Effect of timing training in golf and soccer players:

skill, movement organisation, and brain activity

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Abstract

Background Although trainers and athletes consider 'good timing skills' to be critical for optimal sport performance, little is known in regard to how sport-specific skills may benefit from timing training. Thus, assuming that all motor performances are mediated by an internal timing mechanism, enhanced motor timing is expected to have positive effects on both planning and execution of movement performance, and consequently on complex sports actions as golf or soccer. Accordingly, in order to increase our knowledge of the importance of motor timing and possible effects of timing training, this thesis examines the effects of synchronized metronome training (SMT), thought to improve the execution of motor programs and to enhance motor skills in golf and soccer players.

Methods Study I examined the effects of SMT on motor timing abilities and its potential effect on golf shot accuracy and consistency in 25 experienced male golfers. Additionally, Study II examined the effects of SMT on the spatiotemporal movement organisation and dynamics of the golf swing performance, as captured by kinematic measurements and analyses in thirteen male golfers. Study III examined the effect of SMT on accuracy and variability in a soccer specific, cross-pass task in elite and sub-elite female soccer players. Moreover, the underlying brain activity was assessed by means of functional magnetic resonance imaging (fMRI) to investigate the corresponding neural activity when passively observing the cross-pass task, and the possible pre- to post training effects.

Results SMT was shown to improve motor timing ability, by means of less timing asynchrony and with associated changes in timing variability, in both golf- and soccer-players. Additionally, significant improvements in golf shot and soccer cross-pass performance, by means of significant increase in outcome accuracy combined with a decrease in outcome variability was found. From the kinematic investigation in Study II, results indicate that improved motor timing, as an effect of SMT, lead to a more coordinated and dynamic swing performance, and with decreased variability in the temporal structure of the swing motion. Finally, it was found that SMT induces changes in the activity of the action observation network (AON), underpinning action observation and action prediction, by means of decreased activation within bilateral cerebellum, fusiform gyrus and superior temporal gyrus. These findings hint at a more efficient pattern of neural recruitment during action observation, after SMT.

Conclusion In summary, this thesis provides evidence that four weeks of SMT improved the participant's motor timing and synchronization abilities, and showed influence on both behavioral and neurophysiological motor programs and skill performance in golf and soccer players. Thus, by improved outcome accuracy and decreased variability, affecting the coordinated movement pattern and organisation, as well as affecting the associated underlying brain activation.

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List of papers

This thesis is based on the following papers, which are referred to in the text by their Roman numerals.

- I. Sommer, M. & Rönnqvist, L. (2009). Improved motor-timing: effects of synchronized metronome training on golf-shot accuracy. *Journal of Sports Science & Medicine 8*, 4, 648-656.
- II. Sommer, M., Häger, C., Rönnqvist, C. (2014). Synchronized metronome training induces changes in the kinematic properties of the golf swing. *Sports Biomechanics*, 02/2014, 1-16.
- III. Sommer, M., Häger, C., Olsson, C. J., & Rönnqvist L. (Manuscript). Timing training in female soccer players: effects on motor skill and associated changes in functional brain activity.

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Abbreviations

AE	Absolute Error
AON	Action Observation Network
BOLD	Blood Oxygenation Level Dependent
CNS	Central Nervous System
CTRL	Control Group
EBA	Extrastriate Body Area
fMRI	functional Magnetic Resonance Imaging
HRF	Hemodynamic Response Function
IFG	Inferior Frontal Gyrus
IM	Interactive Metronome
IPL	Inferior Parietal Lobule
IRI	Inter-response Interval
MS	Milliseconds
PMC	Pre Motor Cortex
NpF	Non-preferred Foot
PW	Pitching Wedge
RAS	Rhythmic Auditory Stimulation
SMA	Supplementary Motor Area
SMS	Sensorimotor Synchronisation
SMT	Synchronised Metronome Training
STG	Superior Temporal Gyrus
VE	Variable Error
TV	Target Variability

'We perceive in order to move, but we also move in order to perceive'

- James. J. Gibson, 1979, p.223

Pre-phase

The idea of the doctoral project from which this thesis has emerged was born as I accidentally stumbled upon a paper showing that improvements in motor timing, as an effect of multimodal timing training (Synchronised Metronome Training – SMT), have positive effects on golf shot accuracy (Libkuman, Otani and Steger, 2002). As a former athlete, this particular study grabbed my attention because it pointed at the importance of precise timing, which is required in any sport performance – thus by means of refined movement planning, movement coordination and control, and possible success. The findings also implied that task-specific performance (e.g. golf shot accuracy) may be influenced by more general, non-task specific training (e.g. timing training – SMT).

Although the results presented by Libkuman and colleagues were interesting, it also became apparent that little is known about how SMT may induce changes in the underlying kinematic properties of motor performance. Neither did any knowledge exist in regard to whether the effects of SMT were limited to closed motor skills such as the golf swing, or if it also could have positive effects on open motor skills, for instance in an interceptive cross in football. Moreover, questions in regard to whether SMT would also be beneficial to highly experienced and/or elite athletes, and not limited to novice/intermediate or recreational athletes, and finally, how effects of SMT would be manifested in terms of functional brain plasticity and organisation, were raised.

Therefore, the aim of the present thesis is to highlight these issues.

Introduction

In functional performance, whether defined as athletic excellence in such sports as golf or soccer, for instance, or associated with recovered function after injury, the accomplishment of purposeful motor tasks rests upon wellcoordinated actions. Certainly, any motor skill involves many degrees of freedom related to the large number of muscular-skeletal components involved (Bernstein, 1967). Hence, the coordination of multiple (sub-) movements is essential in order to generate an optimal outcome. However, coordination of movements is possible without a mechanism no orchestrating the work of the individual parts (limbs/joints). In line with this, it is argued that coordination includes and specifies spatio-temporal ordering between component parts (e.g. Jantzen, Oullier and Kelso, 2008), and since movements involve changes in muscle length over time (Mauk & Buomonano, 2004), coordination and timing seem to be inextricably linked. Functional performance also involves the close interaction of sensory processing with the production of complex, multi-joint motor tasks. Indeed, the number of peripheral sources (e.g. eyes, muscles, joints, and the vestibular organs) providing feedback to the CNS during action execution imply that the neural system needs to integrate and coordinate feedback information across multiple modalities (e.g. proprioceptive and visual) in order to generate an optimal outcome, in relation to specific task demands, in a constantly changing environment.

Thus, the present thesis aims to synthesise knowledge related to timing, coordination and motor control – and perception and action – in general, and the effects of timing training on golf and soccer performance, describing the underlying kinematic parameters of performance as well as related changes in brain activation, in particular.

Timing in motor control and coordination

A soccer player is not only required to time and coordinate her movements on the soccer field in relation to the ball and her teammates, as well as her opponents, but she must also handle the spatio-temporal coordination of her own body during soccer-specific tasks, such as passing, trapping, shooting and heading. Thus, the processes of motor coordination and control require an understanding not only of coordination between motor system components, but also coordination between the movement system and the prevailing constraints (e.g. Turvey, 1990; Davids, Handford & Williams, 1994). As such, coordination requires a system-environment interaction with a sensory -motor coupling.

Coordination, in general, refers to a process in which movement system components involved in a specific motor action are combined in a manner that is efficient with respect to the intended goal (Bernstein, 1967; Turvey, 1990). Here, coordination may be operationally defined as the spatiotemporal relationship between two or more coupled agents or components (Jantzen, Oullier and Kelso, 2008); or in dynamic systems terms; as the bringing together of the movement system components into correct (spatiotemporal) relation with each other (Turvey, 1990). Utilising the golf swing as an example, coordination may therefore be described as the coupled movement (however, with specific time-lags between the initiation of the respective body part/effector) in which the player initiates the downswing towards the ball by a left pelvic rotation and shifting weight to the left foot, while bringing the right elbow down towards the body (see Hume, Keogh & Duncan, 2005 for a review). As such, coordination involves variables that specify the spatio-temporal ordering between component parts (Jantzen, Oullier and Kelso, 2008).

Optimal sports skill performances, such as the golf swing or the instep-kick in soccer, entail complex sequential movements, spanning multiple effectors (limbs, muscles and joints), and thus rely on carefully coordinated movements timed in the order of tens to hundreds of milliseconds (c.f. Medina, Carey & Lisberger 2005; Buanmono & Laje, 2010). A high degree of coordination, both within and between limbs, is required for fast, accurate and energy-efficient movement execution. The accuracy in timing of movements between different limbs (e.g. head and foot) and within limbs (e.g. hip, knee and foot) seems to be crucial for skilled performance in both single effector actions and in actions requiring multiple effectors (Schmidt & Wrisberg, 2004). These factors have a significant impact on both the quality (e.g. the spatio-temporal properties of a golf swing) and the outcome of the movement (e.g. golf shot accuracy).

Control refers to the acquired ability of the athlete to vary the parameters of the motor pattern, such as force, speed and duration, to suit specific performance constraints (Newell, 1986). Although the coordination pattern of, for instance, a kicking movement and the control (force of the kick) may remain the same, the actual outcome may differ, since skill involves angling the foot (or the club, in golf) to achieve the intended trajectory of ball flight. Despite the computational challenges concerning handling the numerous degrees of freedom involved in such tasks (Bernstein, 1967), the human brain is able to integrate, translate and coordinate information across multiple sensory modalities and multiple muscles and joints in order to generate the most efficient motor action acquired at a given time (Jantzen, Oullier & Kelso, 2008). For instance, precise integration between visual and

motor systems is paramount for the timing of the kick of a football in motion (Egan, Verheul & Savelsbergh, 2007), and precise audio-motor integration is integral for synchronising movements with external auditory cues (sensorimotor synchronisation: SMS – e.g. Repp & Su, 2013). Thus, and as implied above, the coordination of effectors for optimal performance in a given environment (with several types of constraints being present) is not solely concerned with spatiotemporal coordination of motor actions. It also entails a timely coordination and integration of sensory input from different modalities, and how these relate to the evolving motor action(s). In other words; a perception-action coupling.

As can be implied from the above reasoning, timing seems to be an important variable or property of motor coordination and motor control. Still, the explicit role of timing in motor actions has been questioned in favour of state-dependent theories. Using the instep-kick in soccer as an example, a player will typically drive her leg in a forward movement, including a proximal (hip) to distal (foot) sequence of activation and peak velocity, to kick the ball. According to state-dependent theories (e.g. Hore & Watts, 2005; Diedrichsen, Crscimagna-Hemminger & Shadmehr, 2007), the time-lag between the activation of muscles initiating the forward movement of the thigh (flexing the hip-joint) and the extension of the leg (extending the knee-joint) would be based on a state-dependent control process (proprioceptive feedback entailing angular positions), rather than a timedependent control process. The state/time-dependent divergence is interesting from an action-perception perspective, because the most efficient approach to achieve well-timed movements would be to integrate sensory information from visual, auditory and somatosensory modalities.

Variability in motor performance

Skill is a level of performance in any given task that can be acquired only through practice. In regards to motor actions, the skills of experts are typically different from those of novices in that they are for instance faster, more accurate, more efficient and more cost effective (Yarrow, Brown & Krakauer, 2009). Although the outcome goal of a movement is the same, the movement pattern used to achieve these outcomes may not be repeated in an identical way every time, for instance due to changes in performer, task or environmental constraints. This feature of 'repetition without repetition' (Bernstein, 1967) facilitates adaptations to solve typical motor problems, and is present even on an expert level.

Most sport skill performances are based on a model template that is a representation of the ideal or optimal form of a movement (e.g. the instep-

kick in soccer or the golf swing performance). Typically, the trainer or tutor - during learning - provides the optimal performance of a skill based on how it is executed by experts. Further, any deviations from optimal expert performance/execution then provide information from which a diagnosis of faults can be made (Lees, 2002). However, during the past decade or so, movement variability has been accentuated in the field of motor control research, because of the flexibility and adaptability it offers in regard to achieving a specific (motor/movement) goal or outcome (e.g. Todorov & Jordan, 2002; Davids, Araujo, Glazier & Bartlett 2003, Bartlett, Wheat & Robins, 2007). For a coach or an athlete, the relationship between consistency (being able to achieve the same outcome repeatedly) and variability may at first seem paradoxical; however, it provides an understanding of the importance of adaptability to the prevailing constraints or conditions. Rather than viewing any deviation from a perceived 'common optimal movement pattern' as being some undesirable 'noise in the system', or as a potential weakness in the players technique, one needs to acknowledge that movement variability reflects the adaptability of the performer on the convergence of the environmental, organismic or task constraints acting on the performance at any given time (Newell, 1986; Newell, van Emmerik & McDonald, 1989, Todorov & Jordan, 2002), at least in cases in which variability is defined as an asset in regard to being able to reproduce the same movement pattern during a variety of environmental constraints.

In golf and soccer, the major goal, and challenge, of any player is to consistently and predictably hit the ball in the desired direction for the proper distance, independent of strategy. To do so, the player must optimally organise and repeatedly produce successful complex movements (McHardy & Pollard, 2005). Accordingly, it is suggested that if any invariance of the golf swing kinematics is sought, for example, it should be at ball impact where the outcome is determined (Knight, 2004). This claim makes sense in one way, but still it is beyond doubt that the spatio-temporal properties of the golf swing movement prior to ball impact (i.e. during the first 50% of the downswing movement) will directly influence the properties of the club-ball contact. This fits well with the notion that variability should only be minimised in the (motor) components that have the greatest effect on the variability of the outcome (e.g. Todorov & Jordan, 2002). However, one might ask what parameters of variability in motor execution that have the greatest effect on the variability of the outcome?

Todorov and Jordan presented the theory of optimal feedback control, in which one important feature is the minimum intervention principle. This principle postulates that deviations from an average action (e.g. club or foot

trajectory/position) are only corrected if they interfere with the task performance. Thus, by correcting only task-relevant errors, the model minimises the potential effects of noise. Todorov and Jordan argue that such differential management of variability in motor actions occurs because it is the optimal solution for the performance of the task. In line with this, the Uncontrolled Manifold Hypothesis (Sholz & Schöner, 1999) acknowledges that variability is always present in human movements, but may be of a good or a bad nature. Here, bad variability affects the important performance variable and causes larger outcome errors – and should be avoided, whereas good variability does not result in failure of the main task, and allows for flexibility of performance. However, so far most studies of sport performances have investigated movement variability at i.e. the impact of foot/club and ball, and/or of specific outcome parameters at different phases of the motor production of such skills, and not the underlying movement dynamics and coordination patterns throughout the performance, which indeed may have an equivalent effect on the performance outcome.

Decrease of movement variability and smoother movement trajectory as an effect of rhythmic cuing (RAS – rhythmic auditory stimulation and SMT) has recently been found in hemiparetic reach (Thaut, Kenyon, Hurt, McIntosh & Hoemberg, 2002; Malcolm, et al., 2009) and in children with cerebral palsy (Johansson, Domelöf & Rönnqvist, 2012), respectively. These studies suggest that the coordinative structure of motor performance influences motor output. Accordingly, in Study II of the present thesis, we assessed the stability and variability of coordination in golf swing performance, by means of time-series signals gained from calculations of cross-correlation between different joint motion linkages, as well as accuracy and variability of the golf shot outcome (Study I).

Timing in a sport performance context

From appraising the general non-scientific sports literature it becomes evident that timing is a rather vague and diverse concept. While frequently concluded by both coaches and athletes that it is an important factor for successful performance, there is no consensus in regard to what one refers to. In the domain of golf, timing is one of the main attributes that professional players (e.g. Nicklaus, 1974; Watson, 1998), instructors (e.g. Pelz & Frank, 1999) and scientists (e.g. Neal, Lumsden, Holland & Mason, 2008) believe to be important for an optimal swing. However, it is less well known what this timing component may involve, and it is also shown that there is seemingly no correlation between golfers' own classification (judgment) of a well-timed shot and the temporal properties of their golf swing (Neal et al., 2008). In general, for closed-skill sports such as golf, timing seems to refer to a feeling of a smooth flowing swing, occasionally tapping in to such concepts as swing tempo/duration, or the relative duration of the individual phases of the swing (backswing, downswing and followthrough). In open skill sports such as soccer, timing is usually an expression for being in the right place at the right time, or for instance, the timing of movements in relation to the ball (e.g. during a header or a volley).

From the available scientific literature on research related to timing within the domain of sports, it seems that the most prominent features of timing refer to the ability to control and differentiate the rhythm and tempo of a specific motor action (Martin, 1988; Zachopoulou, Mantis, Serbezis, Teodosiou & Papadimitriou, 2000; Kim, Jagacinski & Lavender, 2011), the sequential order between a series of individual movements, and the time intervals that separate them (generally referred to as motor sequencing – Putnam, 1993, Ferdinands, Kersting & Marshall, 2013, Davids, Lees & Berwitz, 2000; Savelsbergh & Bootsma, 1994), as well as the strength of coupling and phasing between and within segments (temporal intra- and inter-segment coordination) during action (e.g. Beak et al., 2013; Horan & Kavanagh, 2012).

While behavioural studies within sports other than golf, such as tennis (Zachopoulou & Mantise, 2001), soccer (Keramidas, Patsiaouras, Papanikolaou & Nikolaidis, 2004) and fencing (Czajkowski, 2009) indicate that parameters of timing (e.g. rhythm and tempo of limb displacement) greatly influence the outcome quality of the movement, and that choice of time for a specific action to be initiated/performed is decisive for success, less is known about how motor timing abilities may be improved. Similarly, neither is it known how and if improvement in motor timing may be manifested in the underlying brain mechanisms corresponding to these behavioural changes.

Movement tempo and rhythm as features of 'timing' in motor actions

It is suggested that timing is an ability that includes skills in observing, controlling and differentiating the rhythm of a specific motor action, depending on the situational demands (Martin, 1988), and is thus considered one of the most fundamental skills of an athlete (Zachopoulou et al., 2000). Accordingly, golfers are believed to be facilitated by holding the tempo and duration variables of golf swing performance at a constant. Here, it is proposed that the timing structure of a golf swing involves aspects of both tempo and rhythm, where tempo refers to the overall duration of the swing, and rhythm to the relative timing of the different phases of the swing (backswing, downswing and follow-through; Jagacinski et al., 2009). Advanced golfers have been found to display little between- and within-

subject variance in regard to swing tempo (independent of club used), and little variance in swing-rhythm, independent of swing tempo (e.g. Egret, Vincent, Weber, Dujardin & Chollet, 2003; Betzler, Monk, Wallace, Otto & Shan, 2008; Grober and Cholewicki, 2008; Jagacinski et al., 2009). This is a trait proposed as being decisive for effective distance control in golf (Pelz & Frank, 1999). In line with this, Jagacinski, Greenberg and Liao(1997) report a compensatory relationship between the backswing and the downswing, meaning that when the backswing is shorter, the downswing is longer, and vice versa. According to Jagacniski et al. (1997) these patterns suggest that the tempo and rhythm of the shot are not independent and that changing one's tempo may disrupt rhythm.

The aspects of tempo and rhythm in golf are interesting in regard to the SMT intervention utilised in the studies implemented in the present thesis, because the variability of the motor output (inter-response interval), as provided by the IM system, mirrors the subject's ability to keep a steady movement rhythm. Changes in rhythmic skills may induce changes in aspects of the golf swing performance related to swing-tempo and swing-rhythm. The ability of the auditory system to rapidly detect temporal patterns in auditory signals and construct stable rhythmic templates is well known (Thaut & Kenyon, 2003), and it has been shown repeatedly that movements instantaneously entrain to the period of a rhythmic stimulus (for instance a metronome beat). Thus, as in RAS, it may be the case that SMT intervention provides rhythmic cues which give the brain a time constraint to which the duration of the movement is fixed. This process will possibly induce changes in movement speed, and lead to smoother and less variable movement trajectories and muscle recruitment, as seen in post-stroke gait patients (Thaut et al., 2003) and in hemiparetic reach (Johansson et al., 2012). Thus, the rhythm '...not only influences movement timing-time as the central coordinative unit of motor control-but also modulates patterns of muscle activation and control of movement in space' (Thaut, 2013, p. 33).

In regard to soccer-kick performances, rhythm and tempo have predominantly been examined in tasks requiring the subject to kick for a maximum length. It is typically found that these kicks generate higher movement velocities and shorter movement durations than when kicking for accuracy. Also, it is evident that the tempo of preferred-foot kicks is faster than for non-preferred foot kicks (Nunome et al., 2006), pointing at an effect of expertise on the kinematic properties of the kicking performance. However, less is known about how increased timing skills may influence soccer kick performance (e.g. kinematic or kinaesthetic measures) or soccer kick outcome measures (e.g. accuracy, variability or overall success – goals).

Temporal order and sequencing of movements

As previously stated, coordination refers to the process by which movement system components are assembled and brought into proper relation with each other during goal-directed activity (Turvey, 1990). For example, the successful performance of skills in both soccer and golf requires the player to assemble a coordination pattern which facilitates the development of high velocities in the distal (foot/club head) segment. In interceptive actions, this pattern typically describes a proximodistal temporal sequencing at the onset (Hay, 1985) and reach of peak velocity (e.g. Nunome et al., 2006; Neal et al., 2008) of joint movements.

The soccer kick and the golf swing have several commonalities in regard to action execution. For instance, first of all they aim for hitting a ball and they mutually involve a pendulum-like movement entailing a timed proximal-todistal coordination pattern (e.g. Nunome et al., 2006; Egan, Verheul & Savelsbergh, 2007; Kellis & Katis, 2007 for an overview), which influence the final speed, trajectory and spin of the ball, and thus influence the quality of foot/ball contact (see Lees, Asai, Andersen, Nunome & Sterzing, 2010 for a review). Moreover, performance success in both these sports relies on a high degree of outcome accuracy and consistency within a dynamic environment.

In golf, the spatio-temporal layout of the swing performance indicates that in an ideal downswing motion, the proximal body segments (i.e. pelvis, torso) reach peak angular velocity prior to more distal segments (e.g. Springings & Neal, 2000; Nesbit & Serrano, 2005; Cheetham, Rose, Hinrichs, Neal, Mottram, Hurrion & Vint, 2008). Such sequencing of peak segmental angular velocities is essentially a utilisation of the summation of speed principle (Bunn, 1972), and is crucial for obtaining peak club head velocity at the exact point of ball impact. Neal et al. (2008) acknowledge that the length of time between the peak velocities of the different segments/limbs involved in the golf (down) swing is imperative for maximising club head velocity and distance. However, within the downswing movement sequence it is not known which magnitude of inter-segment lags is optimal. Interestingly, Cheetham et al. (2008) found that there was no difference in the means for the time of peak rotational speeds before ball impact between amateur and professional golfers. However, they did find that the standard deviations of the means for amateurs were more than double those of the professionals, implying a less consistent and less coordinated downswing movement in amateur golfers.

Egan et al. (2007) investigated the coordination of internally timed and externally timed soccer kicks (i.e. kicking a stationary ball and a moving ball, respectively). The authors found that the time between maximum hip angle and ball contact (relative timing) was significantly longer/higher in the moving ball condition, probably due to perceptual processes related to the detection of the trajectory of the ball, and the online adjustment of the movement of the own body. Also, an expert/intermediate difference was found for the moving ball condition, with experts proving to have shorter relative timing. In line with this, Nunome et al. (2006) examined time-series data related to the spatio-temporal pattern of movement in the preferred and non-preferred leg in a group of highly skilled youth soccer players (n=5). The authors found a proximal-to-distal pattern of coordination with both the preferred and non-preferred foot. Although not specifically outlined, it could be extracted from the presented data that the time intervals that separated the sequential order between the individual movements were not the same for the two feet. Thus, it may be hypothesised that temporal sequencing of proximodistal inter-limb displacement is moderated by experience. This is based on the fact that the time-series data was different for the two feet (although the overall proximodistal patterns was similar), and because a lower velocity at foot/ball impact was seen for the non-preferred foot, in comparison to the preferred foot. This is in line with the literature on skill acquisition; reporting different stages in the learning process in different sports and a progression of motor control from proximal to distal during the learning process of goal-related tasks (Chow et al., 2007; Hodges et al., 2005).

Intra- and inter-limb coordination as a measure of movement timing in sports

Current advances in the field of non-linear dynamics have shown that collective variables, such as relative phase shifting, are able to capture the underlying spatio-temporal dynamics of inter/intra-joint coordination (e.g. Burgess-Limerick, Abernethy and Neal, 1993). Recent studies show that cross-correlation analysis is a way of revealing the underlying temporal features of movement, and has successfully been applied to continuous kinematic data in order to examine the coordination between head, thorax, and pelvis motion during the downswing of professional golfers (Horan and Kavagnah, 2012).

Similar to commonly used correlation analysis such as Pearsons productmoment, cross-correlations assume a linear relationship between two timeseries for instance velocity of the knee in relation to the ankle in a soccer instep kick. Unlike other correlation techniques, cross-correlations time-shift one variable (e.g. wrist) in relation to the other (e.g. the elbow), and then identify the 'time-lag' (temporal relation) at which the correlation between the two time series is the greatest (Mullineaux, Bartlett, & Bennett, 2001). Accordingly, temporal aspects of coordination have been assessed using cross-correlation functions in, for instance, volleyball serving (Temprado, Della-Grasta, Farrell & Laurent, 1997), relative timing in the triple jump run-up (Maraj, Elliott, Lee & Pollock, 1993), javelin throwing (Morris, 1998), and in a study of foot and shank motion during running (Pohl & Buckley, 2008). Within golf swing performance specifically, inter-segment coupling between continuous time-series signals of head and thorax, and thorax and pelvis (Horan & Kavanagh, 2012), and between and within pelvis and upper torso (Beak, et al., 2013) has been investigated.

For the golf study (Study II) with a focus on golf swing performance, it was hypothesised that any changes in the coordinative structure and the temporal synchronicity between intra-limb couplings and the golf club motion, as an effect of SMT, would be quantifiable with the use of cross-correlation analysis.

Interceptive timing skills

Accurate time estimation in the anticipation of predictable events is vital for motor behaviour. It seems beyond doubt that timing is an important feature in interceptive tasks. For instance, in soccer it is suggested that one important timing-related variable is that of being in the right place at the right time (Savelsbergh and Bootsma, 1994; Davids, 2002). More specifically, I refer to the problem of timing (self-produced) actions with an external event (externally timed actions). While performing a soccer kick of a football in motion, for instance, the player must regulate the coordination of the kick in an ongoing manner on the basis of visual information regarding the ball, but also on the proprioceptive information available from executing the kick (Egan et al., 2007). While the former relates to moving in relation to the spatial and temporal constraints of ball-flight trajectory, the latter event – the kick – is an internally timed process relying on the spatiotemporal coordination of the hip, knee and foot, which has been discussed earlier in the present thesis. When kicking a moving football it takes time for visual information that reaches our eyes to be transformed into muscle contractions, and for muscle contractions to bring the leg to the appropriate place at the appropriate time. Thus, timing the kick requires prediction. The timing precision will therefore depend on how well one can predict the moment of interest at the last moment at which the timing can still be adjusted (Brenner & Smeets, 2011). Thus, motor anticipation requires an internal representation of elapsed (or remaining) time, which refers to

temporal processing, or the decoding of temporal information (Wiener, Matell & Coslett, 2011).

However, these two events can obviously not be separated in the example of performing a soccer kick within a game-setting, and thus, in successfully satisfying the task constraints of kicking a ball for power and/or accuracy, the player must master the interaction of information provided by both the motor (action) and the perceptual systems (Atkinson & Newill, 2000). Although driving a golf club towards a stationary ball is not defined as an interceptive action, it places similar demands on the integration of, and interaction between, action (movement) and perception (e.g. the visual appreciation of the ball and the features of the ground it is lying on).

Motor timing from a theoretical perspective

Timing as a concept refers to how the human brain continuously measures time based on multiple timing systems (e.g. viz., circadian, interval, and millisecond timing), associated with different behaviours and neurological substrates (Mauk & Buonomano, 2004). In relation to motor coordination and control, it is suggested that most motor actions require carefully coordinated movements timed on the order of tens to hundreds of milliseconds, in which the spatio-temporal patterns of muscle activation is orchestrated by some specialised or general neural mechanisms (Buonomano & Laje, 2010). Accordingly, timing seems to be inextricably related to motor control and coordination (e.g. Mauk & Ruiz, 1992; Ivry, 1996; Meegan, Ashlin & Jacobs, 2000; Medina, Carey & Lisberger 2005; Buonomano & Mauk, 2004, Kelso, 1995; Cassentti, 2011; Repp & Su, 2013).

While reviewing the motor timing literature, it becomes clear that the concept *motor timing* almost exclusively refers to either SMS or self-paced rhythmical motor actions (e.g. finger-tapping or circle-drawing) in which response variability is the main outcome measure. Hence, motor timing typically refers to 'the production of timed motor actions or responses, ranging from a simple timed motor response to complex spatio-temporal patterns of muscle activation' (Buonomano & Laje, 2010, p. 520). Thus, motor timing has been understood from a scenario mostly involving a relatively small movement scale, which may pose a challenge in regards to understanding the timing properties, movement dynamics and the associated underlying brain activity of sport performances.

Sensorimotor synchronisation – SMS

In the synchronised metronome training (SMT) paradigm utilised in the studies included in the present thesis, subjects are typically required to produce rhythmic movements (e.g. handclaps) in response to an external rhythmic auditory signal (a fixed metronome beat/pulse). Viewed from a dynamic systems perspective, sensorimotor synchronisation is a form of entrainment of one oscillatory process (motor) by another (perceptual), as a consequence of unilateral coupling between them (Pikovsky, Rosenblum & Kurths, 2001; Wimmers, Beek & van Wieringen, 1992). Phillips-Silver, Aktipis & Bryant (2010) define entrainment as spatio-temporal coordination resulting from rhythmic responsiveness, being dependent upon the abilities to integrate the detection and production of rhythmic information. More specifically, coordinated rhythmic movements require the ability to 1) identify the rhythmic patterns of the signal, 2) produce rhythmic output, and 3) integrate sensory information and motor production, which in turn enables adjustment of motor output based on rhythmic input.

Sensorimotor synchronisation and the entrainment that may arise spontaneously from the detection of rhythmical pacing signals was discussed earlier in this introduction with regard to RAS. From a sports perspective, theories of SMS may well apply to sports in which motor actions are performed in synchrony with rhythmical externally paced events (e.g. competitive dance, certain types of gymnastics and synchronised swimming, to mention a few). In these cases an entrainment process may enhance performance. However, for sports entailing high demands on accuracy in movement timing that is not guided by an external rhythmical event (such as the inter/intra-limb coordination involved in a golf swing, or the timing of interceptive actions in soccer), relevant motor timing theories are scarce. Thus, continuous investigations of the role of timing in sport-specific performance are needed to understand and provide the sporting community with relevant knowledge.

Although it is not my purpose to outline all relevant (or irrelevant) theories related to motor timing, the fact that few (if any) theories or models of motor timing are easily applied to sport performances may be problematic. For instance, as outlined by Rodger and Craig (2011), the majority of studies that examine sensorimotor synchronisation have focused on tapping a finger to an auditory beat (e.g. Aschersleben 2002; Doumas and Wing 2007; Repp 2005; Wing and Kristofferson 1973). This also means that the task of timing motor actions to sensory information (coupling action and perception) has been understood from a scenario involving a relatively small movement scale. It is presumably so that the temporal control of movements of such

small amplitudes is not equal with that of movements made over larger amplitudes (i.e. serial foot-tapping moving between different locations). In agreement with this notion, it has recently been found that sensorimotor tasks (posing higher demands on motor execution) prove a divergent underpinning brain activation in comparison to i.e. finger movements, that pose minimal demands on movement kinematics and dynamics (Hardwick, Rottschy, Miall & Eickhoff, 2013).

Still, not all motor timing theories emerge from SMS tasks, in which movements are performed in synchrony with an external pacing signal. Some finger-tapping tasks, as well as circle-drawing tasks, involve motor production in a self-paced rhythm. Here, the ultimate task of the subject is to produce a rhythmically consistent motor output. In other words; to keep a 'steady beat'. Such studies hint at the participants' rhythmical ability, and the ability for more general temporal processing, and are in line with the notion that timing is an ability that includes skills in observing, controlling and differentiating between the rhythm of a specific motor action (Martin, 1988). Although still concerned with relatively small amplitude movements, these studies are interesting to sport-specific motor actions such as the golf swing, because it is a hypothesis that self-paced tapping involves the timing of integrated sensory (including auditory) consequences of movements (Drewing, Hennings & Aschersleben, 2002). Accordingly, it has been proposed that the kinematic properties of the movement (i.e. during circle drawing) generate the timing structure of emergent timing (e.g. Torre & Balasubramian, 2009), which is also in line with the notion that motor/movement timing is based on a state-dependent control process, proposed by Diedrichsen et al. (2007).

Training motor timing and SMS abilities

A number of interventions that are based on rhythm perception and production (e.g. Rhythmic Auditory Stimulation - RAS, Musical Intonation Therapy - MIT, and Interactive Metronome - IM treatments) invoke SMS by means of auditory pacing (entrainment), in which subjects are trained to synchronise a targeted behaviour (e.g. motor coordination of upper and lower extremities) to an externally provided (auditory) target rhythm. Although these treatments all use similar forms of auditory pacing/entrainment, only the Interactive Metronome (IM) system incorporates real-time performance feedback entailing information about the size and direction of the asynchrony in its training paradigm (synchronised metronome training - SMT). This is suggested as an important property of the SMT, and will be discussed further on in the present thesis.

Several intervention studies have utilised SMT. Here, positive effects have been described by means of improved motor functions and academic skills in school children (Taube, McGrew & Keith, 2007), smoother and shorter movement trajectories in children diagnosed with spastic hemiplegic (Johansson et al., 2012), and increased aspects of motor control (Sharon et al., 2010; Bartscherer & Dole, 2005; Beckelheimer, Dalton, Richter, Hermann & Page, 2013) in different clinical populations. Moreover, the effects of SMT have also been found by means of improved attention and behaviour regulation in children with ADHD (Shaffer et al., 2001; Leisman & Melillo, 2010), for reading achievement and academic performance in school children (Taube, McGrew & Keith, 2007; Ritter, Colson & Park, 2012), and cognitive functioning after blast-related brain injury (Nelson, MacDonald, Stall & Pazdan, 2013). Taken into consideration that the effects of task-specific SMT is found in such a wide array of human performances, one may postulate that SMT impacts on some domain-general mechanism(s) of the brain, subsuming temporal processing, motor timing and time perception. This hypothesis is further enhanced by a number of case studies showing the effects of SMT on clinical disorders associated with poor temporal processing such as ADHD, dyslexia, Alzheimer's, cerebral palsy, Parkinson's disease, schizophrenia, autism, and speech and language disorders such as dysfluency, aphasia and apraxia (see McGrew, 2013 for an overview). Moreover, these findings corroborate data from perceptual learning studies showing that the neural mechanisms underlying mental timing may be fine-tuned or modified with training (Diamond, 2003; Rammsayer & Brandler, 2007), and that interval-specific learning may generalise across modalities, such as somatosensory to auditory (Nagarajan, Blake, Wright, Byl, & Merzenich, 1998), and auditory to motor (Karmarkar & Buonomano, 2003; Meegan, Aslin, & Jacobs, 2000).

In regard to RAS, it has been theorised that rhythmic cueing, and or rhythmic auditory stimulation, (such as SMT) '...appears to enhance motor control in rehabilitation by facilitating planning and execution through a strong entrainment and synchronisation effect of repetitive rhythmic sensory signals on the motor system' (Malcom, Massie & Thaut, 2009, p. 71). The authors argue that the auditory system during rhythmic/timing training builds time traces that serve as a temporal motor template onto which movement can later be mapped. RAS has been showed to entrain central motor processors to cope with the imposed rhythmic timekeeper of the auditory system and to stabilise motor control in a variety of clinical populations. It has been hypothesised that the effects of RAS on gait patterns in PD patients could be achieved by affecting striatal activation (Brown et al., 2006) or via an effect on the cerebellum (Eckert et al., 2005; Brown et al., 2006; Del Olmo et al., 2006).

Although the coordination and control of any motor action will most probably become more efficient as an effect of deliberate practice (Ericsson, Krampe & Tesch-Römer, 1993), less is known in regard to how non-sport specific timing training, as for instance SMT, might influence sport-specific performance. Until now, the effects of SMT in a sports context are limited to golf performance. Here, SMT has been found to improve golf shot accuracy and decrease golf shot variability (Libkuman et al., 2002), indicating that improvements in motor timing as an effect of SMT can seemingly be transferred to an unrelated motor task; in this case the intrinsic movement sequencing during the golf swing performance. This indicates that improved motor timing (SMS ability) as an effect of SMT is transferable to an unrelated motor task through the integration of and interaction between sensory information from multiple modalities, thus, reflecting a means for strengthening the perception-action coupling.

The role of feedback in timing training

Our ability to adjust motor output to the rhythm of the external signal implies that some sort of feedback-based error correction processes compensating for timing errors, in a reactive fashion, are present (van der Steen & Keller, 2013). However, and in line with Zatorre, Chen and Penhune (2007), the accurate timing of movements to an external beat logically seems to include a feedforward prediction of the timing of a forthcoming movement. Because the ultimate task in SMS is to perform a motor response in exact conjunction with a pacing signal, the agent needs to initiate the motor output well before the occurrence of the signal, based on an accurate prediction of the sensory consequence of our motor commands. Such motor actions (e.g. clapping hands in a circular fashion) are thus subjected to a number of online corrections (for instance speeding up/slowing down velocity). Without such error correction processes, variability would accumulate from movement cycle to movement cycle, and result in increasingly large asynchronies, phase drifts, and eventually synchronisation errors (Vorberg and Wing, 1996; Repp, 2005). Accordingly, Repp (2005; 2010) has suggested two distinct error correction processes being present in SMS tasks: period correction and phase correction. Phase corrections are largely unconscious (dorsal) processes that control action (adjustment of the timing of each tap on the basis of previous temporal information), whereas period corrections seem to involve conscious (ventral) processes related to perception and motor planning. In line with this, Bispham (2006) argues that the use of period correction is especially suitable when synchronising movement to a fixed pulse, whereas phase correction may be applied across domains when a deliberate prediction of future events is needed for behavioural synchronisation (e.g. kicking a ball). This is in keeping with the notion that the task of timing movements to a pacing signal with an inter-stimuli interval of > 1 s (such as in the SMT paradigm) favours the work of a conscious timing system (Lewis & Miall, 2003; Repp, 2012), and thus relies on a deliberate prediction of the next metronome beat.

In regard to error correction during SMS, it has been found that tapping with instantaneous information about the size and the direction of the asynchrony of each response (knowledge of results) facilitates the ability to synchronise motor output with rhythmic input, whereas tapping without performance feedback does not reduce asynchrony (Aschersleben, 2000; Mates, Radil & Pöppel, 1992; Aschersleben & Prinz, 1995; 1997; Mates & Aschersleben, 2000). The instantaneous feedback of performance provided by the IM system thus seems paramount for any performance improvement to occur, because instead of participants relying on their own mental estimations of their temporal accuracy, the IM system provides accurate (to 0.5 ms), realtime guide sounds to indicate the temporal accuracy of the rhythmic output (an auditory signal is presented over the headphones each time the subject touches the response key). Thus, sensory feedback from the visual, auditory, tactile, proprioceptive and kinaesthetic modalities, originating from the actual motor production (e.g. a toe-tap or rhythmic, circular handclaps) may not be sufficient to increase performance in SMS tasks (decrease asynchrony). Rather, it seems that the ability to coordinate rhythmic movement with an external rhythm, solely with the aid of our sensory modalities, is only possible to a certain extent. Reducing asynchronies below these 'scores' only appears possible if an external source of feedback, hinting at the direction and magnitude of the asynchrony as they occur, is present. This notion fits well with the concept of knowledge of results, which postulate that information provided over and above those sources of feedback that are naturally received when a response is made is crucial for performance improvement (e.g. Adams, 1968; Ford, Hodges, Huvs & Williams, 2006).

Sport-specific timing/rhythm interventions

In regard to interventions that are sport/task-specific, some studies have, in one way or the other, introduced aspects of rhythm and timing to motor coordination and motor control. For instance Sörgut, Kirazci and Korkusuz (2012) examined the effects of tennis-specific and non-tennis specific rhythmical training on forehand stroke performance consistency, and found that both types of rhythmical training brought about positive tennis-specific effects. Similarly, rhythmical whole-body movement training (running, jumping, hopping, skipping, sliding and leaping in pace with a rhythmical auditory cue) has been found to increase consistency in tennis strokes (Zachopoulou & Mantis, 2001), and effects of ball-control training in synchrony with organic music have been found to increase performance in a soccer dribbling test (Keramidas et al., 2004). Although some of these studies suffer from poor design or lack conceptualisation of the training paradigm (e.g. bouncing a tennis ball at a self-paced tempo), and do not entail any form of feedback in regard to the motor timing performance during training, they are at least attempts at incorporating some aspect of timing and rhythmical training into sports performances. Moreover, the results of these studies support the notion that timing and rhythmicity skills are important for motor coordination and control, and thus for optimal performance. In line with this, Karageorghis & Terry (2001) have stated that one of the main benefits athletes might derive from listening to music during a performance would be an enhanced acquisition of motor skills (that is when the perceived rhythm is matched with required movement patterns).

In more general terms, the influence of music pertaining to its psychophysical effects on sport and exercise domains has been investigated repeatedly. However, these are often more anecdotal in character, entailing case studies (see Terry & Karageorghis, 2006 for a narrative review). Some research has investigated the tendency for humans to respond to the rhythmical qualities of music by synchronising movement patterns to tempo. However, focus has mainly been on the ergogenic and aerobic/anaerobic effects of such entrainment. Therefore, if athletes or exercisers work in time to music, they are likely to work harder for longer periods of time.

Underlying neural mechanisms of motor timing

Although there is still no consensus with regard to whether timing relies on the work of a specialised or a general ability of networks of neurons (Buonomano & Laje, 2010), a neuroanatomical overlap between areas recruited during temporal processing (time perception and estimation) and during motor timing tasks such as sensorimotor synchronisation has been frequently reported (e.g. Schubotz, Friederich & von Cramon, 2000; Chen, Zatorre & Penhune, 2009; Macar, Coull & Vidal, 2006; Rubia & Smith, 2004; Coull, Cheng & Meck, 2011). For instance, in a meta-analysis including studies of timing that report whole-brain analyses, Wiener, Turkeltaubb & Coslett (2010) found an overlap between areas recruited during millisecond-level motor timing and perceptual tasks in, among other areas, the bilateral SMA, bilateral middle frontal gyrus, bilateral IPL, bilateral IFG, basal ganglia and bilateral posterior cerebellum – some of which overlap with those areas also typically activated during action observation paradigms (IPL, SMA and middle frontal gyrus – Casper, Zilles, Laird & Eickhoff, 2011). In their review, Rubia & Smith (2004) suggest that motor timing and time perception are inseparable, because they rely on each other. Thus, functional motor coordination and control is not possible without good temporal perception functions, and vice versa.

Cerebellum

This neuron-dense structure in the bottom of the brain is suggested to contribute to motor coordination and planning, precise motor timing and temporal precision, but does not initiate movement. The cerebellar timing hypothesis is based on the assumption that the cerebellum has a unique representational capability, and is accessed whenever a particular task requires precise timing (Ivry & Schlerf, 2008). Several neuroimaging studies provide evidence for the cerebellum being a part of the core neuronal network supporting motor timing in SMS tasks (Timmann, Watts & Hore, 1999; Ivry, & Keele, 1989; Spencer, Zelaznik, Diedrichsen & Ivry, 2003; Harrington, Lee, Boyd, Rapsack & Knight, 2004; Perrett, Ruiz & Mauk, 1993). In line with this, it is suggested that the timing capabilities of the cerebellum extend beyond motor control into tasks focusing on perceptual processing that require the precise representation of temporal information and sensorimotor learning (for reviews see Salman, 2002; Rubia & Smith, 2004; Repp & Su, 2013). In essence, the cerebellum is known to be critical to producing complex and coordinated movements (Thach 1998; Imfeld et al. 2009), is thought to contribute significantly to the generation of forward models (e.g. Thach 1998; Kawato et al. 2003) that are crucial for motor planning and correction, and finally is believed to have a key role in time perception and time estimation (Medina & Mauk, 2002).

Cerebellum is particularly interesting in the context of timing training and its' effects on motor learning (the soccer cross-pass task), investigated in an action observation paradigm. This because cells/neurons in premotor cortex with mirror properties may code a motoric representation of visuo-motor actions, both during action execution and during observation, suggested to be driven by the cerebellar inverse model (Miall, 2003). Here, neurons within the action observation network (AON) are suggested to send a command to the cerebellum, which then sends its prediction back to the premotor cortex for subsequent motor planning. This is in line with findings from O'Reilly, Mesulam & Nobre (2008), suggesting that the cerebellum works with sensorimotor cortices to aid in efficient prediction by supplying these regions with temporal information about dynamic events.

Neural underpinnings of motor coordination assessed by means of an action observation paradigm

There are several reasons why an action observation paradigm is appropriate for examining the effects of SMT on SMS abilities and soccer-kick performance on a neural level. First, a range of current findings from action observation studies – entailing fMRI investigations – related to the activation of mirror neurons during both the execution and visual perception of an action (e.g. Calvo-Merino, Grezes, Glaser, Passingham & Haggard, 2005; Pilgramm, Lorey, Stark, Munzert, Vaitl & Zentgraf, 2010; Umilta et al., 2010, Abreu et al., 2012), along with their presence in both premotor and inferior parietal cortices, is strong support for the existence of action-specific links that integrate motor and sensory information about specific actions (Kohler et al., 2002; Rizzolatti & Sinigaglia, 2010). It is suggested that the role of the mirror neurons is to establish a functional link between specific sets of sensory and motor information. As such they provide a mechanism for what is considered to be the primary function of the neocortex; the joining together of specific information across modalities (Braitenberg and Schüz, 1998). Second, much of the work in regard to the action-perception coupling has been guided by the 'common-coding' principle, which holds that perception and action are represented in a common format and thus share resources in functional brain architecture (Hommel, Müsseler, Aschersleben, & Prinz, 2001; Prinz, 1990), which is also consistent with the overlapping neural correlates found for perceiving an action - via visual, auditory, or multiple channels - as when executing the same action (Rizzolatti, Fadiga, Fogassi & Gallese, 1996; Rizzolatti & Craighero, 2004). Third, sensorimotor synchronisation tasks entail a temporal integration of action and perception (Krause, Pollok & Schnitzler, 2010; Hove, Fairhurst, Kotz & Keller, 2013), in which movements are timed through a perceptionaction coupling, and thus support a close link between action execution and action observation (Sevdalis & Keller, 2011). Fourth, it is still not possible to record real-time brain activation patterns with high spatial resolution during the performance of large scale movements (such as handclaps or the soccer-kick). Thus, and in summary, an action observation paradigm entailing fMRI analysis is a relevant approach.

Moreover, the potential plasticity of the mirror neuron system, and thus whether the patterns of activation within this system may be susceptible to training-induced changes, is of great importance. Here, findings related to activation patterns being mediated by task-specific experience (Cross, Hamilton & Grafton, 2006:, Calvo-Merino et al., 2005; Wright, Bishop, Jackson, Abernethy, 2010; Urgesi et al., 2010) and studies assessing training-induced changes in hMNS/AON patterns during action observation

(e.g. Hamilton & Grafton, 2006; Catmur, Walsh & Heyes, 2007; Reithler, van Mier, Peters & Goebel, 2007; Engel, Burke, Fiehler, Bien & Rösler, 2008a, 2008b) indicate that the mirror properties of the AON are neither wholly innate nor fixed once acquired; instead they develop through sensorimotor learning (Cross, et al., 2013), and thus could at least hypothetically be susceptible to training-induced changes.

Suffice to say that we do not claim to investigate mirror neuron activity specifically, but rather neural activity of motor or sensory neurons whose discharge is associated with either action execution or action observation, but not both, as is the case for mirror neurons (Kilner & Lemon, 2013). Accordingly, the initial fMRI analysis of Study III in this thesis is of an exploratory character and thus aimed at whole-brain investigations.

Perception in action

Sensory systems provide information about the state of the body as well as features within the environment (perception) that are critical to the regulation of movement (action). This information is clearly integral to the ability to act effectively within an environment (Rosenbaum, 1991). However, scientists have not reached consensus on whether perception aids action or vice versa, and are in even lesser agreement in regards to how the athlete utilises all of this information to act upon it in the most optimal and efficient way. The input of information from multiple sensory modalities (perception) and its relation to motor output (action) is quite intriguing, and it has been claimed that these entities should not be looked at in isolation, and that there is no linear sequence leading from perception to action (Pfeifer & Scheier, 1994). Rather, the relationship between perception and action should be viewed as a continuous coordination.

As all actions are geared towards the future, the athlete needs to correctly predict future events to control them (von Hofsten, 1995). However, a flawless prediction of the future is not possible as the unfolding of the events around us, our own actions, and the interaction between these involve a large number of degrees of freedom. Thus, the athlete is in need of a dynamic and flexible movement plan that is constantly adapting to the changing environment, and evolving with the action at hand (von Hofsten, 1995). Such an adaptation is based on the continuous picking up of task-relevant information (perception), and functions as a guide to steer the action. In this view, the tasks of perception are prospective, and its' main purpose is to provide input to the athlete about upcoming events so the athletes' actions can proceed with smoothness and continuity. An opposing view to this was

presented by John Dewey over 100 years ago. He proposes that the stimulus is not at the beginning, but that there is always an ongoing coordination:

'We begin not with a sensory stimulus, but with a sensorimotor coordination. In a certain sense it is the movement which is primary, and the sensation which is secondary, the movement of the body, head, and eye muscles determining the quality of what is experienced. In other words, the real beginning is with the act of seeing; it is looking, and not a sensation of light.' (Dewey, 1896, pp. 137-138).

In a sport setting, many exploratory actions are generated in order to obtain more information about action values and the environment. Thus, action facilitates perception. However, this is not only true for the traditional action (moving) and perception (mainly visual perception) coupling. The fact that we move and perform limb movements in time and space will also provide other types of sensory information facilitating future actions. Either way, optimal motor performances seem to be dependent on the integration and interaction between timing, coordination, motor control, sensory processing and, thus, a functional perception-action system. Prospective planning involves the dynamic and flexible planning of future actions, being dependent on the perceptual information available. In turn, prospective control involves both planning and perceiving what is going to happen next, and "…is based on knowledge about rules and regularities that govern events in the world and abilities to extract future-oriented information from the senses" (Von Hofsten, 2004, p. 266).

Processing sensory information from multiple modalities

It seems clear that visual perception and action in sports are related to the athlete's need to perceive the spatio-temporal layout of the surrounding environment in order to act upon it successfully. However, there are other forms of sensory information that are equally important. Sensory/perceptual systems provide information about the state of the body (e.g. in space) as well as features within the environment critical to the regulation of movement. This information is clearly integral to the ability to act effectively within an environment (Rosenbaum, 1991). For instance, a successful soccer player is not only required to time and coordinate her movements on the soccer field in relation to the ball and her teammates, as well as her opponents; she must also handle the spatio-temporal coordination of her own body during such soccer-specific tasks as passing, trapping, shooting and heading. These are actions that would require the player to gather, interpret and act upon internal proprioceptive information as well.

The term proprioception is subjected to many definitions. However, it seems clear that it somehow involves the body's own sense of position and motion, which might include body segment static position, displacement, velocity, acceleration, and a muscular sense of force or effort (e.g. Gandevia, McCloskey and Burke, 1992; Reiman and Lephart, 2002). Such sensory information is, as opposed to external stimuli (exteroception), derived from changes to internal structures, and is relayed as electrical impulses from nerve endings (proprioceptors) to the CNS. Ogard (2011) states that ...proprioception is the CNS process of determining the relative position and movement of the limbs and the body...' (p.113), and further explains that accurate information from the somatosensory, vestibular and visual systems is paramount for this process. Accordingly, internal proprioceptive information, in conjunction with vestibular and visual information, facilitates efficient, effective and accurate body-segment movements required to accomplish a given task in a given environment. In keeping with this, it has been shown repeatedly that removing sensory information is detrimental to synchronisation performance (e.g. Aschersleben, 2000; 2001). Thus, sensory information seems to be important for withholding/containing the present SMS ability, but it does not facilitate performance (more than to a certain extent). Similar effects of 'knowledge of results' on performance have been reported in soccer (e.g. Adams, 1968; Ford, Hodges, Huvs & Williams, 2006).

It is a well-recognised view within the timing research domain that motor timing is dependent on a functional ability of temporal processing. Accordingly, the tendency of music and rhythm to elicit movement has been investigated thoroughly (e.g. Luck et al., 2010). A recent study by Manning & Schutz (2013) neatly exemplifies how body movement facilitates timekeeping (see also Krause, Pollok, & Schnitzler, 2010; Repp, 2002; Repp & Knoblich, 2007, 2009). More specifically, they showed that moving to the beat of a metronome also increases the perception of timing, by means of improved time-interval estimation. This fits well with the behaviour of musicians bobbing and twitching to the beat of the music, and is also in keeping with ideas proposed by Cassenti (2011), arguing that the timing of the motor behaviours themselves provides a mechanism for measuring time intervals; i.e. the motor-temporal link theory. Both these aspects speak for SMT as an effective intervention that not only improves SMS ability through training, but also improves time perception through motor training. Also, within the same line of thought, this motor-temporal link may, through sensorimotor integration, explain why the effects of SMT have also been seen on diverse cognitive abilities such as reading fluency and attentional control (e.g. Taube, McGrew & Keith, 2007; Shaffer et al., 2001).

Multimodal training

Multisensory integration was defined by Meredith and Stein (1983) as an increase in neuronal response to a stimulus consisting of a combination of modalities compared with the sum of neuronal responses to each stimulus modality separately. For perceptual experience and behaviour to benefit from the simultaneous stimulation of multiple sensory modalities, integration of the information from these modalities is essential. The interaction, as well as the integration among, different sensory modalities is especially important in a sport context. Sensory modalities interact, functionally reorganise and contribute to new qualities of perception that carry information not inherent in each single modality, which may be pivotal for successful performance.

In line with this, several studies have shown performance enhancement as an effect of multimodal cueing. For instance, Ngo, Pierce & Spence (2012) found that auditory or audio-tactile warning signals enhanced performance in a realistic air-traffic control training scenario. In a sport perspective, Gray (2009) present evidence of improved skill acquisition in baseball batting as an effect of multimodal feedback of performance (tactile, auditory and visual). Similarly, it has been shown by Wing, Doumas, and Welchman (2010) that variability (inter-response intervals) in rhythmically paced finger-tapping was lower with bimodal feedback (auditory and haptic) than when feedback was unimodal (auditory or haptic), which exhibited similar variability. This is also in line with the previously discussed effects of feedback on timing training showed by Aschersleben and colleagues. Overall, these results suggest training with multimodal sensory information feedback may direct an athlete's attention to the relevant cues for successful performance (see also Van Erp, Saturday & Jensen, 2006).

SMT may be defined as a form of multimodal training as it entails the coordinated and timed integration and interaction of several sensory modalities. More specifically, feedback from audio, visual, kinaesthetic and proprioceptive modalities guides the subject in its task to synchronise movements (e.g. circular handclaps) to an externally paced auditory signal.

Action observation as a paradigm for assessing training effects

Recording brain activation patterns in an fMRI action observation paradigm is the closest we can get to assess the underlying brain activation patterns of actual movement (unless small scale movements as i.e. finger-tapping is in focus of investigation), and is thus a proper method of investigation. Given that the participants have physical experience, and thus a motor representation of, the observed action, a more or less similar activation pattern within areas known to be a part of the AON can be expected. This is in line with Keysers & Gazzola (2010) who theorise as follows;

'Whenever we perform an action, all the neurons involved in executing this action will fire at approximately the same time as those involved in seeing, hearing and feeling ourselves perform the action. After repeatedly performing and perceiving ourselves perform the action, Hebbian learning would make many neurons, not only in the vPMC and IPL, but also in the SMA and medial temporal lobe, have the property of being excitable both when we perform the action and when we see or hear someone else perform a similar action. The only prerequisite for such learning would be for a neuron to have connections with both sensory and motor systems—a frequent property in a brain that has evolved to connect perception and action' (pp. 1-2).

Thus, it is reasonable that neurons in other areas (e.g. cerebellum) than the classic AON may be activated during action observation.

Mirror neurons was originally discovered in area F5 of macaque monkevs' premotor cortex, showing to fire both when the monkey performed a specific action (e.g. reaching) as well as when it observed the same action being performed by another monkey or person (Rizzolatti et al., 1996; Rizzolatti & Craighero, 2004). Several research groups have since shown that a similar system appears to exist in humans. Neuroimaging studies have typically demonstrated the existence of a network with mirror properties in the supplementary motor area (SMA), the inferior parietal lobule (IPL), the ventral premotor cortex (vPMC) as well as the inferior frontal gyrus (IFG), proposed to be involved in recognition of voluntary behaviour. This network of mirror neurons is frequently referred to as the action observation network (AON; Cross, Hamilton, Kraemer, Kelley & Grafton, 2009), and is suggested to play a major role in action recognition and understanding (Rizzolatti & Craighero, 2004), action imitation (Iacaboni, 2005), as well as in action prediction (e.g. Urgesi et al., 2010; Wright et al., 2011). Thus, the AON may be essentially viewed as a system or network that translates perception to action through action recognition and understanding, for

consequent preparation of motor responses and movement imitation (Umilta et al., 2001), as well as the decoding of upcoming movements, which in a sport context allows anticipating rather than reacting to an opponent's actions (Abreu et al., 2012).

Learning by doing and observing

Evidence exists to suggest that only actions corresponding to stored motor representations of our own motor commands and their consequences, meaning motor actions that are represented in long-term memory and primary motor cortex (e.g. Jeannerod and Decety, 1995; Jeannerod, 2001) as well as the cerebellum (Wolpert, Miall & Kawato 1998; Pillgram et al., 2010), are effective in activating the AON. It is theorised that the AON is not merely dependent on a direct kinematic copy of an observed action (e.g. Rizzolatti & Sinigaglia, 2010), but rather encode and respond to the end-goal of motor action (e.g. Stevens, Fonlupt, Shiffrar & Decety, 2000; Newman-Norlund et al., 2010; Buccino et al., 2004; Gazzola, Rizzolatti, Wicker & Keysers, 2007; Urgesi et al., 2010; Enticott, Hayley, Bradshaw, Rinehart and Fitzgerald, 2010).

When an individual learns a new skill, he or she acquires new perceptual and motor representations of these skills (Toni, et al., 2002). Thus, hMNS differences in experts and novices basically compare mirror neuron activity between individuals who have acquired such representations, and those who have not or have to a lesser degree. The expertise effect has repeatedly been demonstrated in studies assessing brain regions that are active during action observation related to dance (e.g. Calvo-Merino et al., 2005; Pilgramm et al., 2010), dance vs. capoeira (Calvo-Merino et al., 2006), archery (Kim et al., 2008) and piano playing (Haslinger et al., 2005), as well as studies in which agents are required to anticipate end-point goal and/or action outcomes (e.g. Agliotti et al, 2008; Wu et al., 2012 – basketball; Wright et al., 2010; Wright et al., 2011; Jin et al., 2011 – badminton strokes; Diersch et al, 2013 – figure skating). More than further establishing that the hMNS is activated to process actions that conform to the motor representations of the observer, these studies suggest that motor representations are shaped by specific physical experience (see Olsson & Nyberg, 2010), and that the amount of experience mediates the activity patterns of the AON during action observation and anticipation, which in turn may have a direct impact on performance in diverse sport settings.

Changes in AON activation induced by task-specific training interventions

Studies investigating the effects of task-specific training or interventions on AON activation during action observation either relate to the effects of motor training on AON activity – comprising the action – perception transfer (Prinz, 2001), or to the effects of observational learning on AON activation patterns. Observational learning (repeated visual exposure to the same motor act) has been found to increase AON activation and positively impact rehabilitation of motor deficits after stroke (Ertlet et al., 2007), as well as improving gait speed in multiple sclerosis patients (Brichetto, Pedulla, Fida, Alberta & Tacchino, 2013), and influencing AON activation during observation and prediction of actions we cannot readily reproduce (e.g. gymnastic moves - Cross et al., 2013).

In regard to the effects of task-specific training, increased activation within the AON has for instance been found as an effect of task-specific dance training (Hamilton & Graton, 2006), mirror-movement training (Catmur et al., 2007), and hand trajectory training (Reithler et al., 2007; Engel et al., 2008a, 2008b). The results from these studies fits well into the perceptionaction paradigm 'that assume that the perception of an action activates internal cognitive mechanisms that can also be used in the generation of action' (Hecht, Vogt & Prinz, 2000, pp 3), as they display a transfer of skills from action (motor training) to perception (AON activity) by means of increased AON activation within vPMC, IFG, IPL, STS and SMA/preSMA. Taking into account the common coding theory (Prinz, 1997) and the theory of event coding (Hommel, Müsseler, Aschersleben, & Prinz, 2001) which posit that the final stages of perception and the initial stages of motor control share common representations, in which planned actions are represented in the same format as perceived events, effects of non-task specific training interventions on AON activity during task-specific action observation should be plausible.

The missing link: changes in AON activation induced by non-task specific training

Several studies assess the transfer of skills from action to perception. However, these studies are concerned with training that is task-specific; training that is similar or strongly related to the action consequently being observed. To our knowledge, no studies devoted to investigating transfer effects from a non-task specific training intervention on AON activation during task-specific AO exist. Thus, the current fMRI study is novel in two

important ways: 1) it tests whether the learning of action sequences transfers from X to Y, and 2) it explores whether AON activation should be altered as an effect of non-task specific training. Studies showing the transfer effects from action to perception within the same domain (e.g. Cross et al., 2006 dance training and dance observation; Reithler et al., 2007; Engel et al., 2008) provide some evidence that we should, as they at least confirm that the AON is influenced by motor training. Another indication of transferability is reported by Wiggett et al (2012) considering the transfer effects of firstperson training to third-person observation on AON activity. Here, brain activity within the IFG and IPS during action observation of hand gestures from a third-person perspective was altered as an effect of 80 min firstperson perspective observation (or action) of hand gestures. Also, the fact that the AON display similar activation patterns (e.g. within the IPL, vPMC, STS and IFG) during action observation across many different domains (archery, dance, piano, basketball, etc.), within similar levels of skill, expertise and experience (experts vs novices) point towards the AON having some general traits that are common for a number of actions. Thus, taskspecific AON activation (e.g. observing soccer actions) might be influenced by non-task specific training (e.g. timing training).

Objectives

The main objective of the present thesis was to examine the effects of timing training (SMT) on sport-specific skills in a sample of experienced male golfers and elite- and sub-elite female soccer players.

Timing is a concept that is believed to be paramount for optimal sport performance. However, within the domains of sports, timing is at best a vague concept, and little is known in regard to how performance may be influenced by specific timing training. Studies I and II thus focus on the investigation of these aspects in a sample of experienced male golfers, by employing both golf shot performance assessments and kinematic movement analyses. To further study the capacity of the SMT intervention, the focus was then shifted from a close skill to an open skills sport, and from male athletes to female athletes. Thus, soccer skill performance in elite-/sub-elite female players was incorporated as a measure of examination (Study III). Moreover, as no knowledge exists in regard to how effects of SMT may influence brain plasticity, fMRI investigations of these players' brain activation patterns, comprising an action observation paradigm, were employed to add a third and highly important dimension to the understanding of the effects of SMT on human movement performance.

The following specific research questions were posed:

I) May recent findings in regard to effects of SMT on SMS abilities in nonathletes and recreational golfers also apply to experienced male golf players and elite-/sub-elite female soccer players? (Study I and III)

II) Can SMT positively influence golf shot precision and accompanying variability in a sample of experienced golfers, as previously seen in recreational golfers? (Study I)

III) How are potential effects of SMT manifested in the underlying kinematic properties of golf swing performance? (Study II)

IV) May SMT also positively influence the accuracy and variability of soccer cross-pass outcomes? (Study III)

IV) How are effects of SMT manifested in brain activation underpinning observation of a soccer-specific action? (Study III)

Materials and methods

Methodology-wise, the present thesis is complex as a number of different study designs, statistical methods, and assessment methods are utilised. Therefore, the following sections provide an extensive outline of the studies from a methodological perspective, starting with study designs followed by descriptions of the participants, a detailed description of the assessment methods, the statistical methods applied, and ethical considerations.

Designs

In Study I, the effects of the SMT on golf shot accuracy and variability were explored by means of a randomised pre- and post-test control group design. Before the SMT commenced, the participants' golf shot accuracy, precision and variability, timing and rhythmic ability, and relevant background variables were assessed. Immediately after training completion, a similar post-test battery was applied. For the pre- and post-test shots, kinematic properties of the golf swing execution were also assessed, by means of a movement registration system. This data constitutes Study II.

In Study II, the kinematic pre- and post-test golf swing data analysed was extracted from golf performance by golfers included in the experimental group from Study I. Thus, a one-group, pre- to post-test design was applied. The study design is summarised in Figure 1.

In Study III, the effects of SMT on soccer skill performance was analysed using a randomised pre- and post-test control group design. Here, the initiation of the SMT was preceded by assessments of the participant's cross-pass performance (precision and variability), timing and rhythmic skills, and relevant background variables. Additionally, the participant's brain activation pattern during action observation was assessed by means of fMRI investigations. The same procedure was applied after the SMT period (Figure 2).

All studies were carried out in controlled experimental laboratory settings, with ecological validity in mind (see each respective study for a more thorough summary).

Participants

Study I

A total of twenty-six right-handed, experienced male golfers from the Umeå area (Sweden) were recruited. Their age and golf handicap (hcp) ranged from 20 to 37.1 years and 4.4 to 19.8 hcp, respectively, with golf-playing experience ranging from one to twenty years (Table I).

Study II

The kinematic properties of golf swing performance from the 13 golfers constituting the experimental group from Study I was analysed in the present study. The players had between 4 and 20 years of golf-playing experience and their age and golf handicap ranged between 20.0 and 33.7 years and 5.0 to 19.5 hcp, respectively.

Table 1: participant information with regard to Study I and/or II, age, experience, golf handicap, and relevant physiological measures (e.g. height, weight) is presented. All players had normal or corrected to normal vision. All recruited players completed the experiment. Thus, no drop-outs were registered.

Group	n	Age	Height (cm)	Mass (kg)	Handicap	Experience	Study
SMT	13	27.5 ± 4.6	180.2 ± 3.6	77.0 ± 11.2	12.7 ± 4.9	10.9 ± 4.8	I and II
Control	13	27.7 ± 5.3	183.5 ± 5.9	82.8 ± 12.2	12.3 ± 4.8	7.3 ± 4.1	Ι

Study III

Twenty-five local elite (Swedish Women's Premier League; Damallsvenskan) and sub-elite (Division 1) female soccer players volunteered for this study. Their age and experience ranged between 16.2 and 25.8 years (mean 19.5), and 5.5 to 19.0 (mean 12.4), respectively. All players, except one experimental group participant, reported right-foot preference for soccer skill performance. The participants were from a range of outfield playing positions, and were all involved in regular training and matches. During the period of the study, both the SMT- and the control-group carried on with their regularly scheduled team soccer practice. The elite players had six hours of scheduled soccer practice a week, and the control group 5.5 hours a week, during the four-week intervention period.

Apparatus and measurements

Data associated with motor performances (motor timing abilities, and golf swing and soccer skill execution), movement kinematics and brain imaging was assessed in the present thesis. Because of the respective assessment method's complexity, a clear overview of the methods utilised in the different studies is provided below.

Table 2: Overview of the assessment methods and materials used in the empirical studies.

Materials/Methods	Study I	Study II	Study III	
Hand and footedness assessment	x		x	
Performance measures	Х	Х	х	
Kinematic movement analysis		х		
Synchronised metronome training	Х	х	х	
fMRI investigations			х	

Assessment of golf shot precision and variability (Study I)

Pre- and post-test golf shot performance was established in a golf simulator (P3ProSwing, Bethel, USA) located in a 5 m \times 5 m \times 3.5 m indoor golf lab facilitated by Umeå University. All trials were performed with the participants' own clubs, and the ball was shot from a 22.9 cm x 35.6 cm sensing platform covered with 1.5 cm-high artificial grass. The participants typically executed a full swing and hit a real golf ball that would travel approximately 3 m before hitting a screen. The screen displayed the fairway on which the ball was positioned, as well as the green and the hole with a pin and a flag. The golfers were instructed to aim for the pin, and as they hit their shot an animated trajectory of the golf ball's flight towards the pin was projected on the screen in front of them.

During pilot testing, a number of golf shots performed in the P3ProSwing golf simulator were simultaneously measured by an optoelectronic registration system (ProReflex, Qualisys Inc., Gothenburg, Sweden) by means of the club head velocity and angle at ball impact and compared with the P3ProSwing data. Outcomes from five different clubs (9 iron, 4 iron, pitching wedge, driver and putter) and in total 30 golf shots were analysed

and compared. There was a high significant correlation between the two outcomes measures (overall r = 0.97). The mean velocity differences (km/h) between the two measurements were small, although consistently somewhat slower (both over repeated trials and clubs) for P3ProSwing (mean vel diff = -4.4, -4.2, -3.9, -7.4 and -0.4 km/h, respectively) in comparison to ProReflex outcomes. Similar correlations (overall r = 0.82) and differences were found for the club angle at ball impact (mean diff = 0.3, 0.23, 1.39, 0.89, 1.45 degree) for respective clubs between the two systems. Thus, we considered the outcome measures from the P3Pro simulator to be both valid and consistent.

Assessment of kinematic properties of golf swing performance (Study II)

Eadweard Muybridge (1887) conducted what is thought to be the first photographic analysis of human locomotion over a century ago. Muybridge' sequence of still photographs produced simulated motion, which could be studied further by examining changes in action as it evolved over time (Schmidt & Lee, 2005). Contemporary motion capturing techniques are of course extensively refined and typically involve either optoelectronic or magnetic-based systems. Independent of the system used, the main aim of kinematic analysis of human movement performance is to reveal the underlying properties of the motions or motor actions in focus, and not otherwise visible/detectable to the naked eye (e.g. velocity, acceleration, etc.). As motion capture systems have become commercially available, the number of studies devoted to kinematic analysis of performance within the domain of sports (e.g. cricket, baseball, tennis, skiing, dance, soccer, martial arts, fencing, rowing and gymnastics) has increased dramatically. Here, optoelectronic systems are often preferred over magnetic systems, due to the minimal constraints the wireless reflecting markers pose on the performer and the performance.

Due to optoelectronic recording methods providing a highly detailed picture of both the spatial and temporal profile of movements, kinematic movement registration of this type is a method that has also been widely applied to gaining an insight into the underlying variables that characterise a successful golf swing. Typically, the focus of investigations has been related to temporal (e.g. Egret, et al., 2003; Neal et al., 2008; Nesbit & McGinnis, 2009) and planar (e.g. Nesbit, 2005; Coleman & Anderson, 2007) characteristics of swing performance, movement variability (Horan, Evans & Kavanagh, 2011; Tucker, Andersson & Kenny, 2013), the nature of the coordination between the pelvis, upper torso and upper limb during the golf

swing (e.g. Myers et al., 2008; Horan et al., 2010; Tinmark et al., 2010; Kwon, Han, Como, Lee & Singhal, 2013) and properties related to the sequencing/segmental timing of the different swing phases constituting the full swing (e.g. Neal, et al., 2007; Cheetham et al., 2008).

In general, the optoelectronic systems provide objective and reliable data if measurements are recorded in a well calibrated space and appropriate filters and smoothing techniques are applied to the data to eliminate random errors. Moreover, it is of importance that at least two cameras are monitoring each marker at any given time (Della Croece, Leardini, Chiari & Cappozzo, 2005) to obtain 3D data. Also, the recording frame-rate of the motion capture system must be well-suited for the typical velocity of the segments to be analysed (club head often reaching velocities of 45m/sec). One major limitation of this system is related to soft tissue artefacts where the skin slides on top of the underlying bone as an effect of the high velocity movement of the arms during the swing (and particularly at ball impact), thus creating noise in the 3D data (Kenny, McCloy, Wallace & Otto, 2008). Further, occlusion is an issue, as occluded markers make consequent identifying and tracking of the XYZ positions of these markers difficult (this is mainly a challenge for studies applying a large number of markers within a relatively small measurement volume).

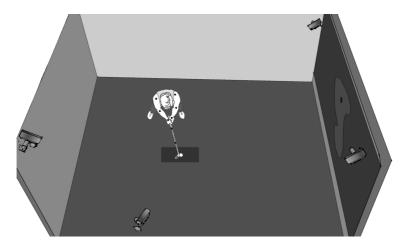


Figure 1: Experimental set up for Study I/II, displaying the four camera motion capture system and the golf simulator set-up.

The above-mentioned issues and concerns were regarded when conducting this study, and thus objective and reliable assessment of data was facilitated. For each golf shot, the swing performance in terms of three dimensional (3D) kinematic data was measured by four cameras (240 Hz) placed around the subject who performed the golf shots (Figure 1).

The motion capture system provided real-time position (XYZ coordinates) and orientation data of six spherical reflective markers attached on anatomical landmarks on the body of the participants (shoulders, elbows, wrists, club shaft and club head). Here, tangential (3D) velocities of the markers attached to the golf club and different arm joints were generated by use of custom written software in MATLAB (Mathworks Inc., Boston, MA). Then, for the purpose of the study, intra-joint coordination in terms of cross-correlations and corresponding phase shifts deliberated from the tangential velocity profiles was calculated.

Assessment of soccer skill performance (Study III)

The participants were required to make a 25-metre cross-pass, aiming for the centre of a dartboard 5 m in diameter, printed on 5 m x 5 m tarpaulin sheet (Figure 2). Balls were, with prior notice, randomly released from one of two ramps at a speed of 3.8 m/s towards a $2.0 \times 2.0 \times 2.3$ metre action zone that the player was required to take her shot within.



Figure 2: Experimental set up Study III

Participants started the tests from a standing position, 2.5 m from the action zone, before jogging or running into the action zone when the ball was released. The players were required to time the approach of the ball, so that the shot was performed within the zone. The participants were instructed to aim the cross-passes at the centre of the floor-mounted target. To enhance ecological validity, no prior touches were allowed to control the ball (Dooan

et al., 2001) before performing the cross-pass. The participants made 26 passes, 13 with each foot, in a counterbalanced and randomised order.

The distance from the ball to the centre of the target was measured in X (direction) and Y (distance) coordinates, with negative X-values denoting the point of impact being to the left of the target, positive X-values to the right, negative Y-values short of the target, and lastly positive Y-values denoting the point of impact overshooting the target. The discrepancy in Xand Y- axes where subsequently used to calculate Absolute Error ($\Sigma \mid x_i -$ T |/n), Target Variability $(\sqrt{\Sigma(x_i - T)^2}/n)$ and Variable Error $(\sqrt{\Sigma(x_i - T)^2}/n)$ M(2/n). Here, the absolute error (AE) measure represents the average deviation of each participant's total number of shots (26) from the target without respect to position. As the spread of the 26 passes provides information about the player's performance consistency, Total Variability, also known as root-mean-square error (TV) and Variable Error (VE) were analysed. TV is a measure of the participant's total spread about the target, representing an overall measure of success in hitting the target, whereas VE denotes the variability of the participant's deviation from his own mean, representing the variability or inconsistency in the accuracy of the crosspasses (Schmidt and Lee, 1999).

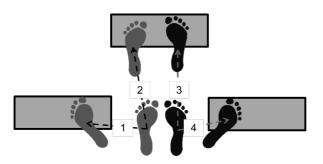
The cross-pass task was chosen for several reasons: 1) it is challenging for players at all levels and thus does not display a risk for obtaining ceiling effects (which was confirmed during pilot testing); 2) it provides an optimal experimental setup for assessing soccer-kick accuracy and variability; 3) performance of this particular task has recently been found to successfully predict player level (Vorland-Pedersen, 2014), and thus demonstrate good reliability and validity; and 4) it is highly relevant for match performance. Moreover it involves supra-second timing (to time the approach of the ball within the action zone with your own run), coordination, motor control and millisecond timing (the inter-limb sequence of isolated movements within the leg that strikes the ball). It is also highly demanding with regards to visuo-motor integration as it involves whole-body control as well as gaze shifts (ball/target). Accordingly, performances that are well timed with good motor control and with adequate focus of attention reflect successful movement planning and sensorimotor integration, resulting in a more precise/accurate performance outcome.

Moreover, and in line with the suggestions of Russell & Kingsley (2011), we quantified the players performance in terms of continuous data (discrepancy from target as measured in metres and centimetres), thus facilitating ecological validity of results, being relevant to players, coaches and sports scientists.

Assessment of timing and rhythmic abilities (studies I-III)

The Interactive Metronome (IM) [®] system assessed the participants' timing and rhythmic skills at pre- and post-test. Here, the participants are requested to perform unilateral and bilateral rhythmic hand and feet movements in conjunction with a computer-generated reference beat, heard through headphones. By use of contact-sensing triggers, including hand gloves and flat plastic footpads, the IM system generates scores on three dependent measures; namely the mean millisecond discrepancy between the participant's responses and the reference beat (timing skills), the interresponse time that is a measure of how close each hit is timed to the previous hit (rhythmic skills), and finally the highest number of times in a row that the participant is able to stay within ± 15 ms of the reference beat (reflecting the degree of stability in performance). A high timing score indicates a larger millisecond discrepancy between the metronome beat and the participant's movements, a score that indicates less accurate timing. Thus, lower timing scores imply better timing. The IM pre- and post-test are standardised assessments developed by the instrument manufacturer, consisting of 14 different tasks, involving uni- and bimanual hand and feet actions (Interactive Metronome, 2012). Prior to each of the 14 tasks included in the pre- and post-tests, the participants were shown a video modelling the appropriate movements, and the tempo of the metronome was set at 54 beats per minute (nominal beat separation; 1111 ms) for all tasks. No guide sounds are available during the tests, except from in Task 14 which is a repeat of Task 1 (clapping both hands). The tests took about 20 minutes to complete.

In Study III, two additional tasks were employed to capture performance on soccer-related foot work. One was a stepping test in which the participants were required to step on the floor-mats in synchrony with the metronome beat, using both feet (see Figure 3). The other was a kicking movement, in



which the participants were required to move (kick with) their dominant foot at a sensor mounted 0.5 m above the ground. This exercise was utilised to mimic a soccer-kick movement.

Figure 3: IM stepping test

Neuroimaging (Study III)

Neuroimaging by means of functional Magnetic Resonance Imaging (fMRI) investigations was first introduced in the early 1990s, providing scientists with a reliable instrument for mapping functions onto the brain. Here, the BOLD (Blood Oxygen Dependent) signal is thought to correspond to neuronally mediated hemodynamic changes that can be modelled as a (non-) linear convolution of some underlying neuronal process, responding to changes in our experimental factors (e.g. type of stimuli, pre- vs. post-test), by a hemodynamic response function (HRF).

Oxygen is delivered to neurons by haemoglobin in capillary red blood cells. When neuronal activity increases there is an increased demand for oxygen and the local response is an increase in blood flow to regions of increased neural activity. For instance, blood flow in the visual cortex is normally modulated in step with neural responses to visual stimuli (Huettel, Song & McCarthy, 2009). Haemoglobin is diamagnetic when oxygenated (Oxy-Hb) but paramagnetic when deoxygenated (De-Oxy-Hb). Thus, the oxygenated blood affects the magnetic field minimally, while deoxygenated blood produces a clearly measurable, additive magnetic field. This difference in magnetic properties leads to small differences in the MR signal of blood, depending on the degree of oxygenation. Since blood oxygenation varies according to the levels of neural activity, these differences can be used to detect brain activity. De-Oxy-Hb is paramagnetic – as its proportion decreases, the MR signal increases and generates what is referred to as the Blood Oxygenation Level Dependent (BOLD) signal.

In the present study, we assessed brain activation patterns corresponding to the observation of a soccer cross-pass task (identical to the cross-pass task that was to be performed during the pre- and post-test soccer skill assessment), contrasting to activation during observation of a rolling football. We applied a blocked design (BD) in which stimuli were presented sequentially within a condition, alternated with a baseline condition as well as different task conditions. These on/off states were alternated throughout the experiment to ensure that signal variation from small changes in scanner sensitivity, head movement or attention shifts have a similar effect on the signal responses associated with each of the different states. To avoid confounding factors we randomised the order in which conditions were presented, and counterbalanced the order in which conditions were presented across subjects, to limit practice and order effects. The main advantage of the BD is that it is statistically powerful (Friston et al., 1999) and straightforward to analyse, as the BOLD signal change related to baseline is relatively large (Buxton, Wong and Frank, 1998). Thus, a relatively low number of trials and subjects are needed. Moreover, the design allows for considerable experimental flexibility, allowing both parametric and multi-factorial designs to be employed. It is also known to have excellent functional contrast-to-noise ratio (Logothetis, 2008).

The intervention

'Would you believe me if I said tapping you right toe to the beat of a metronome will make you a better footballer?' I asked a premiership player last fall. His response was; 'What? No!' Obviously, the tapping your toe to a metronome beat is only half the truth. Add 27,000 repetitions of a variety of whole-body and single limb movements, as well as an important feedback component, and there is the intervention used in the three studies comprised in the present thesis.

General properties of Synchronised Metronome Training (SMT)

The main purpose of the SMT is to improve the participant's motor timing and rhythmicity skills, by means of sensorimotor synchronisation training (producing movements, i.e. handclaps, in response to an external rhythmic auditory signal). The participants' SMS ability is assessed by the 14 motor timing tasks entailed in the IM pre- and post-test regimens. The SMT intervention in studies I/II and III included 12 sessions of training with the IM system, distributed over three 45-50 min sessions a week during a fourweek period after the pre-test. At the completion of training, participants have typically engaged in approximately 27,000 motor repetitions. However, none of these exercises were task-specific (i.e. golf swing or soccer-kick related). During the training sessions, the IM system instantaneously transposes the timing information into discriminative, temporally-based feedback sounds presented in the participant's headphones, continually indicating whether the response was on target, early or late. A contact that matches the beat within ± 15 ms generates a high pitched tone in the centre of the headphones and is simultaneously perceived in both ears. An early contact (a contact that precedes the beat by ≥ 151 ms, or by 150 - 16 ms) generates a very low or low pitch tone in the user's left ear, respectively. A late or very late contact (a contact that follows the beat) generates similar pitch tones in the right ear. These instantaneous guide sounds enable the participant to deliberately correct their timing errors as they occur. Guide sounds were not delivered during pre- and post-test.

After each training session, the participants were shown their scores, designed to work as a motivating feedback for future performance enhancement.

The basic SMT intervention consists of 14 standardised tasks including clapping both hands together, tapping one hand alone against the thigh, alternating toe taps on the footpad, tapping one toe or heel alone on the footpad, alternating between tapping one hand on the thigh and one toe on the footpad, and balancing on one foot while tapping with the toe on the contralateral footpad. Three to four of these tasks were utilized during every session in both studies I/II and III.

Details of the SMT paradigm in study I/II

During each of the first seven sessions, participants performed 4-10 successive exercises involving the basic uni- and bilateral motor tasks mentioned above. Each exercise typically lasted from 2-10 minutes, with the metronome reference beat set to 54 bpm. From session number eight some new reference beat tempos (45, 66 and 78 bmp) and tasks were introduced. These tasks were focusing on the work of the hands/arms, as the main effectors in the performance of a golf swing entail the work of hands and arms (figure 4).



Figure 4: SMT session displaying the handclap-task from Study I

However, none of these tasks were golf-specific in that they mimicked a golf swing. Rather, we avoided golf-like movements and introduced alternative tasks that placed high demands on SMS, motor control and motor planning

(i.e. clapping hands while standing on a balance-board, hitting wall mounted sensors with hands crossing the body midline and clapping hands behind back, 4 beats both hands - 4 beats behind back - 4 beats both hands, etc.).

Details of the SMT paradigm in Study III

In Study III, each training session would typically start off with three to four



basic uni- and bilateral motor tasks. Then, another ten tasks focusing on soccer related foot-work were introduced. In contrast to Study I, these more specialised exercises were implemented already from the first training session. For clarification, these movements were not related to that of kicking a ball, but rather to more general soccer related movements focusing on the work of the feet (e.g. a variety of shuffle steps and stepsequences on multiple floor-mounted sensors), all in synchrony with the metronome reference beat that was set at 54 bpm for most exercises (approximately in 60% of the tasks). A range of different tempos (66 - 100 bpm) was introduced to maintain a challenging and ecologically sound training paradigm.

Figure 5: SMT during Study III (Photo credits: Per A. Adsten)

What is trained in the SMT paradigm?

Within the SMT paradigm participants are required to produce rhythmic movements (e.g. handclaps) in response to an external rhythmic auditory signal (a fixed metronome beat/pulse). According to Phillips-Silver, Aktipis & Bryant (2013) such coordinated rhythmic movements require the ability to 1) identify the rhythmic patterns of the pacing signal, 2) produce rhythmic output, and 3) integrate sensory information and motor production, which, in turn, enables the adjustment of motor output based on rhythmic input. Thus, the coordination of movements with an externally paced rhythm may be defined as a sensorimotor synchronisation (SMS) ability (Repp, 2005; Repp & Su, 2013), containing the basic elements of entrainment (Phillips-Silver et al., 2013), in which movements are timed through action-perception coupling.

Viewed from a motor timing perspective, some of the exercises performed within the SMT paradigm are of an event-based timing character, entailing *discontinuous/discrete* movements with clear endpoints (e.g. tapping one toe, one heel, and any foot-stepping sequence). Such movements are suggested to involve a clock-like neural process, relying on an explicit internal representation of the time interval (Wing and Kristofferson, 1973; Huys et al, 2008). Still, other exercises are of a *continuous/rhythmic* character, entailing circular motions (e.g. clapping hands and tapping hand against the thigh in a circular fashion). These smoothly produced movements are thought to engage emergent timing processes, in which motor timing can be maintained without reference to any explicit representation of the time interval (e.g. Lorås, Sigmundsson, Talcott, Öhberg & Stensdotter, 2012), because the timing possibly emerges from the dynamics of the movement (e.g. Huys et al., 2008; Torre & Balasubramaniam, 2009).

There is some disagreement with regard to whether the rhythmic, circular handclaps utilized in the SMT paradigm are discrete or continuous, and thus relying solely on event-based or emergent timing processes, or both. In my view it could both rely on event-based mechanisms in the meaning that movements are guided by an external auditory event/cue (a pacing signal), but it may also rely on emergent processes because it entails circular, smooth and continuous movements, in a similar fashion to the movements performed in classical circle-drawing tasks. Indeed, for continuous movements performed in synchrony with an external rhythmic pacing signal, it is possible that the dynamics of the circular movements gives rise to direct proprioceptive information that can facilitate the prediction of the upcoming of the "next event". This would be in accordance with theories suggesting that motor timing rely on (effector) state-dependent processes (e.g. Diedrichsen et al., 2007), and also fit well with the theorized role of cerebellum in feed-forward and error correction processes (e.g. Diedrichsen, Hashambhoy, Rane, & Shadmehr, 2005).

Another aspect of event-based timing, relating to the SMT paradigm, is that much of the timing training is performed at a tempo of 54 bpm, which entails an inter-tap interval of 1.1 s. Research suggests that mental interval timing consists of two sub-systems; an automatic timing system processing discontinuous/discrete timing on a millisecond-level, heavily involving the cerebellum, and a cognitively controlled timing system dealing with continuous-event timing (in seconds). Whereas the former is hypothesised to favour an automatic mode of temporal processing, the latter is suggested to involve a cognitive mode (Lewis & Miall, 2003).

SMT seem to tap into both these aspects of temporal processing and motor timing, due to the fact that the tempo of the pacing signal was altered during the training period. At the beginning of the intervention most exercises was performed at 54 bpm (IRI:1100 ms), but faster tempos with shorter interresponse intervals (66 bpm: IRI = 909 ms, 77 bpm: IRI = 779 ms) was introduced as the training proceeded.

Summary of results and brief discussion of findings

Study I, Improved motor timing: effects of synchronized metronome training on golf shot accuracy (Sommer & Rönnqvist, 2009).

Background and aim

As previously described, timing is one of the central attributes that professional players (e.g. Nicklaus, 1974; Watson, 2011), instructors (e.g. Pelz & Frank, 1999) and scientists (e.g. Neal et al., 2008) believe to be important for optimal swing performance and subsequent golf shot accuracy. However, given the focus of importance of timing in the golf-related literature, it is surprising to find so few empirically-based studies investigating the timing properties of the golf swing, and how timing training may affect golf performance. Thus, the aim of the present study was to investigate the effects of SMT on golf shot performance by means of outcome precision and variability.

This work is also an extension of a recent study conducted by Libkuman et al (2002), showing the beneficial effects of SMT on golf shot accuracy. More specifically, the extension included improvements of validity issues related to homogeneity of participant degree of experience, levels of skill (golf hcp), and age range, as well as specificity of instructions ('choose a distance from the pin that is, with some margin, within the reach of your shot ability/range with each club' vs. 'Choose a distance from the pin that reflects how far you are able to hit the ball with each club'). Finally, we added target variability and variable error to the outcome measures being investigated, whereas Libkuman and colleagues only investigated the mean distance between the pin and the ball's final resting place (absolute error).

Method

(I) Pre-test: first the participants' timing and rhythmic skills were assessed by means of the 14 task IM test battery (Figure 6). At the time of the golf pre-test, the participants first set the distance from the ball (fairway) to the pin (it was emphasised that this distance should, with some margin, be within the reach of their shot with each club), then they were instructed to aim for the pin and to proceed at their own pace. All golfers performed 20 shots with each club (pitching wedge, 4 iron and 7 iron, respectively) in a counterbalanced randomised block design. (II) Intervention: the participants were randomly divided into either the intervention group or the control group. The training intervention, aiming to improve the participants' timing and rhythmic skills, lasted for four weeks, with three training sessions each week, adding up to a total of 12 hours of training and approximately 27,000 motor repetitions.

(III) Post-test: the same experimental conditions (timing and rhythmicity tests, golf shot distances, golf clubs used, etc.) used for the pre-test occasion was applied for the post-test.

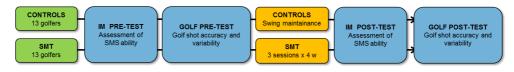


Figure 6: Experimental design Study I

Findings and conclusions

In summary, four weeks of SMT showed evident motor timing improvements, as assessed by the IM testing paradigm. Additionally, significant improvements in golf shot performance by means of significant increase in outcome accuracy combined with a decrease in outcome variability, measured by the distance of the golf ball from the pin and how it varied, were found for the SMT group. No such improvements were found for the golfers in the control group. As with previous studies that employed SMT as an intervention, this study's results provide further evidence that motor timing can be improved by SMT, and further that such timing enhancement also improves golf shot accuracy and variability.

Study II, Synchronized Metronome Training induces changes in the kinematic properties of the golf swing (Sommer, Häger & Rönnqvist, 2013).

Background and aim

One conclusion derived from the investigations of the effects of timing training on golf shot performance (Study I) was that timing training seems to positively influence golf shot accuracy and variability. Thus, we can infer that the four-week SMT has induced changes in some physical parameter(s) of the golf swing execution. This inference is based on the notion that motor control and timing are inextricably related (e.g. Baht & Sanes, 1998; Mauk

& Buomonano, 2004), and as coordination includes and specifies the spatiotemporal ordering between component parts (e.g. Jantzen, Oullier, & Kelso, 2008), precise timing between individual body/limb segments in complex, multi-joint tasks such as the golf swing seems especially crucial.

However, a reasonable question arising from these findings is related to the effects of SMT on the spatio-temporal properties of the golf swing performance. In other words, we can measure the outcome effect of SMT on golf shot accuracy and variability, but what exactly has changed in regard to golf swing performance? Thus, the aim of Study II was to evaluate the possible effects of SMT on the movement dynamics during golf swing performance, as captured by kinematic analysis.

Method

This was accomplished by investigations of the kinematic pre- and post-test golf swing data extracted from golf swing performance made by golfers included in the SMT intervention group from Study I (Figure 7). Here, tangential (3D) velocities of the markers attached to the golf club and different arm joints were generated by use of custom written software in MATLAB (Mathworks Inc., Boston, MA). Timing relationships within each arm and in relation to the club velocity profiles were analysed by means of time-series signals gained from calculations of cross-correlation between different joint motion linkages. Furthermore, the phase-shift (zero-lagging) of each joint pair was assessed to map any changes in the temporal sequencing of the golf swing as a result of SMT.

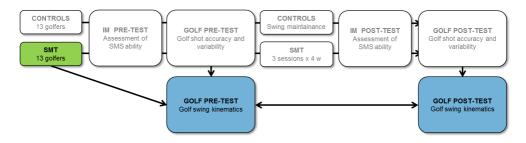


Figure 7: Experimental design Study II

Findings and conclusions

There were significantly higher cross-correlations between joint couplings and concomitant changes to the associated phase-shift differences, as well as reduced phase-shift variability at post-test. No significant effect of SMT was found for the club peak velocities. We suggest that domain-general influences of SMT on the underlying brain-based motor control strategies lead to a more coordinated movement pattern of the golf swing performance, which may explain previous observations of significantly improved golf shot accuracy and decreased variability after SMT.

Study III, The effects of timing training expressed in female soccer players' motor skills and underlying functional brain response (Sommer, Häger, Olsson, & Rönnqvist, 2014).

Background and aim

Findings from studies I and II indicate that improvements in motor timing as an effect of SMT can seemingly be transferred to an unrelated motor task; in this case the intrinsic movement sequencing during the golf swing performance, and consequently the golf shot outcome. Based on the positive effects of SMT on golf performance, we wanted to examine if similar effects of SMT would be evident on a variety of technical soccer skills. Moreover, the findings from the golf studies provide a rationale for investigations of possible changes on a (brain) neuronal level. The primary aim of the present study was to confirm and extend recent findings concerning effects of SMT on sport performances (Libkuman et al., 2002; Sommer & Rönnqvist, 2009; Sommer, Häger & Rönnqvist, 2014). Specifically we asked whether positive effects of SMT on motor timing would transfer to the soccer cross-pass task, by means of enhanced outcome accuracy and consistency. Moreover, we investigated the extent to which SMT modulates the underlying brain activation of soccer cross-pass action observation.

Method

The experimental procedure was divided into three parts (Figure 8).

(I) Pre-test: first, by means of a blocked design fMRI paradigm, we assessed the brain activation associated with the observation of a soccer cross-pass task (identical to the cross-pass task to be performed during pre- and posttest soccer skill assessment), relative to different control conditions. Then, a baseline of the participants' timing and rhythmic skills were assessed by means of the 14 task IM test battery, and finally, we assessed outcome accuracy and variability in the cross-pass task.

(II) Intervention:. The training intervention, aiming to improve the participants timing and rhythmic skills, lasted for four weeks, with three

training sessions each week, adding up to a total of 12 hours of training, and approximately 27,000 motor repetitions. During the period of the study, both the SMT and the control group participants carried on with their regular team soccer practice.

(III) Post-test: the same experimental conditions used for the pre-test occasion were applied for the post-test.

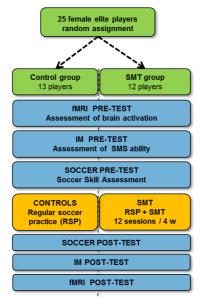


Figure 8: Experimental design Study III

Findings and conclusions

As expected, the SMT group improved their motor timing, as assessed by the IM system. Furthermore, positive effects of SMT were found on cross-pass performance in regard to both outcome accuracy and variability. Of particular interest was the near to linear relationship between improvement in timing and improvement in the cross-pass task.

Significant changes in BOLD signal from pre- to post-test, as an effect of SMT, was found within several brain areas during the cross-pass observation task, the most prominent being those within the cerebellum.

Thus, as the cerebellum have recently been found to be heavily involved in both action production and temporal processing, we argue that SMT reinforces the action-perception coupling and the underlying brain-based motor control strategies that, by means of a more coordinated movement pattern, lead to significantly improved cross-pass accuracy and decreased variability.

General discussion

The aim of the present thesis was to examine five major research questions pertaining to the effects of timing training (SMT) on SMS abilities, and golf and soccer skills;

First, we investigated whether previously reported positive effects of SMT on motor timing in non-athletes and recreational golfers also could be found in high performing athletes who, hypothetically, possess a higher degree of general motor coordination skills. Then, we assessed the effects of SMT on golf shot precision and its associated variability (study I), as well as the kinematic properties of the golf swing performance associated with these outcome measures (Study II). Next, we shifted research focus to female soccer players, to assess possible effects of SMT on the outcome accuracy and variability of a cross-pass task. Finally, we investigated how effects of SMT may be manifested in brain activation patterns associated with passively observing this very same cross-pass task.

The results associated to each of these research questions are considered in turn in the subsequent section.

The effects of SMT on motor timing performance/SMS abilities (as assessed by the IM system)

In line with other studies comprising SMT as an intervention, improved sensorimotor synchronisation abilities (by means of decreased asynchrony and inter-tap variability), was as evident in all subjects undergoing SMT in the present studies. This was a highly expected outcome, considering that skills are acquired through extensive practice (e.g. Ericsson, Krampe & Tesch-Römer, 1993). Although 'practice makes perfect', the properties of the training regimen may have contributed substantially to the observed effects. These properties fits well with the concept of deliberate practice (Ericsson et al., 1993), which state that for effective learning to occur, certain conditions must be fulfilled; the activity should be well-defined, involve an appropriate level of difficulty, and provide opportunities for repetition, error detection and correction, and useful feedback. Accordingly, as all of these conditions apply to the SMT paradigm, with useful (instantaneous, real-time) feedback of performance being the outermost important factor, these effects were expected. The effect of the guide sounds very much fill a feedback function much akin to that of the 'knowledge of results' concept, which refers to information provided over and above those sources of feedback that are naturally received when a response is made (e.g. Adams, 1968; Ford, Hodges, Huys & Williams, 2006).

Corresponding to this, it has been found that both the removal of intrinsic feedback (tactile and kinaesthetic - Aschersleben et al., 2001, 2004) and the presence of extrinsic feedback (additional auditory signal each time the finger touches the tapping key - Aschersleben and Prinz, 1995, 1997; Mates et al., 1992) influence the ability to synchronise taps with external stimuli. In summary, these findings suggest that the timing of the tap is not dependent on a single feedback component but on an integrated perception of all extrinsic and intrinsic feedback components.

With regard to acquiring SMS skills, the results from the studies presented in this thesis suggest that SMS skill acquisition is initially fast, and then even out, with less increase in performance over sessions, until performance reaches an asymptotic level (Figure 9).

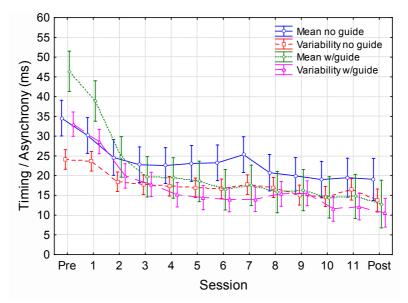


Figure 9: Learning curve from SMT for all participants from both studies I and III as a function of training session, including the four SMS measures; mean deviation from beat with and without guide sounds, and mean inter-response intervals with and without guide sounds.

Thus, changes in skill level is interpreted to occur during training as well as after training, reflecting online skill stabilisation and improvement, and offline motor memory consolidation (Doyon & Benali, 2005). This notion is in line with results presented by Savion-Lemieux and Penhune (2005),

showing small amounts of motor skill practice spread over several days induce long-term retention, which suggest that long-term retention is strongly dependent on successful consolidation. In line with this notion, data from studies I and III suggest that the instantaneously provided feedback signals are initially 'disturbing' to participants, but that they become accustomed to them, and are able to exploit them for refining their SMS skills as the sessions progress. More specifically, the average asynchrony with guide sounds is typically close to 50 ms at pre-test, and then decrease as training proceeds, until they perform better with guide sounds present than without (Figure 9), most often after session number three. It has been hypothesised that this disturbance is due to a 'pseudo-synchronisation effect' (Repp & Su, 2013), in which participants typically start following the feedback sound of their own responses, instead of the externally paced rhythm.

In essence, the SMT intervention trains the subjects' ability to move to a rhythmically paced external signal. The obvious effect of SMT is that these subjects show better timing skills (responses are closer to the external pacing stimuli) and less variability (inter-response intervals). The improved sensorimotor synchronisation is in my view, and in agreement with e.g. Malcolm et al. (2009), an entrainment process which builds a new spatio-temporal motor template onto which movements can later be mapped. Thus, the pacing rhythm may provide precise anticipatory time cues for the brain to plan and organise motor actions onto. Here it is hypothesised that the auditory rhythms of the metronome trigger the firing rates of auditory neurons, which in turn entrain the firing patterns of motor neurons (Thaut, 2013).

However, and contrary to the purpose of the RAS, the SMT intervention does probably not build a temporal motor template for later *sport performances* to be mapped onto. Unless this template is tempo insensitive, or consist of an infinite number of different tempos, motor performance would be locked i.e. in a 54 bpm mode. The most plausible explanation of this transfer is, in my view, related to the effects of SMT on the action-perception coupling, and thus the integration and interaction of sensory information from multiple modalities; SMT may increase the efficiency and organization of the central nervous system circuitry, making the brain's signal processing become more efficient and more consistent.

An alternative explanatory model for improved SMS abilities

Another factor that may play and important role is the notion that SMT positively influence the athlete's ability to selectively attend to a stimulus, without interruption by internal thoughts or external distractions, for extended periods of time. Indeed, the SMT paradigm entail 12 session x 45 minutes of focusing on moving in synchrony with a monotone rhythmic reference beat, while utilizing (instead of being distracted by) the instantaneous feedback sounds, that are meant to facilitate sensorimotor synchronization. This feedback requires the participants to suppress attending to distracting external and internal stimuli. Thus, executive functions must constantly monitor the feedback and update immediate working memory so the subject can adjust and correct their synchronization on a real-time basis (McGrew, 2013). In essence, this is training of attentional control (defined as the ability to defend primary-task systems against interference by thoughts related to the internal or external environment - McVay and Kane, 2010), which may act as a mediator for enhanced working memory capacity (Engle, 2002). In line with this, recent research (e.g. Hunt, 2011) indicate that improved focus (attentional control that maintains goal related information active in working memory) will also improve the efficiency of the working memory – which is suggested to be the most central executive ability for new learning and performance. Thus, the theorized effect of SMT on brain network communication efficiency may also enhance the ability for focusing attention.

From the behavioural outcomes, there are two results supporting the above reasoning; first a significant increase in number of IARs (hits in a row within ± 15 ms of the reference beat) was evident from pre- to post-test (Figure 10).

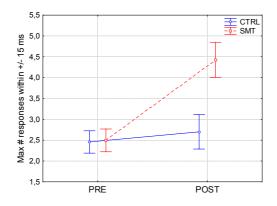


Figure 10: Maximum number of hits in a row within \pm 15 ms, as a function of group and test, vertical bars denoting 90% confident intervals.

Second, the inter-response interval (IRI), reflecting the participants' consistency in sensorimotor synchronisation, was also significantly improved. These results may be interpreted as reflecting the participant's ability to attend to the task at hand. This notion is also in line with Diamond (2003) suggesting that the use of guide sounds in SMT may facilitate 'choice discrimination' and thus increase the ability to exclude irrelevant information. Although being a highly plausible explanation to the effects of SMT on SMS abilities, it is still not clear how enhanced attentional control, facilitating sensorimotor synchronisation, may be transferred to golf swing or cross-pass performance. It may be that that this ability of attentional control can be regarded as a general skill and, thus, is at hand even during the post-training test sessions.

Applying general motor timing theories to understanding sport skill performance

In the introduction section I reasoned upon the fact that motor timing has been understood from studies mostly involving a relatively small movement scale (typically by means of finger-tapping and/or circle-drawing), and that this may pose a challenge in regards to understanding the timing properties, movement dynamics and the associated underlying brain activity of sport skills. In line with this, results from Rodger and Craig (2011) indicate that rhythmically paced motor actions of larger movement magnitudes do not display the usual mean negative asynchrony (MNA) of about 20-60 milliseconds typically reported in other studies (e.g. Aschersleben, 2000). Rather, when movements were made over larger amplitudes, synchronisation errors tended to be more positive. This was also confirmed in the studies included in the present thesis; the participant responses – independent of sport – typically lagged behind the auditory metronome beat by 50-90 ms (before SMT).

These findings may be seen in light of the notion that sensorimotor learning tasks (e.g. rhythmical handclaps or foot-stepping sequences) pose greater demands on movement kinematics and dynamics, while small scale movement variants have relatively minimal motor demands, involving simple responses through primarily isometric contractions of the finger/hand/foot muscles (Hardwick, Rottschy, Miall & Eickhoff, 2013). Hardwick and colleagues conducted a meta-analysis to examine whether differing task demands give raise to different patterns of neural activity. Their findings revealed that for sensorimotor tasks activity was more frequently (however not exclusively) associated with the basal ganglia and cerebellum, which is consistent with their proposed roles in the acquisition

and integration of sensorimotor information (Bloedel, 1992; Bower, 1995; Thaut, Demartin, and Sanes, 2008) and feed-forward and error correction processes (Diedrichsen, Hashambhoy, Rane, & Shadmehr, 2005; Yarrow, Braun & Krakauer, 2009; Ohyama et al., 2003). In contrast, serial reaction time tasks, entailing learning of sequential motor behavious, yielded activity in the dPMC, SMC, SPL and thalamus. These findings further support the notion that an understanding of the timing, coordination and neural mechanisms that underpin skilled sport skills needs to be built upon sport specific investigations, alternatively within a research paradigm that pose similar demands on movement control and motor execution, to facilitate the generalization/specification of study results.

In my view there is a need to clarify the fact that motor timing also entails movements that are self-paced (which is indeed the case in most sporting contexts), not being dependent on an external auditory or visual pacing signal. Thus, whereas *motor timing* is frequently defined as the timing of motor actions in accordance with an rhythmical external event, the concept *'movement timing'* could possibly entail 1) the inter- and intra-limb spatio-temporal coordination of effectors (limbs, muscles and joints) involved in any motor action, and/or 2) the timing of such motor actions in relation to external events (i.e. the movements of an opponent, an approaching football, etc.). Thus, a distinction between *motor* and *movement timing* could be beneficial for future studies investigating aspects of timing in a sport setting.

The effects of SMT on golf shot and cross-pass outcome measures

In the case of Study III our results suggest that, on an elite-/sub-elite level, regularly scheduled soccer practice does not improve performance on the cross-pass task. This is inferred due to the lack of improvement in the control group. For the SMT group, the additional 12 hours of SMT-induced a worthwhile performance change (about 1.5 metres) in regard to the accuracy measure. This effect is large and somehow puzzling due to the fact that the training intervention entailed motor actions that were very different from that of kicking a football.

Taken together, the studies included in this thesis point to positive and worthwhile (Hopkins, 2002) effects of SMT on outcome measures related to accuracy and variability, in both golf and soccer skills. Taken into consideration that the sample of players investigated in the present study consists of elite- and sub-elite players, one may have expected a "ceilingeffect" to occur; that their initial high level of skills would not allow for further skill improvement. However, this was not the case as the mean accuracy and the corresponding variability (VE and TV) was significantly improved (Table X).

Table 3: Collapsed measures of absolute error (AE), variable error (VE and target variability (TV) over the two sports, as a function of group and test (mean \pm SD).

Group/Measure	Pre AE	Post AE	Pre VE	Post VE	Pre TV	Post TV
SMT golf	13,1 ± 3,1	10,5 ± 1, 5*†	8,4 ± 1,9	6,6 ± 1,0*†	9,8 ± 2,0	8,2 ± 1,3*†
CTRL Golf	12,5 ± 2,9	13,1 ± 3,2	$7,9 \pm 1,7$	$7,1 \pm 1,0$	9,3 ± 2,0	$9,7 \pm 2,9$
SMT Soccer	$6, 5 \pm 3, 2$	4,9±2,3*†	$3, 6 \pm 1, 0$	3,0 ± 0,8*	$4, 8 \pm 1, 9$	3,7 ± 1,6*
CTRL Soccer	5, 6 ± 1,6	$5, 9 \pm 1, 8$	3,5 ± 0,8	$3,7 \pm 0,4$	4,3 ± 1,1	4,6 ± 0,9
SMT overall	$9,8 \pm 3,1$	7,7 ± 1,9*†	$11,9 \pm 1,4$	$9,6 \pm 0,9*\dagger$	$14,6 \pm 2,0$	11,9±1,4*†
CTRL overall	9,1 ± 2,3	$9,5 \pm 2,5$	$11,4 \pm 1,2$	$10,8 \pm 0,7$	13,6 ± 1,5	$14,3 \pm 1,9$
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* pre- to post-test difference, p > 0.05

⁺ between-group difference, p > 0.05

While further investigating aspects of accuracy in regard to length (ball landing short of target or overshooting the target) and direction (ball landing left or right of the target), it seems that for both Study I (golf) and Study III (soccer), SMT gives raise to similar effects on these measures. In other words, both length and direction accuracy improve to an equal degree. Thus, SMT seems to decrease the variability in force applied to the kick and golf swing performance, respectively. Moreover, as both the golfers and the soccer players display less variability and higher accuracy in regard to the direction measure, it can be concluded that SMT also gives raise to a more optimal contact between the ball and the foot/club. This fits well with the notion that variability should only be minimised in the (swing) components that have the greatest effect on the variability of the outcome (e.g. Todorov & Jordan, 2002; Knight, 2004).

However, as we did not assess any kinematic properties of the execution of the soccer cross-passes, we cannot provide evidence of possible movement re-organization of such skill execution as an effect of SMT. Still, our results show that a performance enhancement was only evident within the intervention group. Thus, and in line with the findings of changes in the arm movement organizations and dynamics found in golf-swing performance, as an effect of SMT (Study II), we think that such changes might have occurred.

Together, the data indicates that improved motor timing does affect the temporal properties of limb displacement in golf swing and cross-pass performance, producing a more coordinated, efficient and/mechanically sound and dynamic movement, and thus more consistent and accurate performance outcomes. Thus, in line with findings related to the effects of SMT on golf performance (study I and II), it is also possible that SMT reinforces the coordinative structure and the temporal synchronicity within the kicking leg.

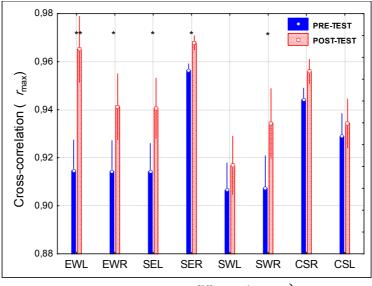
These findings indicate that improved motor timing induces movement performance in an unrelated task. This is in agreement with the assumption of the described phenomena in bimanual polyrhythmic tapping; that there are structural aspects of timing that generalise across different rhythmical tasks (Treffner & Turvy, 1993). Moreover, it is in accordance with findings from perceptual learning studies showing that interval-specific learning may generalize across modalities, such as somatosensory to auditory (Nagarajan, Blake, Wright, Byl, & Merzenich, 1998), or even from a sensory to a motor task (Meegan, Aslin, & Jacobs, 2000).

Accordingly, SMT may influence the (spatio-) temporal properties of a generalised motor program (Schmidt and Lee, 1999), allowing for the production of variations of a particular movement, or class of actions (e.g. kicking or throwing), as they allow the athlete to modify movements in terms of "movement time, movement amplitude and the effector system...used to produce the action" (p. 151), and thus to meet the demand of the prevailing conditions, that being environmental-, organismic- or task-constraints.

An alternative view is the dynamic systems approach (Kelso, 1995), that introduced the notions of stability and non-linearity to explain variability. Based on different constraints, the system will self-organize to find the most stable solution. An increased amount of variability indicates less cooperative behaviour among the components of the system, which eventually can drive the system to new attractor states or behaviourally stable solutions (Harbourne & Stergiou, 2009). Thus, the effects of SMT may be viewed as to strengthen the perception-action coupling by means of a more efficient self-organisation of motor performance (action), and in relation to the prevailing conditions (perception). Here, improved performance may be viewed as the athlete's ability to integrate sensory information from his or her own body during movement (action) with relevant sensory information perceived from the environment (e.g. 'tau' information of the football, or environmental constraints on the golf course). The efficiency of this integration of, and interaction between, multiple sensory modalities may be the ultimate effect of SMT on cross-pass and golf shot outcomes.

The underlying kinematics of the golf swing

Our findings indicate that SMT influences the underlying coordinative structures and the temporal synchronicity of the upper-limb movements involved during the golf swing performance. A consistent finding was the significant higher cross-correlation values of the intra- and inter-joints couplings at the post-test in comparison to the pre-test (Figure 11), and a concomitant significant change in the corresponding shifts from zero lag (Figure 12).



Note: * pre- to post-test difference (p > 0.05)

Figure 11: Mean maximum cross-correlation (r_{max}) as a function of test (pre- and post-test), distributed over the different joint couplings (EWL, elbow-wrist left; EWR, elbow-wrist right; SEL, shoulder-elbow left; SER, shoulder - elbow right; SWL, shoulder-wrist left; SWR, shoulder-wrist right).

These results indicate that improved motor timing as an effect of SMT does influence the dynamics and underlying timing properties of the golf swing motion, mediated by the coordinative structure and the temporal synchrony between joint couplings involved during the golf swing performance. A highly feasible explanation for the observed changes in golf swing dynamics may be attributed to the changes in cerebellar activation, as seen in Study III, involving soccer players. This notion is based on the role of the cerebellum in producing complex and coordinated movements (Thach 1998; Imfeld et al. 2009), and its contribution to the generation of forward models (e.g Miall & Reckess, 2002: Thach 1998; Kawato et al. 2003) that are crucial for motor

planning and correction, as well as its role in time perception and time estimation (e.g. Medina et al., 2005).

The increased intra-joint couplings and the decreased variability in phaseshift from zero lag thus seem to promote a more effective (read preferred, optimal and efficient) movement trajectory of the club and club head towards the ball, as a result of the coordinated coupled work of the two arms and hands.

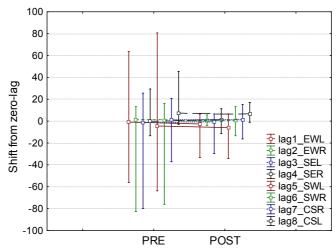


Figure 12: Shifts from Zero-lag corresponding to the r_{max} during the Golf swing movement, Mean (SE), as a function of test (pre- and post-test), distributed over the different joint couplings (EWL=elbow-wrist left; EWR=elbow-wrist right; SEL=shoulder-elbow left; SER=shoulder-elbow right; SWL=shoulder-wrist left; SWR=shoulder-wrist right; CSR=club base-shoulder right; CSL=club base-shoulder left), vertical bars denoting 90% confidence intervals.

This notion is in accordance with the decrease of variability (and smoothing of trajectory), as an effect of rhythmic cueing, that has recently been seen in hemiparetic reach (Thaut et al., 2002; Malcom, Massie & Thaut, 2009). Moreover, the relationship between the temporal and spatial aspects of the two hands seems to have been drawn towards a new state, namely the state that is most appropriate for the performance of the task. This would be analogous to the concept of entrainment, which is based on the notion that the system (the involved limbs, muscles, joints and tendons involved during the golf swing) is drawn towards a movement solution that provides the greatest degree of stability for the system as a whole. This is also in line with a dynamic systems approach to the underpinning elements of SMT, which is based on the same properties as sensorimotor synchronisation, viewed as a form of entrainment of one oscillatory process (motor) by another

(perceptual), as a consequence of unilateral coupling between them (Pikovsky, Rosenblum & Kurths, 2001; Wimmers, Beek & van Wieringen, 1992).

Similarly, and in light of the different takes on whether coordinated movements are dependent or driven by a state- or time-dependent control process (cf. Diedrichsen et al., 2007), the results included in the present thesis suggest that extensive SMT accentuates the coordinative structure and the temporal synchrony (and coupling) between arm joints involved in golf swing performance. These results favour the notion that the coordination (and temporal sequencing) of the multiple joints involved in the execution of golf swing performance (or the soccer cross-pass task) is entirely, or at least to a great extent, governed by time-dependent control processes.

Zelaznik and colleagues (Robertson et al., 1999; Zelaznik, Spencer & Doffin, 2000; Zelaznik, Spencer & Ivry, 2002, 2005) proposed that timing and rhythmic movements are achieved by using different control strategies, depending on the task specificity. Accordingly, during successive timing tasks (such as finger-tapping) every interval is explicitly timed, whereas during continuous rhythmic movement (such as continuous circle drawing) timing is achieved implicitly. This suggest that through auditory feedback of the performance during timing tasks as in SMT, each synchronised interval has to be explicitly timed, by adjusting and fine-tuning the central representation of the timed beat interval. However, when complexity of the movement sequence increases, such as during the golf swing performance, the rhythmic sub-movements seem to consist of both implicit and explicit timing strategies. Our interpretation of the SMT effects found on the kinematic properties (by means of seemingly more tightly coupled joint dynamics during the golf swing) is that it is reinforced implicitly and then consolidated and represented in the motor memory. Thus, this would suggest that the timing training induced neural adaptations (plasticity). Hence, this is in line with McGrew's assumption (2013) that SMT may result in increased brain communication efficiency between brain regions, especially those related to more domain-general motor functions (e.g. cerebellum and the supplementary motor areas).

SMT-induced changes in brain activity/perception – action coupling

In Study III, we attribute the changes in motor timing performance and soccer cross-pass performance to training (SMT)-induced changes of neural activity within the bilateral cerebellum, and to some extent the fusiform

gyrus and the STG. Although we cannot readily state that cerebellum is modulating the motor performance of the cross-pass task. Still, our findings of altered bilateral cerebellar activation post SMT, in addition to the evident correlations between changes in cerebellar activity during action observation and changes in SMS abilities accompanied with increased cross-pass skill, support this notion.

In regard to cerebellar activation during action observation, it is not a common occurrence, or it is seldom reported. One plausible reason for this is that it is not considered to be a part of the action observation network. Nevertheless, some exceptions exist (e.g. Buccino et al., 2004; Grezes, Costes &Decety, 1999; Gallagher & Frith, 2004; Cross et al., 2013) in which cerebellar activation during action observation is present. In the landmark study of Calvo-Merino et al. (2006) it was found that observing moves performed by a dancer of the same sex produced a stronger mirror activation in the premotor, parietal, and cerebellar cortices than did moves performed by the opposite sex. The authors suggested that AON activity is modulated by the motor representation for an observed action, and not only on the visual knowledge of what is observed. Our findings of cerebellar activity during action observation of a soccer-specific task concur with these results. In fact, many studies investigating brain activation during action observation report that a high degree of task-specific expertise is associated with a higher degree of cerebellar activation (e.g. Calvo-Merino et al., 2006; Cross et al., 2013; Wadden, Brown, Maletsky & Boyd, 2013). This is, however, in contrast to the findings from Study III, in which improved SMS ability was found to be associated with a decrease of cerebellar (and fusiform gyrus and STG) activation during soccer cross-pass observation.

Support for decreased cerebellar activation can be found in a study of golf imagery (Ross, Tkach, Ruggieri, Lieber & Lapresto, 2003) which reports that brain activation decreased with increased golf skill levels, particularly in SMA, and cerebellum. Moreover, Jantzen and colleagues (Jantzen, Steinberg & Kelso, 2003; Jantzen, Oullier & Kelso, 2008) have reported that cerebellar activation decreases with training and increases with task difficulty, within a finger-tapping paradigm. Thus, the decrease in cerebellar activation as an effect of SMT found in Study III is interpreted as a more efficient pattern of neural recruitment. This is also in line with neuroimaging studies reporting decreased cerebellar activation as an effect of practice or learning (Doyon et al., 2002;; Jantzen et al., 2003; Nezafat et al., 2001; Ross, Tkach, Ruggieri, Lieber & Lapresto, 2003; Toni et al., 1998; Van Mier et al., 1997, 1998), often hypothesized to be related to reduction in climbing fiber input resulting from decreasing error signal as learning proceeds (Penhune & Doyon, 2005). Thus, as learning endures, the cerebellar mechanisms seem to be less

necessary for producing accurate responses, pointing towards a more efficient pattern of neural recruitment (Koeneke, Lutz, Wustenberg & Jäncke, 2004). This intuitively indicates that when motor coordination patterns are improved, such as during the cross-pass performance in the present study, cerebellar activation should be reduced.

As the cerebellum is known to be critical to producing complex and coordinated movements (Thach 1998; Imfeld et al. 2009), and is thought to contribute significantly to the generation of forward models (e.g Miall & Reckess, 2001; Thach 1998; Kawato et al. 2003) that are crucial for motor planning and correction, and is also believed to have a key role in time perception and time estimation (e.g. Medina & Mauk, 2002), the training-induced changes of cerebellar activation should also logically influence those movements being modulated by it (the cerebellum). This implies that SMT is a means to influencing action through perception, and possibly, in line with the view of Cassenti (2011), also influencing perception through action.

A different approach to the effects of SMT on cerebellar activation during action observation is related to the specific role of cerebellar purkinje cells. As most movements involve the coordinated activation of agonist muscles to initiate motion and antagonist muscles as a brake, these activations require accurate timing to the order of tens of milliseconds. Indeed, pathologies that disrupt the timing between agonist and antagonist actions lead to dysmetric or inaccurate movements. In concurrence with this notion, Thier et al., (2002) have found that for saccadic eye movements, involving agonist muscles to initiate and antagonist muscles to decelerate movement, the activity of cerebellar purkinje cells precisely encodes the onset and offset of a saccade. Accordingly, lesions of the cerebellum, for example, tend to delay the activation of antagonist muscles causing movements to be hypermetric or to overshoot (e.g. Hore et al., 1991), and have been found to increase variability in repetitive finger-tapping (Ivry, Keele & Diener, 1988). Accordingly, in the present studies SMT might have influenced the agonist and antagonist activation in a way that makes the movement trajectory smoother, more synergetic and with less variability. The findings from Study III support this view, indicating that SMT induces changes to the underlying cerebellar activity during action observation, as well as the concomitant improvements in golf and soccer skill performance (read accuracy and variability).

Conclusions

From the present thesis the following conclusions are made:

First, extensive feedback-based timing training (SMT) enhance the ability of synchronising movements with an externally paced auditory signal (sensorimotor synchronisation), even in high performing athletes, that initially display above average timing and rhythmical skills.

Second, it is evident that SMT can positively influences golf shot precision and the associated variability in golfers with low golf handicap and extensive golf experience (Study I).

Third, the underlying movement dynamics of these golf swing performances, as captured by kinematic analysis, indicated that the spatiotemporal properties of the golf swing became more coordinated – manifested through less variance and with decreasing phase shifts between joint couplings at post-test. This indicates that improved motor timing, as an effect of SMT do have effect on the temporal properties of the upper-body motions of golf swing performance, producing a more coordinated and dynamic swing performance (Study II).

Fourth, positive effects of SMT were found on soccer cross-pass skills, by means of worthwhile improvements in both outcome accuracy and variability. These effects were evident even though the players participating were at the elite-/sub-elite level, and despite the cross-pass task being a highly familiar task, often performed during soccer play (Study III).

Fifth, in Study III, we link observed improvements in SMS abilities and soccer cross-pass performance to training (SMT)-induced changes of neural activity within bilateral cerebellum, and to some extent FFG and STG. The decrease of activation within these areas, hint at a more efficient pattern of neural recruitment during action observation as an effect of SMT. In other words, when the motor coordination patterns of these soccer players are improved as an effect of SMT, the cerebellar (and FFG/STG) activation pertaining to the generation of feedforward models, monitoring and error correction, is reduced.

Taken together this thesis suggests that high performing athletes may be able to further fine-tune performance by means of streamlining the temporal mechanisms underpinning motor coordination and control. Indeed, it has been shown in this thesis that successful/optimal performance of motor skills require a precise coordination and control of numerous muscles and sensors guided by the underlying timing centres in the brain, and that the brain neural activity supporting such performance can be fine-tuned and enhanced through (non-task specific) training, in this case SMT.

Finally, and somewhat in contrast to the common notion that specific physical experience is pivotal for motor representations to develop (see Olsson & Nyberg, 2010 for a review), and that the amount of experience modulates the activity pattern of the AON in action observation tasks, the findings from the included studies suggests that brain activity during action observation of one motor domain (soccer) can be influenced by training in another domain (SMT). This implies that SMT taps into the timing related functions of the cerebellum that may sub-serve 1) the efficiency of feedforward and error correction processes (e.g. Diedrichsen, Hashambhoy, Rane, & Shadmehr, 2005; Bastian, 2006; Wolpert, Miall & Kawato, 1998; Yarrow, Braun & Krakauer, 2009), 2) the development of internal models (Imamizu et al., 2003), 3) the acquisition and integration of sensorimotor integration (Bloedel, 1992; Bower, 1995; Thaut, Demartin & Sanes, 2008) that allows predictions about the consequences of motor acts to be made, and enables subsequent motor planning (Miall, 2003), Hence, it facilitates movement timing (e.g. Ivry, 1996; Balasubramanian & Wing, 2004) and the coordination of complex movements (e.g. Thach 1998; Imfeld et al., 2009; Roberts, Bain, Day & Husain, 2012).

Implications

It was concluded that 12 sessions of *non-sport specific timing training* (SMT) seemingly induce changes in the spatio-temporal properties of action execution (golf swing performance) and improve outcome accuracy and variability in both golf and soccer, do have a number of interesting implications. First, it seems obvious that SMT constitutes an efficient complementary training method for golf and soccer during periods of limited and/or impaired sensory motor functions, as well as during off-season. Second, as SMT seems to improve timing skills and movement performance by fine-tuning the timing components (and coordination dynamics) of multijoint movements, this type of training may also be used to improve performance in other activities that require precise (and/or increased) timing abilities.

Finally, the effects of SMT on the activation patterns of the cerebellum (as well as the fusiform gyrus and STG) during action observation imply that AON activity – that has been proposed to facilitate both understanding and inference of intention of observed motor acts (e.g. Rizzolatti & Craighero,

2004) – can be altered and possibly streamlined (made more efficient) by means of SMT. This also suggests that AON activation may be influenced in other ways than through task-specific training (e.g. Calvo-Merino et al., 2005) or observational learning (e.g. Cross et al., 2013). Such knowledge of how SMT can alter brain activity within the AON may be important to enhance training techniques within sports, as well as for enhancing rehabilitative techniques for a number of clinical populations.

Limitations

The studies contained in this thesis have some limitations. Study II would have benefited from an control group in order to be able to evaluate the underlying movement kinematics of golf swing more thoroughly. Second, the sample sizes in all studies are to be considered small. However, the results are strengthened by the fact that the findings were highly comparable in the two different cohorts. Still, replications with larger sample sizes are warranted, especially considering the findings from the fMRI paradigms in Study III. Furthermore, in regard to the action observation paradigm, the orientation of the body of the observed player may have affected neural activity; Kilner, Marchant and Frith (2006) showed that MNS activity in action observation was higher when the actor faced towards the observer than when the actor showed their back to the observer. In the stimuli of the present experiment, the player showed her back to the outcome for the observed motor action.

In Study I, one concern is the lack of a true non-intervention control group. It seems plausible that the swing training group, presented with more restrictive and prescriptive swing dynamics than their prior-established responses, could have caused a temporary decline in their performance on the golfing accuracy task: assuming their swing characteristics were not perfectly in tune with those defined by the Explanar, they might well have reverted from what Fitts and Posner (1967) would have called an autonomous stage to a cognitive or associative stage of skill learning for their swing. Hypothetically, it could have been that the IM intervention had no impact on golf swing per se, and that the improvement observed is due to test familiarity, i.e. that the default for a reasonably experienced group would be to get used to the simulator and score higher on the second occasion. With this view the control group may have (temporarily?) been hindered in their ability to improve because they are attempting to apply their new swing dynamics. This is in line with the dynamic systems approach to how (motor) systems can change over time, as a consequence of destabilised patterns disappearing and new patterns emerging (Kelso, 1995).

In a similar fashion to the control group issue raised above, the one-group, between-test design utilised in Study II poses a similar challenge to the validity of the results.

Another issue is the fact that none of the three studies included in the present thesis utilised a retention-test to assess whether the effects of the SMT diminishes or is consolidated over time. However, the brain imaging data from Study III suggests that the SMT regimen exploits the natural plasticity of the brain to promote the development of new patterns of brain activation (or pathways), and thus, possibly, facilitates increased brain communication efficiency (McGrew, 2013). As the brain of these participants utilises these new patterns or pathways in their sporting activities, I believe the effect of the training is reinforced and refined, rather than diminished, over time.

Future prospects

Future research will be necessary in order to further delineate the effects of SMT, based on the limitations mentioned above. Moreover, it would be of great importance to develop motor timing theories that are based on investigations made on sport-specific performances, rather than applying theories based on finger-tapping and/or circle-drawing studies to sport performances.

If indeed SMT improves temporal skills and movement performance by finetuning the timing components (and coordination dynamics) of multi-joint movements, then this type of training may also be used to improve performance in other activities that require precise (and/or increased) timing abilities. Thus, the effects of SMT should be further delineated with regard to sports that involve interceptive tasks, in which the timing of the individual's own motor action is dependent on the approach of a ball (e.g. tennis and cricket) or the actions of an opponent (e.g. fencing and boxing).

We did examine the immediate effects SMT had on skill performance and brain activity during action observation, but it is possible that the intervention does not provide long-lasting effects in this population, and this should be addressed in future investigations. Also, as the sample of players in the present study entailed elite and sub-elite soccer players and skilled golfers, one may speculate that the gains from SMT on accuracy and variability of the cross-pass outcome would most likely be even better/higher for less experienced or lower level players

Finally, it is worth noting that the IM apparatus is still a 'black-box', in the sense that it is not clear from the IM training whether more repetitions would

bring about greater impact on skill performance as well on neuronal activation patterns. Also, we do not know if similar results may be obtained with fewer repetitions, shorter sessions, other exercises, different reference beat tempos, or individually tailored training programs. Thus, these are important aspects of future research on the effects of timing training within a sport context.

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