decreased from 37% with 10 deg double steps to 6% with 60 deg double-steps. This indicates that directional double-step adaptation is subject to spatial limitations. Noto, Watanabe and Fuchs (1999) found a related effect for double-step adaptation in monkeys by showing that adaptation of saccades transfers to untrained movement directions, but transfer size decreases with increasing distance from the trained direction. The adaptation profile in their experiments resembled the activity profile of directional selective neurons from the frontal eye fields and from the Superior Colliculus. Activity of these neurons is largest for movements to a specific, i.e. the preferred, movement direction and systematically decreases with directional deviations from the preferred direction. Thus, they

concluded that directionally selective neurons in the frontal eye fields or the Superior Colliculus contribute to adaptation of eye movements.

The results from Schmitz et al. (2010) also suggest the feature of directional selectivity for saccadic as well as hand movement adaptation in humans. Therefore, in a next step, Schmitz et al. (2010) compared their data with data on the activity profile of directionally selective neurons in the Superior Colliculus as published by Ottes, Van Gibergen and Eggermont (1986) during movements to specific directional deviations from the preferred movement direction. The adaptation profile achieved in Schmitz et al. (2010) corresponded well to the activity profile reported by Ottes et al. (1986) as well as the adaptation fields reported by Noto et al. (1999). This supports the hypothesis of an involvement of directional selective neurons, in particular from the Superior Colliculus, in human double-step adaptation.

From a functional perspective, directional selectivity can be explained in congruence to the view of a modular architecture of the brain (Bertolero et al., 2015). It is hypothesized that the adaptive (sensorimotor) system is also organized modularly (Flanagan et al., 1999; Ghahramani & Wolpert, 1997) and that motor commands are tailored by the composition of internal models (Haruno, Wolpert & Kawato, 2003) or general-purpose-modules (Bock, 2013). This view explains directional selectivity of adaptation by adaptation of a single module, which is responsible for adaptation in a spatially limited corridor (Bock, 2013; Ghahramani & Wolpert, 1997).

Further result from Schmitz et al. (2010) might be explained by modular composition: when 60 deg target steps were not introduced abruptly, but incrementally through prior 10 deg and 30 deg target steps, adaptation to 60 steps became more successful. A fused output of two directional selective adaptive modules might have made this possible: the mid part of Fig.1 (episodes 11 to 20) from Schmitz et al. (2010) shows that hand adaptation to 30 deg double steps does not differ between participants who adapted in episodes 1 to 10 to 10 deg or 30 deg double steps, indicating that 10 and 30 deg steps activate or adapt the same module. This differs from adaptation to 60 deg, which suggests the involvement of another adaptation module. Therefore, the joint activation of several directionally selective modules might enable subjects to adapt beyond the limits of directional selectivity. Since all of these findings could be shown for eye as well as hand movements, it might be concluded that eye and hand movements use the same or similar mechanisms for the adaptation of movement directions despite their different anatomical and physiological properties.

2.4   Polarity of directional adaptation (Schmitz & Grigorova, 2017)

Directional selectivity has been shown to be a very important feature of sensorimotor adaptation (Eisenberg, Shmuelof, Vaadia & Zohary, 2011; Haar, Donchin & Dinstein, 2015). Rather implicitly than explicitly, numerous studies indicate that polarity of directional adaptation is a further and not less important factor with major implications for the success of adaptation. Important findings on the consolidation of motor memory and antero- and retrograde interference of adaptation come from studies on subsequent adaptations to discordances with opposite polarities (Krakauer, 2009). In most of these studies, a second adaptation to the opposite polarity of a prior sensorimotor discordance did not emerge or eradicated the first adaptation confirming a significant impact of polarity (Galea & Miall, 2006; Martin & Newman, 1980; Seidler, Bloomberg & Stelmach, 2001; Wigmore, Tong & Flanagan, 2002; Woolley, Tresilian, Carson & Riek, 2007). It is possible that polarity represents a specific adaptation mechanism: the first motor response after the introduction of a sensorimotor discordance might be equal for all discordances with the same polarity independent from their size (Fine & Thoroughman, 2006). Considering the tight coupling of the effectors hand and eyes, hand and eye movements might not only share the feature of directionally selectivity but might also use the same mechanisms for the adaptation to opposite polarities.

The article 'Alternating adaptation of eye and hand movements to opposite directed double steps' from Schmitz and Grigorova (2017) investigated whether eye and hand movements have common mechanisms for the adaptation to different directional polarities. Polarity of adaptation seems to hold particular relevance for the joint eye and hand adaptation: adaptation generalizes between these effectors when they subsequently adapt to the same polarity and interferes when they adapt subsequently or concurrently to opposite polarities (Bock et al., 2008; Grigorova, Bock, Ilieva & Schmitz, 2013b). However, polarities had not been balanced across motor systems in either of the mentioned studies. This is a methodological flaw and impedes the inference on the underlying mechanisms. Therefore, Schmitz and Grigorova (2017) applied a new paradigm in which polarities were balanced and hand and eyes adapted alternatingly, i.e. motor system and polarity switched after 20 movements each, 25 times overall. It was scrutinized how both effectors adapt to opposite polarities, as well as how adapted effectors are coordinated when they move separately or concurrently.

When the eyes and the hand moved concurrently, kinematics changed compared to separately performed movements. This confirms a coupling of both effectors as reported – for example – by Epelboin et al. (1997). Furthermore, adaptation of both effectors interfered. The interference was most prominent in one group, which performed hand movements to clockwise directed double steps, because they adapted to the counterclockwise direction,

i.e. the double-step polarity of the eyes. This finding indicates access of the hand to the sensorimotor representation of the eyes. On the other hand, other results indicate that the eyes also accessed the sensorimotor representation of the hand. Mutual access might reflect a tendency of the sensorimotor system to use a single internal representation for joint eye and hand movements, probably to facilitate eye-hand coordination. Several factors have been found to influence whether access occurs: this present and other studies show that it depends on the duration of adaptation, whether movements are performed concurrently or separately and on the availability of feedback (Borisova et al., 2014; Grigorova et al., 2013a, 2013b). A related phenomenon has been shown for hand movements: under some circumstances, symmetrical or asymmetrical transfer occurs, whereas under other circumstances it is completely inhibited. Asymmetric transfer can reflect dominance of one effector over the other (Cotti, Vercher & Guilaum, 2011; Itti, Rees & Tsotsos, 2005; Wang, 2008; Wang & Sainburg, 2006). An observed asymmetry between clockwise and counterclockwise adaptation in the study of Schmitz and Grigorova (2017) might be explained, accordingly.

However, despite the mutual access to sensorimotor representations, both effectors recalibrated their sensorimotor transformation rules independently from each other. This confirms that eye and hand movements use independent mechanisms for the adaptation to opposite polarities. This is plausible, as growth, fatigue, injuries and other factors can exclusively influence a single system for which independent sensorimotor representations seem to be beneficial. Furthermore, the present results underline the capacity of the sensorimotor system to couple eye and hand movements despite divergent recalibrations. This coupling seems to be realized downstream from the locus of recalibration. A possible mechanism is the exchange and the fusion of efference copies based on the actual recalibration statuses of the eyes and of the hand. The exchange of efference copies is supposed to be a key mechanism of sensorimotor control (Shadmehr, Smith & Krakauer, 2010).

2.5   Comparison of two adaptation methods (Schmitz et al., 2012)

The studies of Schmitz et al. (2010) and Schmitz and Grigorova (2017) applied the double-step method to test commonalities of eye and hand movement adaptation. Up to now, only a few studies have investigated double-step adaptation of hand movements. The vast majority of studies used different methods, among which the rotation of feedback is one of the most common. It seemed to be necessary to scrutinize whether the different adaptation methods address the same or different adaptive mechanisms. This was the purpose of the study 'Adaptation of hand movements to double-steps and to distorted visual feedback: Evidence for shared mechanisms' from Schmitz, Bock, Grigorova and Borisova (2012).

A rotation of visual feedback introduces a discordance between visual and proprioceptive feedback and can induce perceptual as well as motor adaptation (Hatada, Rossetti & Miall, 2006). It might be argued that this discordance is artificial and does not occur in natural settings. In contrast, the double-step method does not artificially introduce a sensory discordance. This might explain, why it does not result in perceptual, but rather in pure motor adaptation (Magescas & Prablanc, 2006). Actually, there is a further striking dissimilarity between adaptation to double steps and adaptation to rotated feedback: hand movements can adapt to feedback rotations up to 180 deg (Cunningham, 1989), whereas double-step adaptation is limited to target displacements of less than 60 deg (Schmitz et al., 2010). Therefore, the study from Schmitz et al. (2012) was designed to test whether adaptation with one method transfers to adaptation with the other method, which would signify a common adaptive mechanism. As a second purpose, it was scrutinized, whether rotated feedback adaptation of the hand facilitates double-step adaptation of eye movements as it was the case after double-step adaptation of the hand (Bock et al., 2008). Comparing both adaptation methods might help to bring the well-established research fields on oculomotor (Pélisson, Alahyane, Panouillères & Tilikete, 2010) and hand motor adaptation (Shadmehr & Wise, 2005) together.

With respect to the latter purpose, the results showed that saccadic adaptation was not facilitated by rotated feedback adaptation of the hand. Moreover, during concurrent movements to the same targets, eye and hand movement directions became dissociated by adaptation of the hand to rotated feedback. These findings confirm independent mechanisms for eye and hand movement adaptation, when they adapt to the same polarity. This was recently confirmed in a different study with a different approach (Borisova, Bock & Grigorova, 2014).

However, the major finding of Schmitz et al. (2012) was that adaptation to rotated feedback transferred completely to double-step adaptation and vice versa. Full transfer strongly suggests a common adaptive mechanism for both adaptation methods. Differences in adaptation speed and magnitude were explained in accordance with established reasoning by cognitive strategies (McNay & Willingham, 1998; Redding & Wallace, 1996), although this view has recently been challenged by Schmitz (2016). Despite these findings, it remained unclear, why the hand can adapt to large feedback rotations but only to small double-step sizes. This indicates a discrepancy at the level of directional selectivity. Therefore, both adaptation types were compared in a further study, which specifically focused on that topic.

2.6   Mechanisms for directional selectivity (Schmitz, 2016, part I)

The study 'Interference between adaptation to double steps and adaptation to rotated feedback in spite of differences in directional selectivity' from Schmitz (2016) aimed to specify

two key features of sensorimotor adaptation: directional selectivity and interference of successive adaptations. Studies on transfer as well as on incrementally increasing sensorimotor discordances have shown that task designs and specific instructions influence directional selectivity and reduce interference between two successive adaptations to opposite polarities. In that context, cognitive (Bedard & Song, 2013; Imamizu et al., 2007) as well as sensorimotor factors (Bedford, 1993; Heuer & Hegele, 2008, 2011; Imamizu, Uno & Kawato, 1995) were discussed. Schmitz (2016) specifically investigated the impact of visual information provided and the direction of motor adaptation (polarity), as well as the role of executive functions on directional selectivity and interference. The same, although marginally modified, adaptation methods as in Schmitz et al. (2012) were applied. Directional selectivity was assessed by comparing the adaptation rate between three equally spaced targets. Interference was induced by successive adaptations to two opposite polarities (Cunningham & Welch, 1994).

The direction, to which participants adapted their movements, clearly determined at which target adaptation proceeded best. When movements adapted to the clockwise direction, they adapted best at the most clockwise located target. When movements adapted to the counterclockwise direction, they adapted best at the most counterclockwise located target. This reflects asymmetric generalization between target directions as shown by Imamizu et al. (1995) and Heuer and Hegele (2008, 2011) for adaptation to rotated feedback at a single target direction. The results from Schmitz (2016) now amend these findings for multiple target directions. Furthermore, they confirm the phenomenon for the method of double-step adaptation, at which it manifests even more clearly than for rotated feedback adaptation.

The mechanisms for this generalization pattern are discussed. A modular organization of the adaptive system might account for the specific results: according to Ghahramani and Wolpert (1997) as well as Bock (2013), movements to different target directions activate different directionally specific adaptation modules, whose output is weighted to specify motor commands to neighboring directions. It is further conceivable that the motor command for a movement to a certain target direction adapts to such an extent that the adapted direction (i.e. the new direction) corresponds to a movement direction, which had been previously associated with a different target direction in space and thus affects a further directionally selective module. This module might also adapt (Krakauer, Pine, Ghilardi & Ghez, 2000), which would explain the better adaptation rate at targets in the direction of motor adaptation.

The target-specific adaptation pattern was also influenced by the visual information provided. A possible explanation is that the discordance between visual and proprioceptive information might have induced additional perceptual after-effects (Henrique & Cressmann,

2012). Such after-effects are modality-specific as they develop in specific time scales (Hatada et al., 2006), and are directionally selective, because they decrease with increasing distance between tested and trained target direction (Cressmann & Henrique, 2015). Their emergence would have influenced the results from Schmitz (2016) and thus might explain the differences between adaptation to rotated feedback and double steps. For an alternative explanation might be considered that the visual information emphasized different task features during the adaptation tasks: adaptation to rotated feedback affected the perception of one's own movement direction, whereas double-step adaptation acted at the level of the target representation.

Taken together, adaptation to rotated feedback seems to involve the same and probably more adaptive modules than adaptation to double steps. Important insights into the probable locus of these modules in the brain are provided by the studies of Haar et al. (2015) and Eisenberg et al. (2011). Haar et al. (2015) investigated by functional magnetic resonance imaging (fMRI) how a visuomotor rotation affects the neuronal representation of directional selectivity in the brain. They found that 'motor areas' (primary motor cortex, dorsal premotor cortex, the supplementary motor area and the cerebellum) represented the direction of arm movements, 'visual areas' (early visual cortex in the occipital pole as well as superior parietal occipital cortex) represented the target location and the posterior parietal cortex (PPC) represented both target and movement direction. Adaptation to 45 deg rotated feedback changed the activity of neurons in the PPC but not in the other areas. In further detail, neuronal populations in the medial intraparietal sulcus showed different activity patterns in response to the same visual input as well as the same performed movement direction as before adaptation. Therefore, the authors concluded that neurons in the PPC code the altered visuomotor mapping. The important role of the PPC during adaptation is confirmed by the studies of Cressmann and Henrique (2012) and Henrique and Cressmann (2015), who identified the PPC as the locus of the adaptive recalibration with directionally selective features. According to Eisenberg et al. (2011), also the primary motor cortex (M1) seems to contribute to sensorimotor representations and might be a further instance for the modular composition of adaptation to rotated feedback. Not only movement directions, but also task-specific visual information seems to be encoded in M1, because some neurons are activated by specific movement directions independent from the visual information provided, whereas other neurons respond to visual aspects of reaches (either visual target location or the direction of feedback trajectory) independent from movement direction (ibidem).

Taken together, empirical data from behavioral and brain-imaging studies suggest the existence of directional selective adaptive units, here referred to as modules. Some instances of the adaptive sensorimotor system are activated during movements to specific directions

whereas others are activated by visual task components or by both. Accordingly, the results from Schmitz (2016) show that adaptation to double steps involves the same modules as adaptation to rotated feedback. However, the more symmetrical generalization scheme after adaptation to rotated feedback suggests that the latter involves further modules. This would sufficiently explain the difference between the two adaptation methods reported by Schmitz et al. (2012). In that study, the targets were spaced by 45 deg across the whole circle of 360 deg. With rotated feedback, adaptation to each target direction generalizes to clockwise as well as counterclockwise located targets and thus should have enhanced the overall adaptation rate (Krakauer et al., 2000) compared to double-step adaptation, which generalizes only to one direction. Furthermore, the results of Schmitz (2016) did not indicate that one adaptation method had encouraged participants to apply cognitive strategies. Enhanced cognitive strategies should have been reflected in enhanced reaction times as shown by Fernandez-Ruiz, Wong, Armstrong and Flanagan (2011), but this was not the case. Moreover, interactions between participants' cognitive abilities and adaptation method became not significant, whereas independent from adaptation method, covariations between cognitive abilities (executive functions) and several adaptation measures became significant. This is the topic of the next chapter.

2.7 The role of executive functions in a modular concept for sensorimotor adaptation (Schmitz, 2016, part II)

The term 'executive functions' describes cognitive functions of higher order that enable flexible and adapted behavior; for example, when automatized behavior proves detrimental (Diamond, 2013). In the study on directional selectivity and interference, Schmitz (2016) assessed executive functions of visuospatial planning, verbal working memory, inhibition, perseveration, figural fluency and cognitive flexibility as well as the basic cognitive functions of sustained attention and cognitive processing speed. These abilities were merged by factor analysis to four independent factors, and it was tested whether they explain variance of different measures from sensorimotor adaptation. One factor, predominantly representing perseveration, shared variance with target-specific recalibration. Another factor, loaded by inhibition and cognitive flexibility, which represent two main executive functions (Anderson, Jacobs & Anderson, 2008; Spreen & Strauss, 1998), partially predicted the amount of interference between subsequent adaptations to opposite polarities, as well as interference of target-specific recalibrations. Variance of the latter effect was further explained by participants' visuospatial planning abilities.

The learning of a new internal model makes it necessary to suppress already acquired internal models that are incompatible with the new one (Imamizu et al., 2007). Accordingly, the results from Schmitz (2016) imply that executive functions are related to the ability to

suppress and switch between internal models and thus flexibly modify motor behavior in response to changed task demands. Moreover, the covariations with target-specific adaptation patterns indicate a specific role of the executive functions inhibition, mental flexibility and visuospatial planning for the composition of directionally selective modules. These findings provide a new view on the interplay between sensorimotor and cognitive abilities, which had formerly been described at a general level in relation to cognitive learning, cognitive corrections or strategic control (Bedford, 1993; McNay & Willingham, 1998; Redding & Wallace, 1996; Weiner et al., 1983).

Simon and Bock (2015, 2016) have recently shown that the concept of Chein and Schneider (2012) on cognitive learning and control can explain findings from sensorimotor adaptation fairly well. Schmitz' (2016) findings now can amend this concept: the embeddedness of adaptive modules in directionally selective neurons as implied by the results of Noto et al. (1999), Schmitz et al. (2010), Eisenberg et al. (2011) and Haar et al. (2015), fits to Chein's and Schneider's view on a representation system, which is responsible for basic input-output associations. In contrast, the idea of quickly established compositions of adaptive modules, which might represent the mechanism that enables participants to adapt beyond the limits of directional selectivity and shape the width of spatial generalization, complies with the description of more flexible, higher-order input-output associations characteristic for fast-acting higher hierarchies (Chein & Schneider, 2012). This latter association between sensorimotor features and higher hierarchies of cognition is further supported by reports on the impact of executive functions (Schmitz, 2016), the instruction to apply a new transformation rule (Heuer & Hegele, 2008, 2011), divided attention (Bedard & Song, 2013) and intention (Day, Roemmich, Taylor & Bastian, 2016) on spatial generalization.

2.8   Interim conclusion

Implications for future research as well as practical applications can be derived from this line of research with different degrees of concretization. It is hypothesized that sensorimotor control and adaptation are composed of directionally selective units or modules (Bizzi & Cheung, 2013; Bock, 2013). These modules can be addressed by different adaptation methods. The feature of directional selectivity becomes clearly evident when the double-step method is applied, probably because this method induces pure motor adaptation (Magescas & Prablanc, 2006). It is less obviously revealed in studies that apply a rotation of feedback (Schmitz, 2016), probably because this method also induces perceptual effects (Simani et al., 2007), even though perceptual effects might also be directionally selective (Cressmann & Henrique, 2015). Considering the findings of Haar et al. (2015), which showed that rotated feedback adaptation alters the response of directionally selective neuronal populations in the PPC, it might hold interest to investigate whether the PPC is

the locus for the perceptual or the motor components of adaptation. An fMRI-study with a combined double-step-rotated feedback paradigm might be adequate to address this question.

As shown for hand and eye movements, directional selectivity is a feature of the movement representations and the adaptive mechanisms of different effectors (Schmitz et al., 2010). As the eyes and hands are anatomically very different, it seems to be independent of effector specific muscle activation patterns. Thus, the applied adaptation paradigms seem to address general movement functions making transfer effects from the trained to untrained domains probable. Further research is necessary to reveal whether directional selectivity also occurs during the learning and training of sport-specific skills. It might be possible that spatial accuracy training of eye and hand movements results in spatially limited effects around to the trained movement direction; for example, in darts. This would imply the necessity of a training with different movement or gaze directions, respectively. Moreover, directional selectivity might hold particular importance in situations in which movement direction is a key parameter; for example, during the training of feints with diverging eye and body movements or the training of no-look passes. In such contexts, incremental training – i.e. the training with increasing affordances – might be beneficial because it enables adapting beyond the limits of directional selectivity (Schmitz et al., 2010). Further factors associated with the ability to bypass limits of directional selectivity have been identified and might be considered: the polarity of motor adaptation, the design of task-specific visual information and cognitive functions like the tendency to perseverate behavior, inhibition, cognitive flexibility and visual spatial planning abilities (Schmitz, 2016).

The correlations between executive functions and the width of spatial adaptation illustrate that participants with different cognitive abilities learn with different efficiency. As shown by Bock and Schmitz (2011) and Krakauer et al. (2000), wider generalization is associated with faster learning rates in sensorimotor adaptation tasks. Therefore, these executive functions seem to predict whether a practitioner is a fast or a slow motor learner. From this point of view, it would hold interest to analyze whether similar correlations can be found in other domains and scrutinize whether sport prowess is related to the expression of executive functions. Indications are given by reports on correlations between executive functions and sport success in young elite soccer players (Vestberg, Reinebo, Maurex, Ingvar & Petrovic, 2017).

Although the present results do not allow conclusion with respect to causality, it might be hypothesized that deliberate exposure to motor incompatibilities can be applied to address and train specific executive functions or that the training of specific executive functions en-hances motor skills and sensorimotor adaptation. The latter has been scrutinized by

Anguera et al. (2012), who investigated whether improving working memory improves sensorimotor adaptation. This could not be shown, whereas cognitive fatigue had a significant effect on adaptation. Future studies therefore should investigate the effect of sensorimotor training on executive functions.

Of further interest are the results on adaptation to opposite polarities. It had previously been shown that the switching between two internal models with opposite polarities entails costs and requires extensive training to be performed efficiently. Whereas adaptation to a single sensorimotor discordance typically plateaus within a single session, multiple adaptation sessions are necessary to reduce polarity related switch costs (Cunningham & Welch, 1994, Imamizu et al., 2007). For the case of adaptation to opposite polarities, the borders between motor adaptation and other types of learning become blurred (Bastian, 2008). Adaptation to opposite polarities progresses very slowly. The adaptation rate complies to the time course of learning at the hierarchy of the representation system as described by Chein and Schneider (2012). The lack of adaptability during the switching from one polarity to the other as well as the relative inefficiency of most of the so-called cues regarding a facilitation of switching, further indicates that the underlying adaptation mechanism is only weakly connected to higher learning hierarchies. This contrasts with the results on directional selectivity, for which such a connectivity can be assumed (see above). Therefore, the features of directional selectivity and polarity seem to use different adaptation or learning mechanisms. Accordingly, Wolpert, Diedrichsen and Flanagan (2011, p. 7) regard directional selectivity related to motor primitives, which represent "neuronal control modules that can be flexibly combined to generate a large repertoire of behaviors". Thereby, motor primitives can be formed by the joint activity patterns of a set neurons, in that case directionally selective neurons, which are located in a variety of brain areas (Haar et al., 2015). In contrast, adaptation to opposite polarities is understood as a "credit assignment problem: the question of how to attribute an error signal to underlying causes" (Wolpert et al., 2011, p. 7). Some factors seem to facilitate such an assignment: explicit knowledge (Imamizu et al., 2007) and executive functions (Schmitz, 2016) but also specific cues, such as the arm used during adaptation (Prablanc, Tzavaras & Jeannerod, 1975). This view sheds new light on the study from Schmitz and Grigorova (2017) who investigated hand and eye movement adaptation to opposite polarities: the intention to move the eyes or the hand might serve as cue, whose association with a specific polarity is one important aspect to be learned. The lack of adaptation of eyes and hand to opposite polarities reported by Grigorova et al. (2013b) and Borisova et al. (2014) might have been due to the inability to learn such a cue association, whereas the paradigm of alternating eye-hand exposure in the study of Schmitz and Grigorova (2017) facilitated this learning.

Schmitz and Grigorova (2017) further showed that the sensorimotor system couples effectors even when their movement representations are differently calibrated. The tight coupling of hand and eyes during goal-directed movements and the tendency of the sensorimotor system to inhibit divergent recalibrations might be considered during the training of skills related to eye-hand coordination. Eye and hand movements cannot easily be trained independently from each other; in contrast, crosstalk between the hand- and the oculomotor system has to be expected (Gorbet & Sergio, 2009) and controlled. This might hold particular importance in sport disciplines like badminton, which put high demands on visual perception and manual actions and thus on the oculomotor and the hand motor system (Ahmad Rudin & Sharipan, 2015).

The studies of Schmitz et al. (2012) and Schmitz (2016) confirm that sensorimotor adaptation can be induced by the double steps method, which does not introduce a sensorimotor discordance. These studies further show that such discordance-free adaptation addresses the same adaptive mechanisms as a discordance-based adaptation. This offers the opportunity to apply paradigms on sensorimotor adaptation in natural sport and rehabilitation settings. The development of testable predictions for complex environments and the designing of controllable and ecologically valid test situations are major challenges in this context. However, recently, Babic, Oztop and Kawato (2016) developed a paradigm for the adaptation of whole body movements to a force field and thus succeeded respectively. Furthermore, sensorimotor adaptation paradigms are applied in patients with hemineglect to improve spatial perception, patients with locomotor deficits to achieve a more symmetrical walking pattern and patients with arm paresis to normalize reaching or simply for testing the adaptability of the central nervous system (Bastian, 2008). Notably, for stroke patients with hemineglect, the reported benefit from wearing prism glasses might come from the interplay of hand and eye representations (Serino, Angeli, Frassinetti & Ladavas, 2006). Hereto, the present results provide important insights.

The observation that discordance-free and discordance-based adaptation methods address the same adaptive mechanism might have implications for developing virtual realities. This might hold particular value for surgery, for sport disciplines that require perceptuomotor transformations or the learning of force fields or in which the athletes are systematically exposed to altered gravity, which occurs in situations with high acceleration and deceleration. For these cases, specific virtual realties and environments might be developed that allow controlling the stimulation during the training of motor skills and enable expecting a high transferability to natural environments with and without discordances.

Added value is given to the research on sensorimotor adaptation itself. By showing that the double-step method, commonly applied for the research on the oculomotor system, and the

method of rotated feedback, typically applied for research on the hand motor system, address similar adaptive mechanisms, it becomes possible to connect the research on both motor systems. Eye movements belong to the most elementary human movements. They can be well described and experimentally controlled. The more complex hand movements allow the usage of tools as well as interactions with the environment and hold major importance for the ability to act. The connectivity of adaptation mechanisms allows researchers to choose the most adequate method to investigate learning and adaptation mechanisms in a continuity from simplest movements to most complex actions.

Finally, Schmitz (2016) demonstrated that the combined research on sensorimotor and cognitive adaptive mechanisms serves the understanding of sensorimotor representations. It was argued that sensorimotor adaptation addresses representations of different complexity probably located at different hierarchies. These hierarchies seem to interact; for example, in order to recruit sensorimotor modules during the generation of a motor command (Battaglia-Mayer et al., 2003; Haruno et al., 2003).

3   Supporting action perception and performance

The previous studies investigated mechanisms for sensorimotor learning by analyzing basic actions (goal-directed saccades or mouse guided cursor movements) and provided insights into the structure of the adaptive sensorimotor system. Although these mechanisms are associated with the acquisition of internal representations for new tools (Imamizu et al., 2000), further mechanisms contribute to perception, control and learning of gross-motor movements. A general feature of learning and control seems to be "the ability to dynamically and selectively activate specific brain areas in a coordinated fashion" (Chein & Schneider, 2012, p. 78). Accordingly, the task-related control of information processing seems to be one crucial aspect. Methods and technologies that allow controlling movement information thus might be utilized to constitute perceptual representations and enhance motor learning by promoting the information structure formation and emphasizing information which is particularly relevant for successful performance. The method of sonification might be such a method, because it allows selectively generating additional movement information or augmenting information from other modalities.

Sonification can be defined as the transmission of data relations into sound relations to facilitate communication in various contexts (Kramer et al., 1999). Effenberg (1996, 2004) developed a theoretical framework for the design of auditory information to improve movement perception and action. He speaks of movement sonification when auditory stimuli are designed spatially and temporally congruent as well as structurally equivalent to proprioceptive or visual movement information (Effenberg, 1996). Movement sonification can enhance accuracy in motor perception and control (Effenberg, 2005) as well as pattern

discrimination (Vinken et al., 2013) and improve motor learning (Effenberg, Fehse, Schmitz, Krueger & Mechling, 2016; Sigrist, Rauter, Marchal-Crespo, Riener & Wolf, 2015). According to Scheef et al. (2009), some effects induced by sonification of dynamic movement parameters can be explained by increased neuronal activity in multimodal motion processing areas in the brain.

The studies from the next line of research elucidate how sonifications of kinematic movement parameters affect perception and motor behavior. They further show that this method can be applied to investigate representations of gross motor movements, to induce internal action simulations and to modify intra- as well as inter-individual coordination.

3.1 Brain activity during the observation of sonified movements (Schmitz et al., 2013)

A study from Schmitz, Mohammadi, Hammer, Heldmann, Samii, Münte and Effenberg (2013) investigated perceptual effects as well as brain activity induced by sonification of gross-motor cyclic movements. The sonification was based on kinematic movement parameters of a world champion during breast stroking. The relative positions of the wrists and the ankles in relation to the pelvis determined sound pitch, whereby the relative velocities of these joints modified the sound amplitude. Kinematic movement data were also used to create a visual avatar, which was presented in addition to the sonification yielding an audiovisual movement stimulus. Seventeen participants (non-experts) were instructed to estimate velocity differences of two audiovisual avatars appearing on consecutive videos. In the congruent condition, the auditory stimulus component was the sonification and in the incongruent condition an accord covering the same timbre and pitch as the sonification.

The results showed that the participants made more accurate judgments in the audiovisual congruent than the incongruent condition. This suggests enhanced perceptual processing of the sonified stimulus. A fMRI-analysis (functional magnetic resonance imaging analysis) revealed that the congruent stimulus induced an increase of activity in the medial and superior temporal sulcus. These are audiovisual integration areas (Noesselt et al., 2007), and their activation might explain the enhanced perceptual processing (Frassinetti, Bolognini & Ladavas, 2002).

A subsequent connectivity analysis revealed the activation of a widespread neuronal network during the observation of sonified movements. The network included key-players of the striato-thalamo-frontal motor loop (Buccino et al., 2001; DeLong, Georgopoulos & Crutcher, 1983) as well as parts of the action observation and the mirror neuron system. This supports a hypothesis of the existence of an audiovisual mirror neuron system (Bangert et al., 2006) and suggests its involvement in the processing of the audiovisual motion stimuli

from Schmitz et al. (2013). It is assumed that the mirror neuron system contributes to an internal simulation of the observed movement (Buccino et al., 2001; Jeannerod, 1994). Furthermore, it is supposed to reflect the interface between perception and action and supports the understanding of actions (Buccino et al., 2004; Rizzolatti, Fogassi & Gallese, 2001).

It has to be noted that the connectivity analysis for the control condition indicated activation of the same network by the control stimulus, although this activity was lower and the network less widespread than in the experimental condition, particularly with respect to the motor loop. This means that the movement sonification altered neuronal network activity and particularly addressed brain areas associated with the preparation and execution of movements. In that context, it is interesting to note that the participants never had perceived a sonification in relation to their own movements before. Therefore, the sonification of sport actions seems to activate the striato-thalamo-frontal motor loop in observers without modality-specific expertise. This might indicate a possible internal simulation of the observed breaststroke movements based on internal movement representations in non-experts (Loula, Prasad, Harber & Shiffrar, 2005).

3.2   Perceiving the effects of sonified movements (Schmitz & Effenberg, 2012)

Internal movement representations and the estimation of action effects were topics of a study from Schmitz and Effenberg (2012). The study investigated whether a sonification of selected movement parameters from indoor rowing provides sufficient information to allow rowers the estimation of movement effects, whether the estimation accuracy depends on how familiar the rowers are with the heard movements and whether they can identify sonifications of their own movements. According to established reasoning, the latter aspects allow conclusions on internal simulations of the perceived action (Knoblich, Seigerschmidt, Flach & Prinz, 2002). The sonification used had originally been developed by Effenberg, Fehse and Weber (2011) to investigate motor learning in indoor rowing. It was based on a transformation of the grip force, the footrest force, the sliding seat position and the grip amplitude to sound frequency and sound amplitude.

The participants, which all were experienced rowers, listened with eyes closed to sonifications of their own movements and sonifications of other persons. They were instructed to identify their own sonifications and estimate velocity differences of non-visible (virtual) pace boats driven by the rowing movements. All participants were familiar with the concept of the pace boat from their own ergometer training as the ergometer display typically illustrates the velocity of the virtual boat. Here, the ergometer display was concealed from view.

Participants' estimations correlated significantly better with virtual boat velocity (R^2=0.80) than with other directly sonified parameters. Since boat velocity had not been mapped onto sound directly, it was concluded that the participants were able to infer the boat velocity from the sonifications. The detection rate of one's own movements was significantly above chance level and matched those of other studies (Knoblich et al., 2002). A memorization of individual sound traces as explanation of the result is unlikely, for several reasons: first, by mapping the individual parameter minima and maxima inter-individually on the same sound frequencies, the stimuli became highly standardized; and second, the participants had rowed for several hundred cycles, and less than 2% of them were used in the identification task. Therefore, the significant identification rates indicate that the participants were able to set the sonification in relation to their internal movement representations.

This study supports the hypothesis that the observation of sonified movements activates internal movement representations and induces internal action simulations. Based on the results, practical applications are discussed. A special focus is laid on the potential of sonification for the prediction of action effects. As social interactions largely depend on predictions (Brown & Bruene, 2012), movement sonifications might be particularly relevant for inter-individual action coordination.

3.3 Sonification for action coordination (Schmitz & Effenberg, 2017b)

A chapter on sound joined interactions from Schmitz and Effenberg (2017b) addresses the question whether sonification might serve as a tool to study and improve interpersonal interactions. It is part of an interdisciplinary book on intercorporeality, interkinesthesia and enaction. As interpersonal interactions are based on close connections between perception, anticipation and motor actions (Brown & Bruene, 2012), the chapter starts with a review on the impact of movement sonification on perception and action, before its potential for social enactment and intercorporeality is discussed.

A postulation of the enactment approach is that perception unfolds during the movement and during interactions with the world. According to McGann (2014), social interactions not only depend on the abilities of the individuals, but also on the interaction dynamics between them, which result from the tendency to synchronize movements with each other. Such a tendency becomes evident, when two individuals in rocking chairs unintentionally begin to synchronize their rocking frequencies (Demos, Chaffin, Begosh, Daniels & Marsh, 2012). The concept of intercorporeality goes even further as it describes the sharing of perceptions and actions and the connectivity of bodies beyond their physical limits (Fuchs, 2016), which makes it possible to infer unobservable intentions, perceptions and beliefs from observable bodily movements (Tanaka, 2013). The concept of intercorporeality as well as the enactment approach explain interactions and synchronizations without representations,

which complies to the concept of socialized sensorimotor contingencies (Kaspar, König Schwandt & König, 2014). In Schmitz and Effenberg (2017b) it is argued that movement sonification supports intercorporeality by providing movement information in exactly the same way for all interaction partners, thus ensuring that they share a perceptual experience. Furthermore, it is stated that the method of sonification represents an effective tool to investigate predictions from intercorporeality empirically: based on the manifold possibilities to design movement sonifications, different frameworks can be constituted, which allow the investigation of social interactions with different grades of complexity.

Empirical data highlight the potential of sonification for movement pattern discrimination and synchronization. One study shows that 50 minutes of training with a sonification as real-time feedback subsequently enables elite rowers to correctly discriminate six persons by their sonifications. Since the sonifications were standardized and differed only with respect to the parameter time course, the identifications were seemingly based on a differentiated analysis of the movement patterns. Data from a second study suggest that movement synchronization in time depends on how the interaction partners perceive each other, i.e. on the movement parameters provided: experienced rowers were instructed to synchronize their movements on an indoor rower with sonifications of an elite rower. One sonification was similar to that used by Schmitz and Effenberg (2012). The second sonification was created interactively with expert coaches and emphasized the grip force during the drive phase as well as parts of the sliding seat movement. The results showed that sonification type determined synchronization accuracy and constancy as well as movement rhythm. Participants' statements provided insights into how they perceived the sonifications and how they managed to deal with it. Statements and data suggest that interaction dynamics over-rode individual behavioral tendencies, which created tensions in some participants. This complies to what McGann (2014) describes for social enactment. Moreover, half of the participants developed a holistic view on the sonified rower, which might reflect the forming of a gestalt from the heard.

Schmitz and Effenberg (2017b) provide a new research approach as well as a method to address interpersonal coordination. It is shown that different sonifications can provide different frameworks to study interpersonal synchronization. Systematic variations of sonifications might be applied to investigate the effects of perceiving different movement parameters on the synchronization of sport-specific movements.

3.4 Mechanisms of sonification based synchronization of sport-specific movements (Schmitz & Effenberg, 2017a)

A systematic approach to study interpersonal coordination comes from music science. For a systematic investigation of interpersonal coordination, D'Ausilio, Novembre, Fadiga and

Keller (2014) propose to combine research paradigms with different grades of internal and ecological validity. Fundamental mechanisms of interpersonal coordination can be investigated in experiments in which two persons perform together (bi-directional synchronization) or a single person performs to a musical recording of another person (uni-directional synchronization). The benefit of the latter is that it becomes possible to control the information stream and provide exactly the same movement information to all participants. The degree of complexity of interactions increases in small groups, e.g. ensembles, in groups with a conductor, or in bands with audience. By systematically increasing the interacting units (group size, groups with/without conductor or audience), ecological validity increases incrementally. However, this advantage is accompanied by a reduction of internal validity, which leads to more confusion in causal explanatory models.

This approach from the field of music science might be adapted to sport science research with sonification. The study 'Coxswain 2.0 – movement–acoustic dimensions of interpersonal coordination in team sports' from Schmitz and Effenberg (2017a) focused on the basic paradigm from d'Ausilio et al. (2014) and analyzed uni-directional synchronization to recordings of another person. The paradigm is amended by a study of perceptual effects: Schmitz et al. (2013) and Schmitz and Effenberg (2012) suggested that the perception of sonified actions induces internal action simulations. By combining tasks for movement synchronization and motor perception, it becomes possible to infer on action-perception couplings. Thereto, a special focus was placed upon a differentiated impact of different sets of movement parameters.

In detail, the study scrutinized the impact of kinematic and dynamic sonifications on uni-directional rowing synchronization, the estimation of movement frequencies and self-identification. Participants rowed on an indoor rower while listening to sonifications of kinematic or dynamic parameters of an elite athlete or in a control condition to a discrete sound indicating the onset of the drive phase. The results showed a negative mean asynchrony of 25 ms between the sonified rower's and the participants' movements in the control condition, which means that the participants started their drive phase on average 25 ms earlier. With a dynamic sonification, negative mean asynchrony increased by about 200 ms. With the kinematic sonification, mean asynchrony became positive as participants started their drive phase about 70 ms later than the model. Thus, the continuous sonification per se as well as the selection of movement parameters affected the synchronization performance.

In a second session, participants listened to sonifications of kinematic and dynamic parameters of their own movements and those of other persons. They were instructed to identify themselves and estimate the heard rowing frequencies. Although participants proved able to discriminate movement patterns of different persons based on a standardized sonification

of single rowing cycles, which confirms the findings from Schmitz and Effenberg (2017b) on pattern discrimination, only few of them succeeded in self-identification. Differences between kinematic and dynamic stimuli were not significant in any of the conditions. However, perceptual performance depended on whether own movements were heard or those of other persons. This own-other effect became significant when two covariates were considered: one was the mean asynchrony during movement synchronization and the second the self-identification rate. These results confirm the hypothesis of an internal simulation of the observed movements. Furthermore, the covariations permit hypotheses about the structure of the representations used for the simulation. The results indicate that movement representations are supramodal and at least partially independent from kinematic as well as dynamic movement parameters. Moreover, they seem to have independent components related to the temporal calibration of perception-action couplings, the inner temporal structure of the movement as well as a at least one component, which is independent from these two.

Effects for sport practice are discussed. Possible applications are the uni-directional alignment of movements from several rowers within a boat by providing a model technique in real-time or bi-directional coordination, when they listen to sonifications of each other. By applying different sonification techniques, movements might be inter-individually calibrated. With respect to the variability of performance, the perception of movement frequencies and also synchronization performance might be best supported with a kinematic sonification. Practical effects can be expected: a sonification of boat acceleration has already been applied to improve the boat velocity during on-water rowing. Positive effects were explained by increased synchronization of the rowers, although synchronization could not be measured directly (Schaffert, 2011). Furthermore, it was recently shown that audiovisual rowing models in combination with auditory real-time feedback can improve skill acquisition in rowing (Effenberg et al., 2016; Sigrist et al., 2015).

3.5   Interim conclusion on the mechanisms of sonification

The former studies provide new insights into the mechanisms addressed by sonification of human movements. The specific neural activity reported by Schmitz et al. (2013), the empirical indications of an internal simulation of movements in Schmitz and Effenberg (2012, 2017a) as well as the results of Schmitz and Effenberg (2017b) on action pattern discrimination support the notion that the central nervous system processes sonified movement information as biological motion information. The findings indicate an involvement of motor representations during internal action simulations despite a lack of perceptuomotor expertise and implies that motor representations are at least partially supramodal. This is in contrast to the view on the storage of modality-specific information at the level of

sensorimotor representations (Land et al., 2013), but corresponds to views on the mechanisms of sensorimotor adaptation (Schmitz & Bock, 2014) as well as sensorimotor contingencies. Hereto, Kaspar et al. (2014, p. 48) state: "In principle, it is irrelevant through which sensory channel the information is provided; what matters is that the stimulation obeys the sensorimotor rules of the sense to be substituted." This view also suggests that it is possible to address movement representations by a never experienced modality, as long as the motion information provided is structurally equivalent to other sensory information associated with the representation.

The effect of auditory information on motor behavior is typically explained by audiomotor couplings (Rodriguez-Fornells et al., 2012). Audiomotor couplings become evident by the activation of motor areas in the brain in response to auditory stimuli and activation of auditory areas during silently performed movements. Indications for audiomotor couplings are given after 20 minutes of training already, but to establish them firmly extensive audiomotor training is required (Bangert & Altenmüller, 2003). Noteworthy, audiomotor training also enhances perceptual discriminability of auditory features, and this to a greater extent than purely auditory training (Lappe, Herholz, Trainor & Pantev, 2008). Considering these findings from the field of music for the interpretation of the results from the sonification studies, it becomes apparent that audiomotor couplings can only explain parts of the results from Schmitz and Effenberg (2012, 2017b): the extraordinary performance during pattern discrimination reported by Schmitz and Effenberg (2017b) and the better self-identification in Schmitz and Effenberg (2012) compared to Schmitz and Effenberg (2017a).

This mechanism does not seem to be the explanation for the results of those studies, in which the auditory stimuli provided information in a hitherto-unexperienced modality. Due to a lack of specific training, the emergence of audiomotor couplings is not plausible. In the case of Schmitz et al. (2013), the congruency of visual and auditory information probably might have induced an audiovisual coupling. However, here again the short exposure to audiovisual stimuli has to be considered: before the fMRI session, participants had only observed 45 audiovisual congruent stimuli, which corresponds to a total exposure time of 225 s. This is insufficient to expect a stable binding of sensory information. Thus, the formation of new basic sensorimotor associations cannot be assumed as cause for the observed effects and an alternative interpretation has to be derived.

Immediate effects on perception and action from stimuli in a hitherto-unexperienced modality suggest that sensory information can be flexibly linked to established movement representations. Flexibility of action-perception couplings has also been described by Poljac, van Schie & Bekkering (2009). The flexibility might be mediated by a network similar to the cognitive control network proposed by Chein and Schneider (2012): this network has

a variable-binding property that "allows learned behaviors to be applied in novel environments and to be adapted to accommodate novel information" (p. 82). Furthermore, it supports the emergence of new associations within ten to a few hundred trials, and thus might explain fast-acting sonification effects; finally, its activity is reflected by neuronal activation within a network including the PPC, the thalamus and the basal ganglia, which are also activated by the observation of sonified movements (Schmitz et al., 2013). The PPC might hold particular relevance: it comprises the superior parietal lobule as well as the inferior parietal lobule (Vingerhoets, 2014). A sub-part of the inferior parietal lobule – the supramarginal gyrus – is specifically activated by kinematic (Schmitz et al., 2013) as well as dynamic movement sonifications (Scheef et al., 2009). This region is also associated with internal movement representations as its activity distinguishes perception of own and unknown movement kinematics (Bischoff, Zentgraf, Lorey et al., 2012; Macuga & Frey, 2011). In contrast to the processing of human movements, pitch-coded information of non-human motion activates the superior parietal lobe (Sadaghiani, Maier & Noppeney, 2009).

These studies suggest that biological motion information can be transferred into novel modalities and that sonification of only a few parameters is sufficient to activate the mechanisms for biological motion processing. The results also indicate that the signal structure or parameter time course is – probably implicitly – recognized by the perceptuo-motor system. Sonifications might be applied to investigate and address a variety of movement types, in particular gross motor movements with high ecological validity: Young, Roger and Craig (2012) as well as Schmitz and Effenberg (2017a) show that participants can derive kinematic and kinetic features from artificial movement sounds and use these sounds to regulate their movement patterns online. Such findings allow predicting practical effects for improving training in sport and therapy.

4   Improving motor skills

4.1   Sonification for neurorehabilitation (Brock et al., 2012; Schmitz et al., 2014)

The impact of movement sonification on different aspects of perception as well as motor control and learning indicate its great potential for neurorehabilitation. In this field, stroke hold special significance, as the second most common cause of death. More than 75% of all patients survive a stroke, but have to rely on health care support afterwards (Busch, Schienkiewitz, Nowossadeck & Göswald, 2013). Effective rehabilitation methods hold not only individual but also overall economic significance.

Arm functions are often impaired and hamper patients during their activities of daily living (Jorgensen, Nakayama, Raaschou, Vive-Larsen, Stoier & Olsen, 1995). Therefore, these

methods hold particular importance that support the rehabilitation of arm functions like reaching and grasping. Bastian (2008) highlights the relevance of methods related to sensorimotor adaptation and sensorimotor learning for stroke rehabilitation and refers to empirical evidence of their impact on functional recovery. The efficacy might be explained by their effects on proprioception, because more than the half of the patients have somatosensory deficits (Connell, 2007). Proprioceptive adaptation can even be induced during passively performed arm movements, as long as movement feedback is provided adequately (Cressmann & Henrique, 2012). As movement sonification has the potential to substitute proprioception (Danna & Velay, 2017) and can be applied to modify simple as well as complex movement patterns (Effenberg et al., 2016; Oscari, Secoli, Avanzini, Rosati & Reinkensmeyer, 2012; Schmitz & Effenberg, 2017b), it might have significant impact on the recovery of arm functions in stroke patients.

The two manuscripts 'If motion sounds: Movement sonification based on inertial motion data' from Brock, Schmitz, Baumann and Effenberg (2012) and 'A mobile sonification system for stroke rehabilitation' from Schmitz, Kröger and Effenberg (2012) describe the theoretical and technical background of a mobile sonification system for stroke rehabilitation. The sonification system aims to provide auditory feedback on behaviorally relevant arm movement parameters continuously, wirelessly and in real-time (here < 100 s latency). The system is based on seven inertial sensors attached to the fore and upper arms, both shoulders and the sternum. The sensors are connected to a mobile transmitter, which sends the data wirelessly to a laptop for data fusion, analysis and sound synthesis. The produced sound can be transmitted wirelessly to the patient. The system has been designed for ambulatory use, thus, patients can walk around freely and theoretically wear the system during activities of daily living, which would significantly extend the exposure time. The perceptual effects of a precursor sonification have been investigated by Vinken et al. (2013), who showed that participants, which had never listened to the sonifications before, are able to discriminate arm actions purely based on the sonification.

The system is characterized by a great flexibility and adaptability. It can be chosen from more than hundred movement parameters for sonification. The parameter number results from the implementation of several reference frames (allocentric versus egocentric, cartesian versus spherical) with several possible origins (shoulder, elbow, wrist, trunk or absolute positions in the room). For the for real-time feedback of arm movements, three-dimensional coordinates of the wrist in a trunk-centered spherical reference frame as well as wrist velocity were chosen. The parameter selection considered the findings from Graziano (2001) and Lacquaniti et al. (1995) on the neuronal control of hand and arm movements. The sound feature selection was based on ecological psychoacoustic considerations as described in Effenberg (2004) and Vinken et al. (2013): elevation was mapped onto sound

frequency, radial amplitude defined the brightness of the sound and azimuth angle the panning. Finally, wrist velocity was mapped onto sound amplitude. For applications other than stroke rehabilitation, other reference frames, parameters and sound mappings might be chosen.

Seven patients, two to four weeks post stroke, participated in a pilot study. They suffered from hemiparesis and had low to moderate motor impairments. Clinical test scores were chosen as primary outcome variables. This is a usual procedure that allows inferring whether an intervention results in an improvement of general arm functions or only in an enhanced task-specific tool-use performance. The Nine Hole Peg Test was applied for the assessment of fine motor skills, the Box and Block Test for gross-motor arm skills and the Action Research Arm Test for general arm functions. These tests were applied before and after the intervention with or without sonification. The intervention included five training sessions of 20 minutes duration on consecutive days. In the first ten minutes, the patients reached with their arm to defined positions in three-dimensional space. In the second ten minutes, they grasped and replaced a ball from one to 26 other positions distributed across a cubic space of 51 cm^3. Only the impaired arm was trained. The real-time sonification was provided during the intervention to four patients. The three remaining patients served as control without sonification.

None of the patients felt negatively affected by the sonification system; instead, some reported to enjoy the sonification. The results proved significantly enhanced performance in the Box and Block Test only after the intervention with the sonification. Although the sample size was small, these results are encouraging, inter alia, because they were achieved after only 100 minutes of training. Nevertheless, results should be replicated in a larger clinical trial. Therefore, a clinical trial has been developed and pre-registered in the German Register for Clinical Studies, recently ('Movement sonification in stroke rehabilitation', DRKS00011419). Two studies from a project partner confirm the impact of sonification during stroke rehabilitation: both studies used the same motion analysis system with a related, musical sonification in the rehabilitation of stroke patients, and reported significant effects on arm functions (Scholz, Rhode, Großbach, Rollnick & Altenmüller, 2015: Scholz et al., 2016).

The features of mobility, flexibility as well as robustness (i.e. the sensors tolerate gravitational forces up to 18G) allow applying the system in a variety of contexts such as different fields of rehabilitation (neurological or orthopedic disorders), the learning and refinement of motor skills and interpersonal coordination.

4.2   Character acquisition (Effenberg et al., 2015)

Previous studies provided empirical evidence of the impact of movement sonification on perception and action in a variety of contexts (Effenberg, 2005; Schmitz et al., 2013; Schmitz & Effenberg, 2017a; Scholz et al., 2016; Vinken et al., 2013). According to Oscari et al. (2012), artificial auditory feedback about hand movements can be used for the adaptation of hand movement control. Furthermore, Effenberg et al. (2016) and Sigrist et al. (2015) have shown that sonification can support the learning of gross-motor movements. Thus, sonification might also be applied to improve the learning of complex fine motor skills. The article "Soundscript – Movement Sonification to support the acquisition of characters by multisensory integration" from Effenberg, Schmitz, Baumann, Rosenhahn and Kröger (2015, p. 230) presents a method designed to facilitate writing acquisition. Writing is an important cultural technique, which requires skills beyond purely perceptuomotor capabilities. However, as the acquisition of characters represents the first step in a longstanding learning process, it seems reasonable to focus on this aspect.

The SoundScript method combines a visuomotor approach with a sonification approach. Key features include dynamic character presentation and real-time feedback of performance in the visual and the auditory modality. As a model for the final shape to be produced, characters are typically presented in the form of static images. By instructing characters in a way in which a skilled person would produce them, not only the final shapes become perceivable but also the spatio-temporal features of character production. This might support children's understanding of how a specific character can be written efficiently, because the observation of biological motion can activate specific regions in the brain that support action understanding (Steven, Funlopt, Shiffrar & Decety, 1999).

A second feature of the method is movement sonification, which is applied during character instruction as well as during its reproduction. By sonification, the visual writing trace is amended by a spatio-temporally equivalent sound trace. The spatial and temporal proximity as well as time-varying similarities in the patterning of visual and auditory information might address multisensory integration mechanisms in the brain and thus enhance the character representation (Calvert, Brammer & Iversen, 1998). Furthermore, MacPherson and Collins (2009) see a particular benefit of methods that support the rhythmic-temporal control of actions during skill acquisition. Movement sonification can modify the rhythmic structure of a movement (Schmitz & Effenberg, 2017b) and enhance the learning of a specific movement rhythm (Effenberg et al., 2016).

Children are provided with audiovisual real-time feedback about their movements. Whereas the visual information has to be transformed from the vertical instruction plane to the horizontal reproduction plane, which increases the demands for sensorimotor control (Tippett,

Krajewski & Sergio, 2007), auditory information has not to be transformed and might be used without additional transformation costs. The homogenous relationship of instruction and feedback further facilitates the comparison of the previously observed and the reproduced characters. Another possible advantage of auditory movement information is related to a basic sensorimotor learning mechanism: According to Shadmehr et al. (2010), sensorimotor learning is driven by the perceived error between predicted and actually performed movement. Thus, it is related to the to the expected outcome of the movement. Expectations are based on prior experience. The experience of one's own writing traces during character reproduction might be strengthened by the additional sound trace. Therefore, the sound might support the internal modeling of the expected sensory feedback (feedforward modeling) for the next movement, the perception of one's own performance and thereby the sensing of the prediction error.

The possible impact of audiovisual instruction and feedback on character acquisition was scrutinized in a study with fifteen kindergartners. The children were divided up into three treatment groups. All of them saw a visual dynamic instruction of the characters. Two groups were also provided with sound. The *Control* group heard no sound, *Static* group a non-modulated sound and *Sonification* group a sonification of the written trace. In the latter group, spatial coordinates of the pen tip on the surface as well as its absolute velocity were mapped onto pitch, spectral composition and amplitude of a synthesized sound. The children practiced the writing of the characters 'a', 'k' and 'm' on five days for 30 minutes each. Performance was measured with the methods of dynamic time warping (DTW) and shape matching (Senin, 2008; Tappert, Suen & Wakahara, 1990).

The analysis revealed a significant improvement in the *Sonification* group. Significance was achieved after analysis with DTW that considers spatio-temporal similarities between instructed and reproduced movement. No effect was observed after analysis with a shape matching algorithm that compares final shapes. These findings suggest that spatio-temporal features of the writing trace had been improved by the sonification method. No improvements became evident in the other groups.

The results indicate that the SoundScript method effectively supports character acquisition, probably by addressing inverse as well as feedforward models of motor control. Due to large intra-individual variability, it was not possible to analyze the time course of learning in the present study in further detail. However, according to Yavari et al. (2013), a feedforward model is quickly and an inverse model slowly acquired. Thus, detailed analyses of the time course of learning in future studies might allow distinguishing between the two processes and inferring about the underlying learning mechanism. This would further help to under-stand how character representations are established and develop specific methods for

different types of impairments, such as dyslexia and dysgraphia. With respect to the practical effects, the method might help to improve the learning of writing in pre-school (Effenberg et al., 2015) and school children with or without impairments (Danna et al., 2014). Added value to theory is given by providing empirical evidence of the acquisition of fine motor skills based on artificial auditory information.

5   Final conclusions

Many brain functions, in particular motor functions, seem to represent compositions of multiple sub-processes, which are described in literature as special purpose modules (Bertolero et al., 2015; Bock, 2013; Flanagan et al., 1999; Wolpert et al., 2011). Therefore, the overall discussion across studies laid a special focus on modularity. The hierarchical model on cognitive control and learning from Chein and Schneider (2012) served as reference to locate the mechanisms of change. It was argued that motor functions of different complexity can be well described by modular approaches in combination with hierarchical multilevel models. This can be shown for basic (saccades, hand and arm movements) as well as complex sport movements.

5.1   Modularity in the hand- and the oculomotor system

The studies from Schmitz (2016) and Schmitz et al. (2010) show that directional selectivity is an important feature of sensorimotor control. Adaptations of reactive saccades and goal-directed hand movements result in spatially limited adaptation effects, which are very similar across effectors. Directional selective adaptation and motor control processes are explained with reference to directional selective neuronal populations in the brain (Eisenberg et al., 2012; Haar et al., 2015; Noto et al., 1999). These can be understood as basic functional units which are called modules or motor primitives (Bock, 2013; Haar et al., 2015; Wolpert et al., 2011). Their formation as well as adaptation can be explained by Hebbian learning. This seems to be the dominant learning mechanism of basic learn- and control hierarchies which are "composed of … localized circuits … [or] modules" (Chein & Schneider, 2012, p. 80).

Modularity ostensibly suggests a fragmented organization of adaptation as well as of motor control, but hand movements do not reveal such fragmentation during everyday actions. The present thesis identified sensorimotor (pre-activation of directional selective modules, task-specific visual information and the polarity of movement directions) as well as cognitive aspects (diverse executive functions) as factors that probably support the sensorimotor system during the composition of directionally selective modules and overcoming directional selectivity. Further factors related to cognition are discussed in literature (Bedard & Song, 2013; Day et al., 2016). When adaptation exceeds the boundaries of directional selectivity

as shown in Schmitz et al. (2010) and Schmitz (2016), mechanisms seem to be involved which flexibly manage sensorimotor input-output associations. Such mechanisms are described for higher control and learning hierarchies (Chein & Scheider, 2012; Haruno, Wolpert & Kawato, 2003), which act in shorter timescales than a basic representation system. Therefore, the present findings indicate that beside the slow recalibration of sensorimotor modules their flexible composition represents further, fast-acting adaptation mechanism. Further research is necessary to investigate the mechanisms that regulate modular composition comprehensively.

How modular composed sensorimotor representations and sensorimotor adaptation are intertwined is shown by the study of Schmitz and Grigorova (2017). During adaptation, hand movements are influenced by the sensorimotor representation of saccade directions and vice versa. The tendency to couple both effectors even in situations when the eyes are fixated and only the hand moves or the hand is at rest and only the eyes move, might reflect a tendency of the sensorimotor system to establish a common representation for eye and hand movement control (Gorbet & Sergio, 2009, 2016). A possible explanation for these specific results might be illustrated with Figure 1. Eye movements might train one sensori-motor module and hand movements a similar, however, different module. Joint eye and hand movements are governed by a mechanism represented by the next larger triangle that is partially composed of the trained modules. Eye-hand coordination is influenced by both modules. Due to the overall tendency to couple both effectors, also separately performed eye or hand movements seem to use the mechanism of eye-hand coordination (i.e. the larger triangle). Eye-hand coupling manifests as crosstalk between movement representa-tions during adaptation. Training of sufficient duration, as well as further factors as described in section 2.8, enable the sensorimotor system to decouple both effectors and specifically access single modules (i.e. smaller triangle).

Modular concepts have relevance for complex hand and arm functions as indicated by the studies from Brock et al., (2012), Effenberg et al. (2015) as well as Schmitz et al. (2014). Brock et al. (2012) and Schmitz et al. (2014) described the concept of a method aiming at the recovery of arm functions in stroke patients. In order to address multisensory integration mechanisms in the brain, a mobile system for real-time feedback on arm movements was developed, which provides auditory information about three-dimensional coordinates of the hand in a trunk-centered reference frame. This spherical parameter set had been proven to be behaviorally relevant, and the movement parameters direction, elevation and amplitude seem to be controlled by independent neuronal populations in the brain (Lacquaniti et al., 1995). Thus, this approach is based on a modular structure of arm movement control. A pilot study provided indications for an impact of this sonification method on grasping actions in stroke patients. Data from a large clinical trial with a related method were recently

published by colleagues, and provide further empirical evidence of the feasibility and impact of arm sonification systems in stroke rehabilitation (Scholz et al., 2016). In future, these arm sonifications might be further improved by considering the features of directional selectivity and polarity of arm movements; for example, by sonifying spatial corridors with a tuning width similar to directional selective modules or by addressing the mechanism of polarity through different sonifications for movements to the right or the left. Thereby, the modularity of motor control would be taken into account to a greater extent. Feedback on modular features of arm movement control might be particularly important for stroke rehabilitation, because a large number of stroke-induced impairments of arms functions can be well explained by a disruption of the orchestration of modules (Cheung et al., 2012): modules in the central and peripheral nervous system are assumed to govern the coordinated activity of muscles and thus build the basis for muscle synergies (Bizzi & Cheung, 2013). Stroke seems to affect muscle synergies in several ways. Cheung et al. (2012) were able to accurately describe and explain stroke-impaired arm functions by three independent patterns of muscle synergies: depending on the severity of impairment as well as the temporal interval between stroke event and test date, muscle synergies of the impaired arm either matched, represented fragmented or represented merged muscle synergies of the unimpaired arm. According to the authors, these components might represent good indicators for the recovery of arm functions. Therefore, they might also be targeted by feedback-based intervention methods.

A modular approach might also be used to explain and increase the effectiveness of the SoundScript method (Effenberg et al., 2015). With the goal to support character acquisition in children, cartesian coordinates of a pen on a digitizer tablet are mapped onto sound which provides an additional auditory information during character instruction and a real-time feedback to the children. Thereby, multisensory integration mechanisms might strengthen the representation of the instructed character as well as the representation of the own action. Moreover, it can be argued that the homogenous acoustics during instruction and own movement enables the central nervous system to establish an auditory perception--action reference frame. Following the view of Tagliabue and McIntyre (2014) on multisensory integration, this reference frame allows a further, however, modality-specific comparison of target movement and own movement. In next step, the outcome of this comparison is integrated with the outcomes of multiple comparisons performed in other reference frames and thereby optimizes the hand movement. The authors understand this process as a modular approach to multisensory integration for hand movement control.

In a study with fifteen kindergartners, Effenberg et al. (2015) provided empirical evidence for the benefit of this method during the acquisition of three exemplary characters. Effects were significant for spatio-temporal features of writing but not the static shapes of

characters. The finding that auditory information improved the way how children produced characters raises the question, whether character acquisition might be further supported by sonifications that specifically emphasize the character production process. Therefore, future approaches might address the modular mechanisms of movement regulation, for example, by sonifying polar coordinates in a hand-centered reference frame or with the initial pen position as origin. There are indications that hand movement control is based on the control of polar coordinates within a hand-centered reference frame (e.g. Krakauer et al., 2000; Wang & Sainburg, 2005) and that sensorimotor abilities contribute to the legibility of hand writing in children (Daly, Kelley & Krauss, 2003).

5.2   Multimodal and modular representations of sport movements

The significant covariations between synchronization performance in indoor rowing, self-identification rate and the own-other effect in Schmitz and Effenberg (2017a) suggest that also internal representations of sports movements are composed of independent modules. One module seems to be related to the timing of movements, which represents the temporal calibration status of perception-acting couplings. The results of the synchronization task in the study of Schmitz and Effenberg (2017a) are consistent with this view. The listening to sonifications of different movement parameters of another person results in different temporal asynchronies, probably because kinematic and dynamic sonifications lead to the integration of different timing modules into a modular composed representation of the other's movement.

A further covariation suggests that one modular component of internal representations is related with the individual movement pattern. This finding makes it possible to connect the present research with the cognitive architecture of movements proposed by Schack and collegues (Schack, 2004; Schack & Ritter, 2009). In their view, mental representations are composed of 'Basic Action Concepts' (BAC). BACs are described as being the mental counterpart of body postures and basic movement components, which are closely related with individual movement patterns (Land et al., 2013). The authors themselves refer to modular concepts of mental representations and regard the change of mental repre-sentations through practice and training as functional adaptation of complex actions (Schack et al., 2016, p. 207).

Further research might amend neuroscientific concepts of modularity and further develop a modular concept of sport specific movement representations. This would not only broaden the knowledge about the structure of complex movement representations, but also provide starting points for practical applications and goal-directed interventions for the shaping of single modules or to address modular composition. Thereby, besides individual movement coordination, interpersonal coordination might become an important topic of future

research. This holds particular relevance for sport science, because most sport disciplines require and support interpersonal interactions.

5.3   Fast- and slow-acting mechanisms of change

The results of the present thesis indicate that internal simulations of sport specific movements occur without modality-specific expertise. These findings suggest that internal simulations can be performed independently from modality-specific sensorimotor associations and rather unfamiliar sensory input can be linked to internal movement representations. At least in case of the perception of sonified gross-motor actions, such associations might be mediated by higher hierarchies like the cognitive control network described by Chein and Schneider (2012). This would have several theoretical consequences. These authors argue that mechanisms on different hierarchies act in different timescales, which corresponds to current views on the mechanisms for sensorimotor adaptation and learning. Fast- and slow-acting mechanisms seem to differ with respect to memory consolidation: fast mechanisms yield poor and slow strong retention (Bastian, 2008; Bock & Schmitz, 2011; Chein & Schneider, 2012; Ethier, Zee & Shadmehr, 2008; Lee & Schweighofer, 2009; Smith et al., 2006, Simon & Bock, 2016; Yavari et al., 2013). Nevertheless, fast- and slow-acting mechanisms are intertwined. Fast-acting mechanisms seem to foster the acquisition of long-term representations, which emerge in perceptual, perceptuomotor as well as motor regions of the central nervous system at cortical and subcortical levels (Flint et al., 2016; Francois, Grau-Sanchez, Duarte & Rodriguez-Fornells, 2015). Once these routines have been established, learning seems to be more strongly driven by slower mechanisms (Chein & Schneider, 2012). The studies presented in chapter 3 of this thesis suggest that a sonification of movements addresses fast-acting mechanisms (Schmitz et al., 2013; Schmitz and Effenberg, 2012, 2017a, 2017b) and links to well-established internal representations. Thereby, it can unfold its potential without the need to form new perceptuomotor representations by long-term training. However, as fast-acting mechanisms typically yield poor retention (Ethier, et al., 2008; Smith et al., 2006), it might be assumed that this linkage to already established representations diminishes after auditory stimulation has ended; but this might not be necessarily the case or detrimental as indicated by the results of a recent study: Effenberg at al. (2016) observed a performance benefit induced by sonification during the learning of indoor rowing from the first learning session on. The benefit persisted for several weeks of training and resulted in increased performance even three weeks post training. This quick performance increase indicates the involvement of fast-acting learning mechanisms. Considering the effects that can be achieved by sonifications of rowing actions (chapter 3), the rowing sonification in Effenberg et al. (2016) might have speeded up the acquisition of early behavioral routines or the integration of

modules that are relevant for the learning context. This example shows that there might be a particular value of methods that address fast-acting learning mechanisms despite their probable low retention.

The interplay between fast- and slow-acting mechanisms might reflect the interplay between hierarchies. Several studies indicate that established perceptuomotor couplings facilitate higher-level perceptual processes (Herholz, Boh & Panev, 2011; Schmitz & Effenberg, 2012, 2017b; Sevdalis & Keller, 2014). Once firmly established, they seem to provide the basis for particular competences related to perception and cognition: it has been shown for musical as well as sport experts that established representations support perceptual performance in training-specific as well as adjacent domains (Francois et al., 2015; Mann, Williams, Ward & Janelle, 2007; Tan et al., 2017). Furthermore, years of perceptuomotor training seem to facilitate domain-specific perceptual learning (Blazquez, Kim & Yakusheva, 2017): musicians with 13 years of expertise – but not novices – show altered brain activity after 10 minutes of novel sound pattern learning. The authors explain this effect by a more efficient updating of internal representations across hierarchies, whereby perceptual learning is driven by a prediction error that "is passed back up the hierarchy to refine the [prediction or feedforward] model" (Blazquez et al., 2017, p. 527). Therefore, the optimization of the interactions between hierarchies might be important for achieving high performance in sport.

Taken together, the studies of this thesis amend the knowledge on internal representations, the mechanisms of change as well as their interplay. The results indicate that different components or types of representations contribute to the perception of gross-motor sport movements. Furthermore, it has been shown how learning and control mechanisms can be addressed to alter the control of different types of movements and actions: reactive saccades, goal-directed hand movements, complex manual actions as well as complex sport movements. The contribution of functional different and hierarchically-organized entities to even the simplest action and their possible mutual influence opens the opportunity to access perceptuomotor control with different approaches. The proposed sensori- and perceptuomotor methods allow designing perceptual settings and thereby addressing different hierarchies of motor control. They seem to be powerful tools for the optimization, regulation and shaping of performance in sport as well as adjacent domains.

6   Summary

Complexity in sport situations is a challenge for research on motor behavior in sport and for the development of methods for improving performance. To understand the mechanisms of motor performance, it is necessary to combine basic and applied research approaches and to investigate motor behavior on multiple levels. The present thesis follows a multiple-level approach by investigating mechanisms of motor control, movement representations and mechanisms of change at different levels of complexity. The aim is to analyze features of basic movements, to find out how they are embedded within complex movement types and to develop practical applications for the improvement of motor learning processes. This is made possible by combining two methods that allowed to modify perceptual settings and thereby controlling information processing: Visuomotor methods were used for investigation and adaptation of representations of fine motor skills. The method of sonification was applied to analyze and modify gross motor and complex movements as well as interpersonal coordination.

The results indicate that simple movements such as reactive saccades and two-dimensional hand movements are controlled by lower sensorimotor as well as higher cognitive hierarchies. Moreover, they revealed that motor functions are structured modularly. Extensive practice allows access to slow-acting learning and control mechanisms which yield persistent effects on motor behavior. Fast-acting mechanisms can be activated by a specific arrangement of perceptual information and the pre-activation of basic sensorimotor modules. Specific executive functions might support this effect.

Results on sonification indicate that this method predominantly addresses higher hierarchies which is reflected in the quick effects achieved on the perceptual and motor level even without specific methodological knowledge. Based on these results, two systems for the improvement of motor functions in sport and adjacent disciplines have been developed. Studies provide empirical evidence for their impact on gross motor skills in stroke rehabilitation and fine motor skills during writing acquisition. Furthermore, approaches for a targeted improvement of interpersonal coordination (joint action) are presented.

The combined results of this thesis show that a modification of perceptual settings make it possible to study a variety of movements in a continuity from most simple to most complex. The findings can be embedded into hierarchical models of motor control which allow the systematic development of methods with great flexibility to improve motor competencies and to shape motor behavior in the field of sport and adjacent domains.

7   Cumulus

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