VILNIUS UNIVERSITY

LIFE SCIENCES CENTER

INSTITUTE OF BIOSCIENCES

Masters of Neurobiology, II course student

Egidijus LINKEVIČIUS

Master thesis

The influence of proprioception on precision of goal-directed arm movements

Thesis supervisor:

Prof. dr. A. Alaburda

Vilnius 2020

The influence of proprioception on precision of goal-directed arm movements

Thesis prepared at

Vilnius University, Life Sciences Center, Institute of Biosciences

Egidijus LINKEVIČIUS /________/

Supervisor:

Prof. dr. A. ALABURDA /________/

TABLE OF CONTENTS

ABBREVIATIONS

CNS	Central nervous system
EDS	Ehlers - Danlos syndrome
GTO	Golgi tendon organs
PMd	Dorsal premotor cortex
PMv	Ventral premotor cortex
PPC	Posterior parietal cortex

INTRODUCTION

Sensation of limb position provides crucial information for the control of the limb movements and overall interaction with the environment (Fuentes & Bastian, 2010). This leads to proprioception playing an important role in goal directed movements. However, proprioception is affected by noise of the nervous system, which causes problems with information processing and makes the information gathered from proprioception imprecise (Marini et al., 2016; van Beers et al., 2002). The imprecise perception of the body limbs can cause errors in later stages of movement generation and lead to imprecise movements (van Beers et al., 2004). This raises a question, how imprecision of proprioception influences precise movements.

Even though information from the proprioception is imprecise, goal directed movements are constantly updated by feedback loops, which let evaluate the consequences of given motor commands and correct the ongoing movements (Desmurget & Grafton, 2000; Neggers & Bekkering, 1999). This leads to CNS adaptability to choose movements that are less influenced by noise and avoid the ones that provide high variability in the given task (Thorp et al., 2017). This suggest that CNS shapes the movements to compensate the impreciseness of proprioception and result in precise movements.

In this study, a dart throwing model will be used to illustrate how potential proprioception errors may influence task completion success rates, as dart throwing is a simple action that requires high movement precision, it is driven mainly by the upper limb and it is less affected by the muscle fatigue, as darts are very light (Tamei et al., 2011).

Aim and Objectives of the Study

The aim of this study is to evaluate the influence of proprioception on precision of arm movements in dart throwing.

In order to achieve this aim, three objectives were formulated:

1. To create a model of arm movements in dart throwing.
2. Evaluate the influence of proprioception imprecision on precision of arm movements in dart throwing.
3. Evaluate the dart throwing strategies to compensate the impreciseness of proprioception.

ROLE OF PROPRIOCEPTION IN GOAL-DIRECTED MOVEMENTS

1.1. The sense of position and movement

Many movements generated in daily-life involve combining visual information about a target with proprioception and visual information about the effector (Kuling et al., 2016). For example, when picking a mug, visual information provides the location of the mug (the target), which is combined with the visual and proprioceptive information about the position of the hand (the effector). Limb movements and changing of limb positions causes deformation of the tissues around relevant joint that include skin, muscles, joint capsules, fascia and ligaments (Proske & Gandevia, 2012). These tissues are innervated by mechanically sensitive receptors and provide a combination of multiple information sources to the brain (Fuentes & Bastian, 2010; Kuling et al., 2016; Proske & Gandevia, 2012). The combination of sources is beneficial since it separates the judged position of the limb from external forces, and thus, giving the ability to move to specific position, while carrying the weights of held objects (Kuling et al., 2016).

Proprioception – the sense of body position and self-movement in the absence of vision – is an essential ability in order to successfully control movements and interact with the environment (Fuentes & Bastian, 2010; Moscatelli et al., 2019). The receptors that provide conscious information about the proprioception are known as proprioceptors and these senses include the sense of limb position and movement, tension or force, effort and balance (Proske & Gandevia, 2012). There are four main types of proprioceptors that provide information about the movement and position of the limb: muscle spindles, Golgi tendon, joint receptors, and skin receptors.

1.2. Muscle spindles and Golgi tendon

Muscle spindles and Golgi tendon organs (GTO) are receptors that send signals to the brain regarding the changes in the muscle, i.e. muscle spindles contribute to sensing length and velocity of the muscle, while GTO send signals about the force and heaviness of the muscle - muscle stretches depolarize these receptors and muscle contractions decrease activity of the receptors (Fuentes & Bastian, 2010; Prochazka, 2015; Proske & Gandevia, 2012).

Muscle spindles surround muscle fibers that produce the forces for bodily movement (see Fig. 1.1a). Within the muscle spindles there are Gamma motoneurons, who are activated by fusimotor neurons that cause these motoneurons to pull on spindles that contain stretch-sensitive spindle group Ia and II afferents (Prochazka, 2015). In the absence of a muscle length change *static* fusimotor neurons increase activity of group Ia and II afferents. Also, *static* fusimotor neurons control Ia afferent sensitivity to muscle length changes, while *dynamic* fusimotor neurons are responsible for II afferents (Prochazka, 2015). Less is known about *dynamic* fusimotor neurons influence on afferents.

Golgi tendon organs, unlike muscle spindles, do not modulate their sensitivity (Prochazka, 2015). GTO are tension-sensitive receptors that provide information about muscle tension by Ib afferents to the CNS (Mileusnic & Loeb, 2006). They are located at the myo-tendinous and myo-aponeurotic junctions of skeletal muscles, where Ib fibers intertwine with collagen fibrils, which are connected to tendon or aponeurosis at one end and muscles fibers at the other end (Fig. 1.1b) (Jami, 1988; Mileusnic & Loeb, 2006). The contraction of these muscle fibers cause stain in collagen fibrils, which leads to deformation of sensory terminals, making tendon organs efficient in signaling fast variations of contractile force (Jami, 1988). The firing rate is summed with several Ib afferents and this information is carried by afferent neurons from tendon organs (Jami, 1988; Prochazka, 2015).

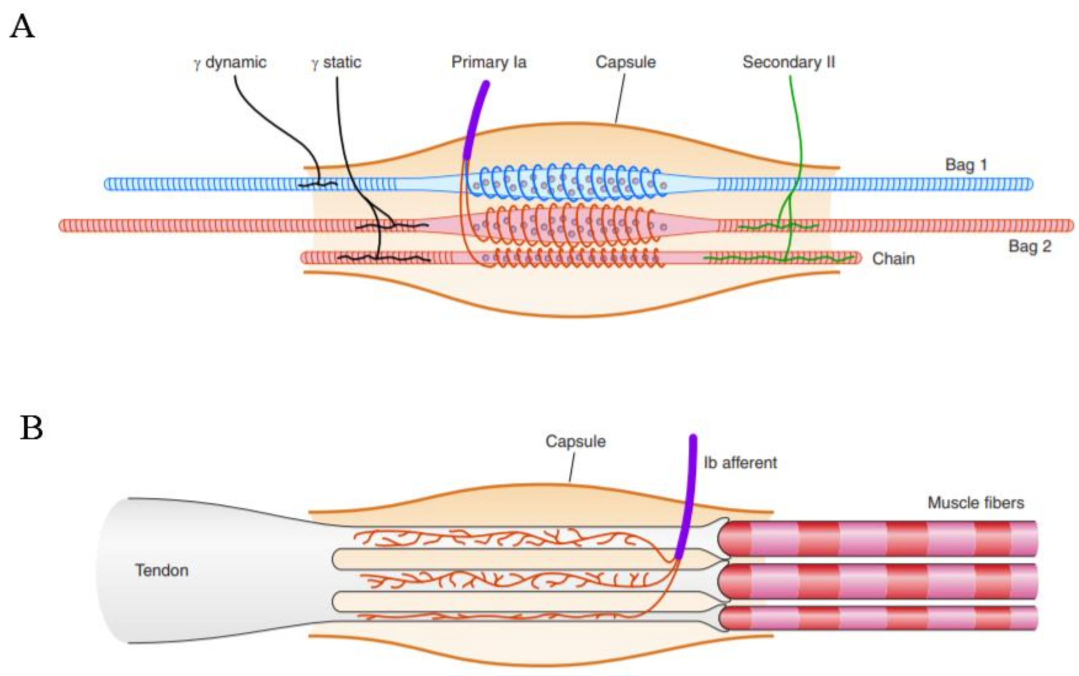

Fig. 1.1. Representation of muscle spindle and Golgi tendon organ. **(A)** Muscle spindles consist of group Ia afferents, which spiral around γ-dynamic and γ-static fusimotor fibers, and group II afferents, which innervate γ-static fusimotor fibers. Muscle spindles are located inside of a capsule. **(B)** Golgi tendon Ib afferent inside the capsule intertwine with collagen fibrils that are connected with tendon on one side and muscle fibers on the other (Adapted from Proske & Gandevia, 2012).

It is argued that feedback from Group Ia/II muscle spindle afferents and Group Ib Golgi tendon afferents play the major role in proprioception (Clark et al., 1985; Fuentes & Bastian, 2010; Proske & Gandevia, 2012; Proske, 2015). Feedback from muscle spindles alone provide information about changes in muscle length, making it a poor controller for joint position and movement, and thus, only a combination of spindles and Golgi tendon afferents can be effectively used for feedback during movement and postural tasks (Kistemaker et al., 2013). When muscle is stretched, proprioception activity increases and brain interprets that muscle length increased, and this results in a sensation that joint is flexed or extended (Tsay et al., 2014). Adaptation processes, however, causes gradually fading sensation, meaning that over time muscles can be interpreted as becoming shorter; for example, elbow flexor muscles could be perceived as indicating more flexed elbow and elbow extensor muscles – a more extended elbow (Tsay et al., 2014).

1.3. Joint receptors

According to Newton (1982) there are four types of joint receptors:

1) Type I mechanoreceptors provide information to the CNS in resting and active conditions and they activate upon joint movement, muscle contraction or joint pressure gradient.
2) Type II receptors respond to joint movement and send two bursts of action potentials to signal the beginning and the end of the movement.
3) Type III receptors usually are inactive and respond only to extreme ranges of active or passive movements.
4) Type IV receptors remain inactive until extreme mechanical deformation or chemical/ mechanical irritations of the joints are present.

During movement joint rotation stretches the joint capsule and this leads to activation of mechanoreceptors, specifically Ruffini-like receptors (Type I), which detect speed and direction of movement, and Paciniform receptors (Type II), which detect small and accelerating movements (Newton, 1982; Proske & Gandevia, 2012). However, most of the afferent joint receptors respond to extreme ranges of the joint movements, which makes their position signaling ambiguous (Fuentes & Bastian, 2010; Newton, 1982; Proske & Gandevia, 2012). For example, it has been found that elbow angle estimates are biased towards extreme positions (Fuentes & Bastian, 2010). It is believed that this could prevent movements beyond a joint's range of motion, since a research showed that there is a greater chance of incorrectly perceiving elbow angle when the arm is farther away from the visual workspace, meaning that this bias estimation protects system from harmful extensions of the limbs (Fuentes & Bastian, 2010).

Even though an experiment (Clark et al., 1985) showed that joint anesthesia provided no noticeable difference on the ability to detect movements, which would indicate that joint receptors' role on proprioception is insignificant, Proske and Gandevia (2012) disagreed by arguing that under some circumstances skin and joint receptors provide more important input than muscle spindle afferents. During circumstances where muscular receptors are unable to detect movements of the limbs, slowly adapting receptors within the joint capsule, such as Type I, III and IV joint receptors, mediates part of remaining kinaesthetic performance (Ferrell et al., 1987; Newton, 1982).

1.4. Skin receptors

Although it was believed that the main role of touch is to gather information about the properties of the external world, skin receptors can act both as proprioceptors and exteroceptors (perceive status of the external world) (Moscatelli et al., 2019; Proske, 2015). Interaction with external object causes deformation in the skin, which provides information about body position (Moscatelli et al., 2019). For example, in the conditions, where the environment has known or assumed properties, cutaneous signals guide movements toward the desired targets, in other words, when searching for the light-switch in the dark, contact with specific characteristics of the wall can provide information about the position of the arm (Moscatelli et al., 2019).

Also, mechanoreceptors in the skin respond to stretch of the skin due to flexion or extension of the joints (Collins et al., 2005; Fuentes & Bastian, 2010; Moscatelli et al., 2019; Proske & Gandevia, 2012; Proske, 2015). Joint rotation causes nearby skin to tighten on one side of the joint and loosen on the other side, and thus, this deformation stimulates mechanoreceptors in the skin (Fuentes & Bastian, 2010; Proske & Gandevia, 2012). There is a linear relationship between cutaneous afferent activity and joint rotation, meaning that as a joint approaches extreme position, cutaneous receptors signaling increases because skin will be most stretched in the extreme position (Fuentes & Bastian, 2010).

Even though cutaneous receptors accurately inform joint position and movement (Collins et al., 2005), their contribution to position sense is considered to be less important than the input from muscle spindles (Proske & Gandevia, 2012). It was believed that cutaneous receptors are important for perception of distal joints, i.e. perception of finger movements because cutaneous receptors are necessary to identify individual joint angles (Collins et al., 2000). However, it has been found that proximal and distal cutaneous feedback is integrated with muscle receptor feedback in order to provide information of joint position and movements (Collins et al., 2005). Also, the research conducted by Kuling and colleagues (2016) indicated that although muscle spindles and joint receptors produced normal afferent information, subjects perceived a difference in the position of the hand when the skin receptors were inhibited. This suggest that skin receptors are an important factor in sensing the position of the limbs (Kuling et al., 2016).

CONTRIBUTIONS OF VISION AND PROPRIOCEPTION TO THE CONTROL OF GOAL-DIRECTED ARM MOVEMENTS PRECISION

Some movement or position senses are independent of task demands and for this reason they are controlled by peripheral proprioceptive signals. On the other hand, there are tasks that require precise movements or position senses, and thus, they depend on brain integration of sensory and motor signals (Fuentes & Bastian, 2010). In order to perform a precise movement, motor commands require information from the environment and from the arm. Information about the position and movement of the arm are gathered from proprioceptors (muscle spindles, Golgi tendon organs, joint receptors and skin receptors) and vision (Neggers & Bekkering, 1999; Sober & Sabes, 2003; Touzalin-Chretien et al., 2010). It is believed that in estimating hand position and gathering information from the environment the major role is played by the visual system (Touzalin-Chretien et al., 2010). Information from the vision needs to be transformed into motor commands (Blohm & Crawford, 2007; van Beers et al., 2002). This transformations undergoes three stages (Blohm & Crawford, 2007; van Beers et al., 2002):

1) Brain constructs internal representation of arm and target positions.
2) Arm and target positions are compared and transformed to motor commands.
3) Muscle contractions are generated.

2.1. Estimation of arm position

Before producing a goal-directed movement, position of the arm and the target should be estimated by integrating signals from the proprioceptors and vision (Sober & Sabes, 2003; Touzalin-Chretien et al., 2010). This estimation is required in order to determine the desired movement vector and to transform the movement vector to motor commands (Blohm & Crawford, 2007; Sober & Sabes, 2003). The movement vector is computed by finding the difference between estimated initial arm position and target location and adding behavioral constraints (Listing's law and Donders' law) (Blohm & Crawford, 2007; Sober & Sabes, 2003). These constraints sets a full orientation of the eyes and the head and help to determine the relationship between desired movement vector and retinal signaling (Blohm & Crawford, 2007).

Bellan et al. (2015) showed that participants first localized their hands towards the last seen location of their hands, proving that the vision plays dominant role in localizing arm position and can bypass the information about the limb position from the proprioception (Bellan et al., 2015; Touzalin-Chretien et al., 2010). However, in a research conducted by Clayton, Jones and Henriques (2015) precision of hand position relative to a visual reference of subjects with Ehlers – Danlos syndrome (EDS) was tested. EDS is similar to joint hypermobility syndrome and is characterized by musculoskeletal complaints (joint and/ or spinal pain), joint instability (dislocation or subluxation) and soft tissue injuries, meaning that they may have proprioception impairments (Clayton et al., 2015; Gazit et al., 2016). It was found that EDS patients were able to locate their hand as accurately as the control group, however their precision was significantly worse than healthy subjects (Clayton et al., 2015). This research shows that people with proprioception impairment are not able to precisely locate their limbs, which implies the necessity of proprioception in arm localization. This suggests, that both visual and proprioceptive information may be used to estimate the position of the arm.

Visual and proprioceptive integration encoding arm movement may seem redundant, however this feedback provides an ability to the brain to weight each signal and evaluate their relative precision (Sober & Sabes, 2003). For example, Izumizaki and colleagues (2010) conducted an experiment, where they measured accuracy between subjects, who gathered information only from visual system and only from proprioceptors. The research indicated that in different situations vision and proprioception were used interchangeably to determine limb position. More specifically, when subjects saw their indicator arm moving into matching position, the accuracy improved insignificantly regarding being blindfolded. However, when the same task was provided entirely visually, the accuracy was significantly better (Izumizaki et al., 2010). This indicates that the brain is possibly weighting the signals from both sensors and evaluate which provides more information. When visually perceived arm position differs from the actual position, the reliability gradually shifts over time from the visually encoded information to proprioceptively encoded information in order to increase accuracy in localizing the real arm position (Bellan et al., 2015; Sober & Sabes, 2003; Touzalin-Chretien et al., 2010).

By integrating the information gathered from vision and proprioception, the brain is able to accurately represent position and movement of the limbs (Han et al., 2016; Limanowski & Blankenburg, 2016). In their study Limanowski and Blankenburg (2016) indicated that posterior parietal cortex (PPC) and ventral premotor cortex (PMv) encode the position of upper limbs (Fig. 2.1), where PMv represents "higher-level" functions and PPC integrates multisensory information. Also, PPC is believed to provide gaze-centered representation, which is known as representation of the object's position in space relative to their location on retina (Blohm & Crawford, 2007). This representation plays an important role in goal-directed movement planning and memory by providing arm position signal (Blohm & Crawford, 2007).

2.2. Visuomotor transformation

For goal-directed movement to reach the target, it is necessary that visuomotor transformation generates motor commands. This transformation is mediated by neurons located in PPC and PMd (Fig. 2.1), which provide information about the target and upper limb position (Fujiwara et al., 2017). It could be suggested that PPC integrates information from the vision and proprioception about arm position and sends a motor command via dorsal pathway from the PPC (Fujiwara et al., 2017; Limanowski & Blankenburg, 2016; Sober & Sabes, 2003). However, PPC is believed to only be involved in the later phases of corrective movements, suggesting primary movement to be mediated by visual information through superior colliculus via reticulospinal pathway (Gu et al., 2017). Dessing et al. (2009) have found that movement biases toward the eyes are being generated, while the representation of the target is being evaluated.

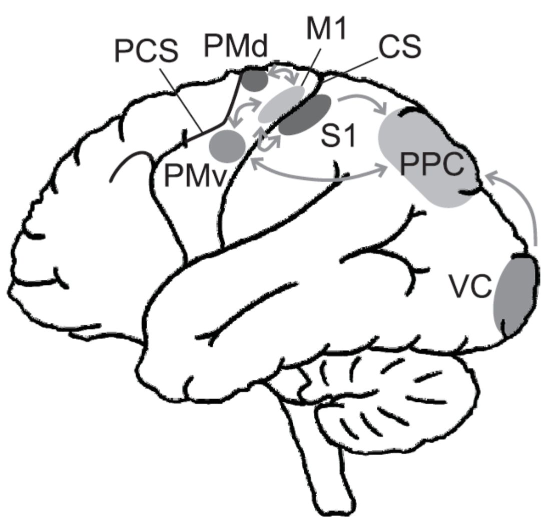

Fig 2.1. Representation of visuomotor transformation areas. Visual cortex (VC); posterior parietal cortex (PPC); central sulcus (CS); precentral sulcus (PCS); primary somatosensory area (S1); primary motor cortex area (M1); ventral premotor cortex (PMv); dorsal premotor cortex (PMd) (Adapted from Blohm & Crawford, 2007).

The visual system gathers external information through retina and produces movement direction and distance from the initial arm position to the target in retinal coordinates (r*R*) (Fig. 2.2) (Neggers & Bekkering, 1999; Sainburg et al., 2003). Movement direction is represented by a vector with a origin at the current arm location, whilst movement distance is affected by the recent experiences in workspace range, and thus is being planned before the movement (Blohm & Crawford, 2007; Sainburg et al., 2003; Sober & Sabes, 2003). Since arm movement directions are relative to the position of the shoulder, a shoulder-centered representation of the motor plan is necessary (Blohm & Crawford, 2007). This transformation could be related to the projections from the PMd to M1 (Blohm & Crawford, 2007; Fujiwara et al., 2017).

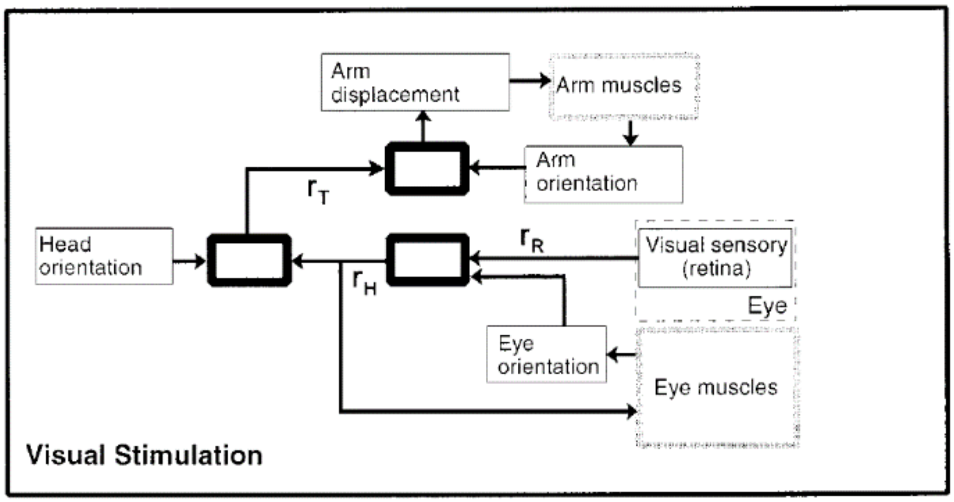

Fig. 2.2. A scheme of visual information transformation to arm movement. The signal r_R represents the target position in retina; r_H represents the target with respect to the head; r_T represents the target with respect to the trunk (Adapted from Neggers & Bekkering, 1999)

The brain takes into account extraretinal signals to compensate 3D eye misalignment coordinates and head rotation in order to transform the visual information of the target into target position with respect to the trunk (r_T) (Leclercq et al., 2012; Neggers & Bekkering, 1999). With regards to the arm displacement, this signal can provide muscle contractions to move the arm to the target. Due to inaccuracies in compensating extraretinal signals and biases, the visuomotor transformation may differ among individuals (Dessing et al., 2009; Leclercq et al., 2012).

2.3. Errors in vision and proprioception

Goal-directed movements are initially planned, and this plan is constantly updated by feedback loops (Desmurget & Grafton, 2000). These loops integrate the information from the vision, proprioceptors and present motor condition and evaluate the consequences of given motor commands and guide ongoing movements, providing the ability to make precise aiming movements in changing environment (Desmurget & Grafton, 2000; Neggers & Bekkering, 1999).

The visual information about initial hand location is primarily used for planning movement distance and specifying direction of targeted movements (Bagesteiro et al., 2006; Lateiner & Sainburg, 2003; Monaco et al., 2010; Sainburg et al., 2003).

Proprioception, on the other hand, provide information necessary to determine the duration of initial acceleration, which also scaled with peak velocity and movement distance (Bagesteiro et al., 2006; Lateiner & Sainburg, 2003; Marini et al., 2016; Monaco et al., 2010; Sainburg et al., 2003). The proprioceptive information is used for corrections of rapid and unseen movements (Bagesteiro et al., 2006). Complex signals from proprioception are transferred via large-diameter myelinated axons of these receptors through the spinal cord, where they branch to spinal gray matter and ipsilateral dorsal column of medulla, which reach thalamus that connects with the primary somatic sensory cortex, where the perception of target position is being established (Kandel et al., 2013; Marini et al., 2016; Proske & Gandevia, 2012). However, sensory signals, necessary for sensorimotor transformation, are corrupted by noise and penetrate every level of nervous system, causing problems for information processing (Marini et al., 2016).

Errors arises in every step of directed arm movements. They can occur due to incorrectly estimating target or present arm position and this incorrect estimation will influence later levels of visuomotor transformation, causing movements to be imprecise (van Beers et al., 2002). There are three stages for errors to arise in: localization, planning and execution (van Beers et al., 2004).

While it was found that the mean endpoint of the movement variance reached 68 mm^2, it has been estimated that motor systems can detect eye position smaller than 0.5° arc, which would transfer to visual localization uncertainty being smaller than variance of 20 mm^2, which could get even smaller due to ability to continuously gather visual information about the current arm and target locations and integrate it with the information provided via proprioception (Hansen & Skavenski, 1977; van Beers et al., 2004). However, it should be considered the location of the target, since the 0.5° arc eye uncertainty transfers to higher variances for the targets that are further away, meaning that precision decreases with increasing distance, leading to visual system being less precise in judging distance than direction (van Beers et al., 2002, 2004). It is *vice versa* for proprioception, since it is more precise in localizing in distance than in azimuth, even though the precision decreases with increasing distance from the shoulder (van Beers et al., 2002).

Errors in movement planning decrease with motor adaptation and sensory recalibration, as this allows to refine motor commands that are sent to the muscles (Barkley et al., 2014; van Beers et al., 2004). As mentioned, the brain integrates information from the vision and proprioception (Bellan et al., 2015; Sober & Sabes, 2003; Touzalin-Chretien et al., 2010). This lets the brain to recalibrate proprioception based on available visual information and to compensate localization information for the head-roll rotation, static ocular counter-roll and misalignment between spatial and retinal coordinates (Barkley et al., 2014; Leclercq et al., 2012; Thorp et al., 2017). However, this compensation in not perfect because the head-roll angles can be overestimated and ocular counter-roll angles can be underestimated (Leclercq et al., 2012).

It is believed that noise in movement execution causes main variability in movement endpoint because this noise combines noises in magnitude and in duration of motor output (van Beers et al., 2004). This implies that successful goal directed arm movement depends on chosen trajectory of the arm movement, which is driven by noise minimization (Thorp et al., 2017; van Beers et al., 2004).

Errors that occur at different levels of visuomotor transformation can change between different individuals (Dessing et al., 2009). This may happen due to CNS ability to learn to choose movements that are less affected by noise (Thorp et al., 2017). An experiment conducted by Thorp et al. (2017) showed that CNS form control policies in a manner that avoids movements that are responsible for task-specific variability. This can be useful for shaping the learning of high-dimensional movements, however, improvements of such learning are mainly observed in the initial adaptation period (Kuatsjah et al., 2019; Thorp et al., 2017).

DART-THROWING FOR EVALUATION OF PRECISION OF PROPRIOCEPTION

Goal directed movements are highly variable, even though the movement may be trained and performed in constant conditions (Loosch, 1999). However, it was shown that in sports activities, for example basketball throwing (Sevrez & Bourdin, 2015), table tennis, fencing (Bańkosz & Szumielewicz, 2014), etc., people manage to decrease their movement variability, meaning that they can provide precise and accurate movements. It was found that the precision of the movement is related to the level of proprioceptive ability since higher movement precision requires higher sensitivity of perception of the limbs (Bańkosz & Szumielewicz, 2014; Sevrez & Bourdin, 2015). This implies an ability to transfer precision of one movement to another in the same limb as it was shown in an experiment conducted by Rienhoff et al. (2013), who found that more accurate basketball player were also more accurate in dart throwing.

As it was suggested that precision is interchangeable between similar movements in the same limb, in order to evaluate the influence of proprioception on precision of movements, it was decided to study dart throwing for couple of reasons: dart throwing is a simple action that requires high movement precision, it is driven mainly by the upper limb and it is less affected by the muscle fatigue, as darts are very light (Tamei et al., 2011).

Dart throwing involves a wrist motion, called dart-throwing motion (DTM), which is a movement in oblique axis from a radially deviated-extended position to flexion and ulnarly deviated position (Leventhal et al., 2010; Vardakastani et al., 2018). However, more body parts may be involved in throwing movement depending on the throwing distance, i. e., short distances require force that could be generated solely by elbow muscles, while further distances require more force that could be generated by implementing muscles of upper and lower body (Nakagawa et al., 2015; Sevrez & Bourdin, 2015; Tumialis et al., 2020). More specifically, in a longer dart throw joints in ankle, knee, hip and shoulder sum their individual speeds of their motions through interactions between the joints and pass the speed to the distal joints (Nakagawa et al., 2015; Sevrez & Bourdin, 2015). While the correlation of proximal joints generate the force needed for the throw, distal joints (elbow, wrist and fingers) regulate the velocity and angle of projection of the dart throw (Nakagawa et al., 2015; Sevrez & Bourdin, 2015).

For a consistently successful dart throwing, the throwers need to correctly localize the target and the arm, plan and execute the movement (Sarlegna & Sainburg, 2009; Sevrez &

Bourdin, 2015; van Beers et al., 2004). Visual information is mainly used in primary stages to define the kinematic plan, while execution of this plan is based on proprioceptive information (Sarlegna & Sainburg, 2009). This leads to proprioceptors organizing compensatory behavior between joints in the body in order to stabilize the endpoint position of the throwing limb (Fuentes & Bastian, 2010; Nakagawa et al., 2015; Sevrez & Bourdin, 2015). Proprioception could support compensatory variability and reduce the scattering of the movement outcome due to variability in movement performance (Loosch, 1999; Sevrez & Bourdin, 2015).

The result of the thrown dart can be determined by combining the velocity, position and direction of the motion in the time of dart release (Nasu et al., 2014). These parameters are influenced by the hand trajectory of the throwing arm and the release timing (Nasu et al., 2014). Subjects in the same skill level can have different joint torque patterns that are based on their throwing form, preferred speed and different body parameters (Tamei et al., 2011). Different joint torque patterns as well as different distance and self-body height estimations may require distinct generation of muscle forces, which can cause decrease in precision of specific movements (Smirnov et al., 2019; Tumialis et al., 2020). This leads to two dart throwing strategies being implemented.

One strategy involves a pre-planned hand trajectory moving in a high speed that compensates timing variability (Nasu et al., 2014; Tran et al., 2019). The hand moves in a small radius of curvature and the dart is being released close to the zenith of the hand’s path while the dart flows in a straighter line and is less affected by the gravity (Nasu et al., 2014; Smeets et al., 2002; Tran et al., 2019).

Another strategy relies on reduced timing variability, meaning that the dart is thrown with a lower speed and in a higher arc to compensate the influence of gravity (Nasu et al., 2014; Tran et al., 2019). This strategy reaches timing error as low as 1 ms (Nasu et al., 2014).

As these dart throwing strategies come from differences of the throwers, this suggests that the dart throwing strategies may be used to compensate the imprecision of proprioception in dart throwing movements.

METHODS

In order to evaluate the influence of imprecision of proprioception on the precision of the movements, a dart throwing model was proposed (see Fig. 4.1). The model is based on equations that were analytically conducted and were derived from the basic laws of physics. The calculations for the study were done using Microsoft Excel 365, by manipulating the variable's values it was possible to observe changes in the graphs, which were interpreted throughout the study.

At first, the velocity needed to perfectly hit the target was calculated using:

$$V^2 = \frac{g(l_0+l_a)^2}{2\cos\alpha\sin\alpha(l_0+l_a)-2\cos\alpha^2[H-(h_0+h_a)]}, \quad (1)$$

where V – velocity, α – release angle, h_a – length between the elbow and the dart, h_0 – height at which the elbow is being held, I_a – distance between the elbow and the dart, I_0 – distance between the elbow and the target, g – gravity, H – height at which the dart lands. Then the values of this velocity were used to predict where the dart will land, while accounting for error in the velocity and/or to the angle of the throw.

Parameters

Values of the parameters were taken based on World Darts Federation (WDF) rules, with all the parameters regarding the dart thrower themselves being standardized.

The distance between the throw line (the elbow of the throwing arm in this case) and the target (I_0) is 2,37 m in accordance with the rules of the WDF (*WDF Rules – WDF*, n.d.). However, in this model the distance is increased up to 6 m to include more body parts in the throw and increase the duration of the throw movement, as this would increase the influence of proprioception on the results of the throw (Eduardo Campos et al., 2019; Nakagawa et al., 2015).

Target

The target has set boundaries, consisting of the bullseye (which includes both red and green circles) in the center of the circle and several outer layers extending outwards from it, if the dart lands at the designated “bullseye” - the throw is counted as successful. According to the rules of WDF, the height of the bullseye on the dartboard (H_0) should be 1,73 m from the ground and 3,2 cm in diameter (D) (*WDF Rules – WDF*, n.d.). Hits that land outside of this border are counted as errors with a value depending on the landing distance from the center of the target.

RESULTS

Model

The model was made to predict where the dart will land when a throw is performed with different values of the parameters. Figure 5.1 illustrates all parameters in the model with their values according to WDF.

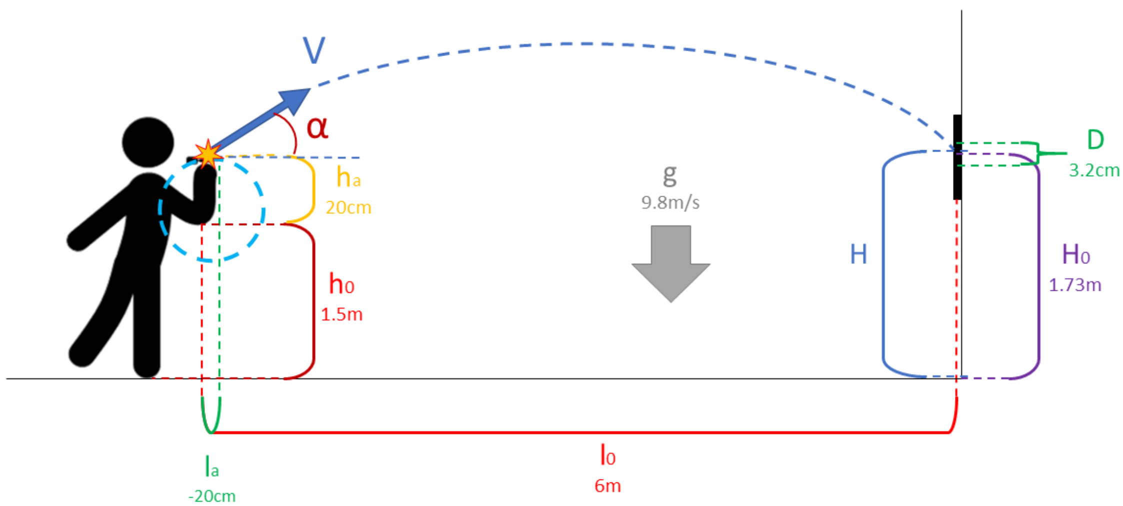

Fig. 5.1. Parameters in the model and their values (V – velocity, α - angle, h_a – length between the elbow and the dart, h_0 – height at which the elbow is being held, I_a – distance of arm leaning back before the throw, I_0 – distance between the elbow and the target, g – gravity, H_0 – height at which the target is present, H – height at which the dart lands, D – width of the target).

This model takes into account only vertical axis for several reasons. Firstly, professional dart throwers' results of their throws mostly scatter in a vertical axis (Loosch, 1999). This suggests that there are no external factors in horizontal axis that affect the dart once it is released and dart throwers learn to throw with little distribution, which increases difficulty in evaluating proprioception influence. Secondly, horizontal axis is independent of the speed of the throw (Smeets et al., 2002). Finally, including the horizontal axis increases the complexity of the model, but provides little additional information regarding the precision of the throw.

In this model, the dart thrower gathers information required for the throw, such as their current height in relation to the target, distance from the target and the height of the target itself, via the visual system (Bagesteiro et al., 2006; Lateiner & Sainburg, 2003; Monaco et al., 2010; Sainburg et al., 2003). It is assumed that the dart throwing movement consists of the throwing arm moving in a circle at a constant speed, with the elbow acting as the anchor in the center. The movement culminating with the release the dart at a specific time. Once the dart is released, it moves in a parabolic trajectory at the same speed throughout the flight without being affected by air resistance, to any meaningful degree, until it reaches the target. Assuming that the dart is released at 90° angle between the throwing arm and the dart, the angle of the dart release (α) depends on the location the arm reaches in the circle at the moment of release (see Fig 5.2).

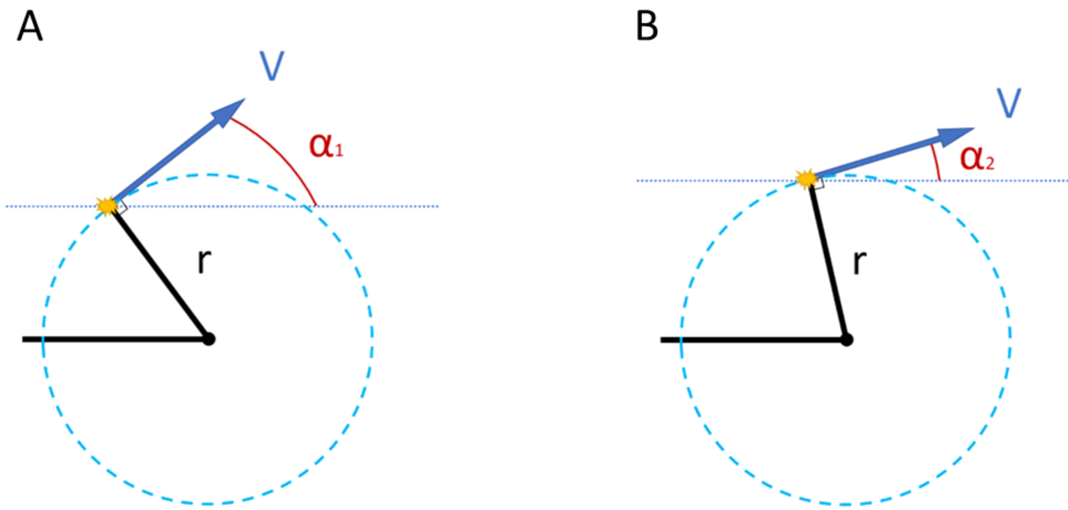

Fig. 5.2. Model of arm releasing a dart ($\alpha_1 > \alpha_2$) (V – velocity, α - angle, r – length of a forearm). **(A)** When dart is released early, the angle of the throw is high. **(B)** When dart is released late, the angle of the throw is low.

The dart lands on the target depending on the velocity (V) of the dart movement and the angle at which the dart was released (α). Both velocity and the angle of the dart throw are influenced by proprioceptive information, which suggests that the velocity and the angle are affected by the imprecision of proprioception. In other words, to successfully land a throw, a dart thrower needs to control the velocity and the angle of the throw.

The location where the dart lands with a throw is calculated by a derivative of formula (1):

$$H(V,\alpha) = (h_0 + h_a) + \tan\alpha\,(l_0 + l_a) - \frac{g(l_0+l_a)^2}{2V^2\cos\alpha^2}, \quad (2)$$

where H – height where the dart lands, V – velocity, α – release angle, h_a – length between the elbow and the dart, h_0 – height at which the elbow is held, I_a – distance between the elbow and the dart, I_0 – distance between the elbow and the target, g – gravity.

Assuming the information from the visual system is correct, the imprecision in throwing the dart comes from imprecision in proprioception that causes errors in the velocity and the angle of the throw (Bagesteiro et al., 2006; Bellan et al., 2015; Lateiner & Sainburg, 2003; Monaco et al., 2010; Touzalin-Chretien et al., 2010). This influence of proprioception on the precision of the dart throwing motion is what the study will refer to as 'error of the throw'. The value of error of the throw is calculated by:

$$\Delta H = H_0 - H, \quad (3)$$

where ΔH – error of the throw, H – height where the dart lands, H_0 – height at which the target is present.

Dependency of velocity and angle

The dart movement is affected by gravity (9,8 m/s), thus it forces the thrower to compensate it by increasing the velocity (V) or by increasing the throwing angle (α) in order to perfectly hit the target (Nasu et al., 2014; Tran et al., 2019). Depending on one parameter, the other one is adapted in a way that the target would be reached. The dependency of velocity and angle is determined by formula (1). The results of this formula are shown in Figure 5.3

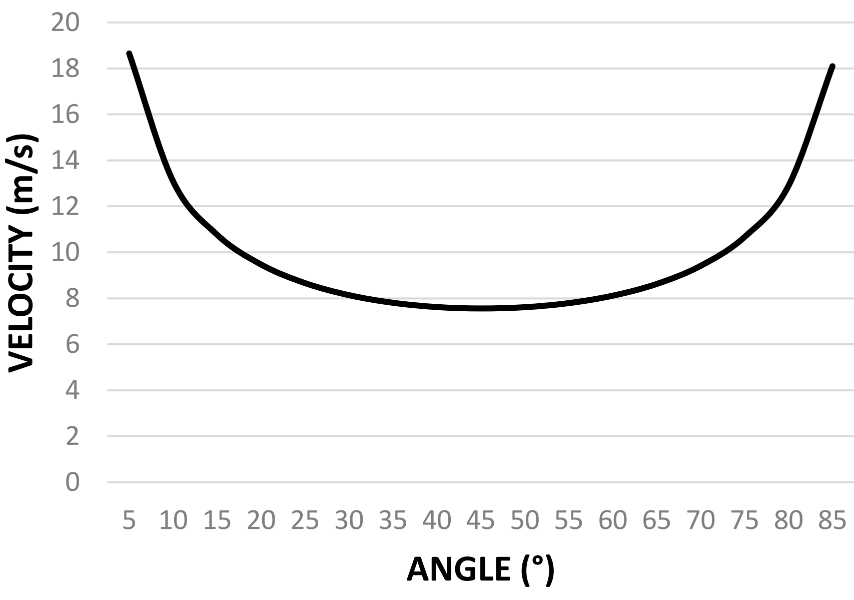

Fig. 5.3. Dependency of velocity and throwing angle.

The graph provides information about the dependency of velocity and angle of the dart release to hit the target. It is shown that there are two values of the velocity that could meet each value of the angle of the throw (with an exception of 45° angle, which is met by only one value of velocity). However, each value of the angle of the throw is met by only one value of the velocity. This implies that there are two strategies of throwing a dart at the same velocity.

The graph is not linear which suggests that there are preferences of the velocity that depend on the throwing angle. According to the graph, the throwing angle is the least affected by velocity at angles lower than 7,5° and higher than 82,5° (where velocity higher than 15 m/s is needed in order to hit the target) and is most affected at angles between 40° and 50° (where velocity is lower than 8 m/s. This suggests that throwing performance is most influenced by the changes in the velocity at throwing angles below 7,5° and above 82,5°, while at the angles between 40° and 50° velocity has the least effect.

Effect of adding 5 % error to the velocity and the angle

Once the dependency of velocity and throwing angle was clarified, 5 % error (proprioception has less than 5,5 imprecision (Fuentes & Bastian, 2010), which, assuming that there is a 90° width dart releasing window, was transformed into approx. 6 % error and decreased down to 5 % for simplicity) was added to each of these parameters in order to evaluate the influence of error of proprioception on the velocity and the throwing angle and on overall precision of the throw (see Fig. 5.4 and 5.5). In this model both positive (+5 %) and negative (-5 %) values of the error were added to describe wider range of scattering of the results.

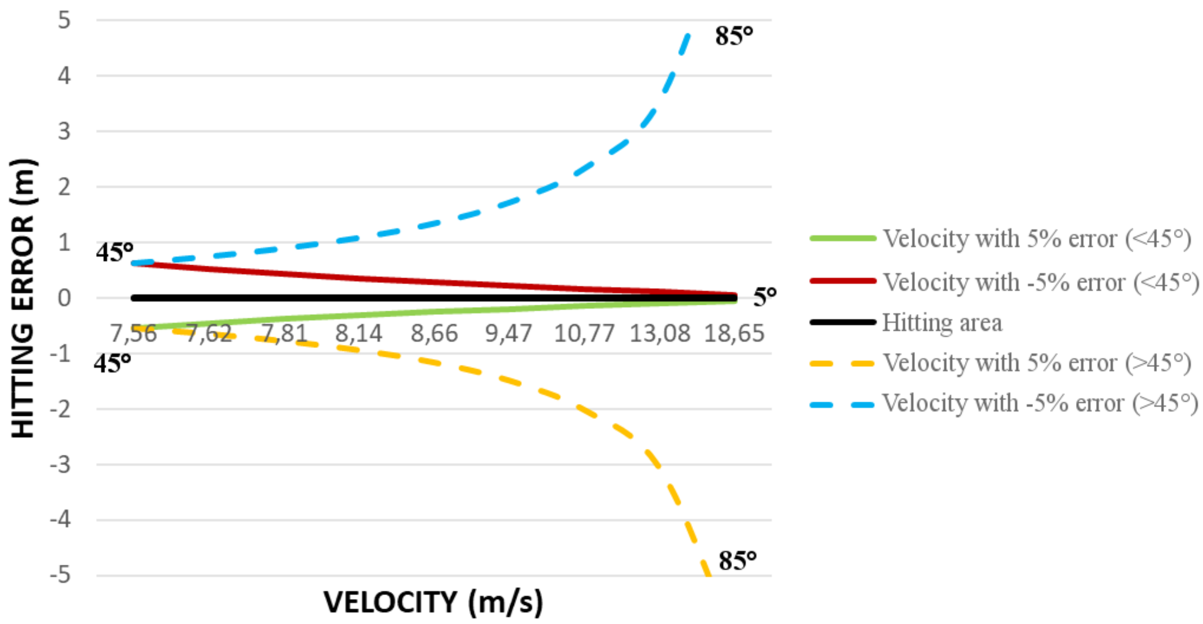

Fig. 5.4. Effect of adding 5 % error to the velocity.

The solid lines in the Fig. 5.4 show the value of the dart hitting the target in throwing angles below 45° when 5 % error was added to the velocity, with the angle of the throw being the one needed to successfully hit the target. The green line provides information on adding positive error (+5 %), while the red line – negative error (-5 %). The graph shows that in throwing angles below 45° adding the same amount of error on the velocity has more influence on hitting the target when the velocities are lower and less effect on higher velocities.

The dashed lines in the graph show the effect of adding 5 % error to the velocity, while the angle of the throw was the one needed to successfully hit the target and the throwing angles are above 45°. The yellow dashed line provides information on adding positive error (+5 %), while the blue dashed line – negative error (-5 %). It is shown that in throwing angles above 45° adding the same amount of error in the velocity exponentially decreases the chance of hitting the target as velocity increases.

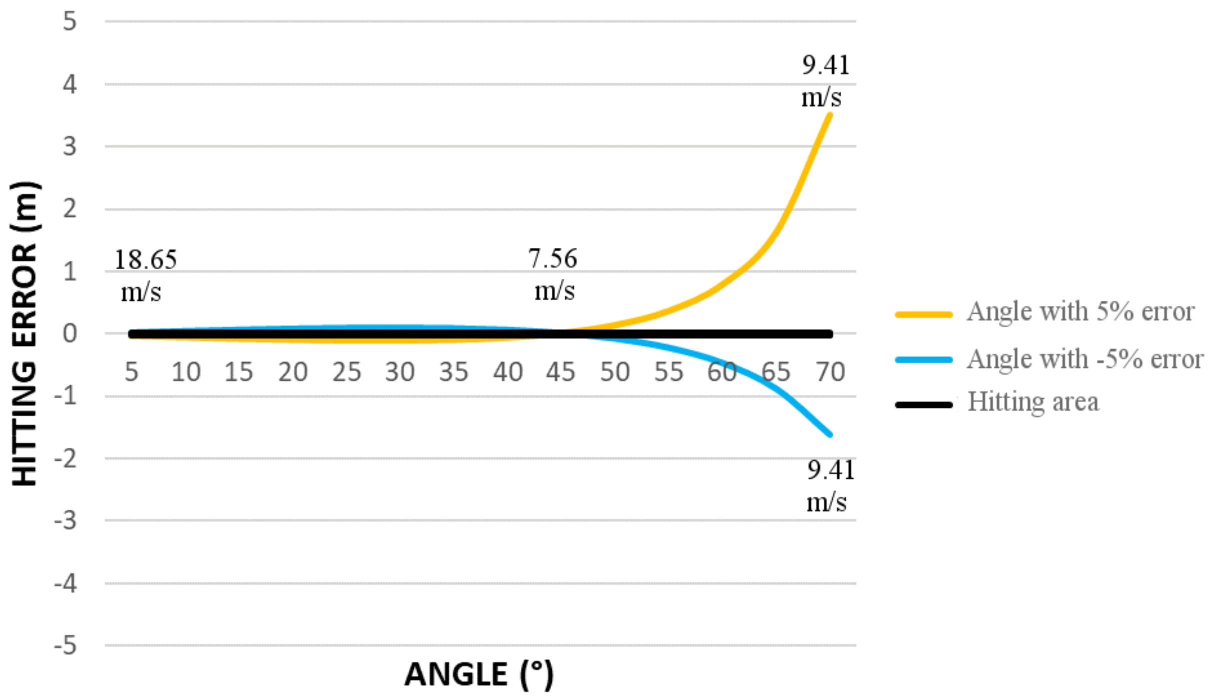

Fig. 5.5. Effect of adding 5 % error to the angle.

Information on the influence of adding 5 % error to the throwing angle, while the velocity was the one needed to land the dart successfully, on hitting the target error is provided in Figure 5.5.The yellow line shows the effect of adding positive error (+5 %) to the angle, while blue line – negative error (-5 %). Adding the error has little effect on throwing angles below 5° and on 45° angle. The angles between 5° and 45° are more influenced by the 5% error, where approx. 30° is the most sensitive to errors angle in this range. The same amount of error to the throwing angles above 45° exponentially increases the margin of error in hitting the target.

Overall, dart throwing is the least affected by proprioception errors when the throwing angle is lower than 5° and the throwing velocity is high.

Adding the boundaries of the target

The target has boundaries that are 3,2 cm in diameter. This boundary compensates a small portion of the throwing errors by increasing area of the target. To evaluate the quantity that added area of target compensates, formula (1) was used to calculate the dependency of velocity and angle to hit both the upper and the lower boundary of the target. This evaluation is illustrated in Figure 5.6.

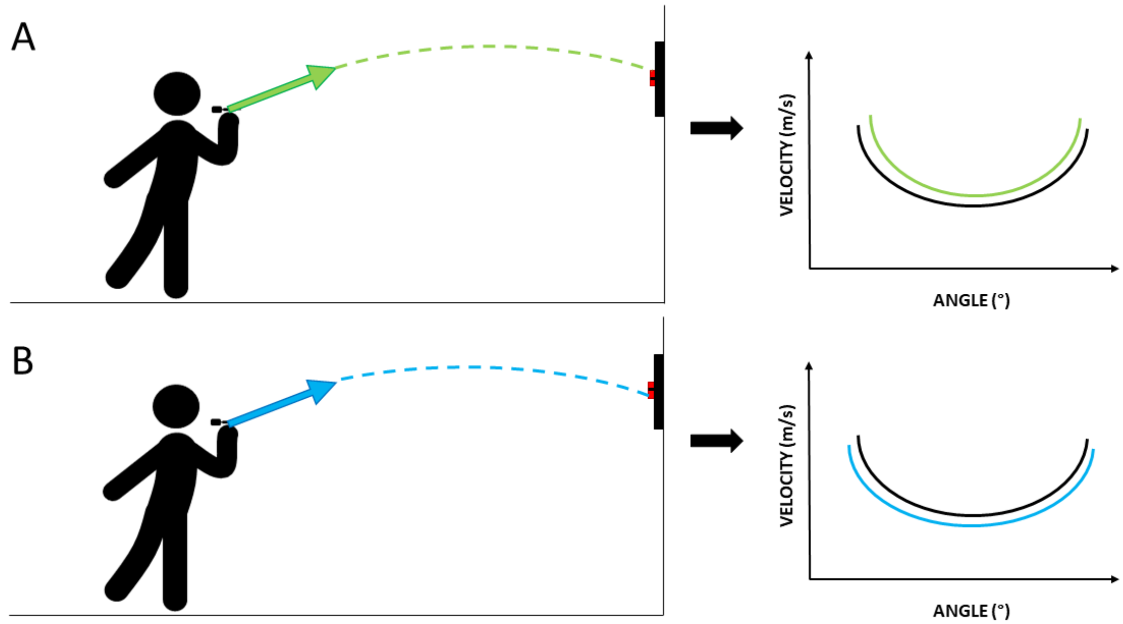

Fig. 5.6. Evaluation of error compensation by providing boundaries to the target. **(A)** Hitting the upper boundary of the target. **(B)** Hitting the lower boundary of the target.

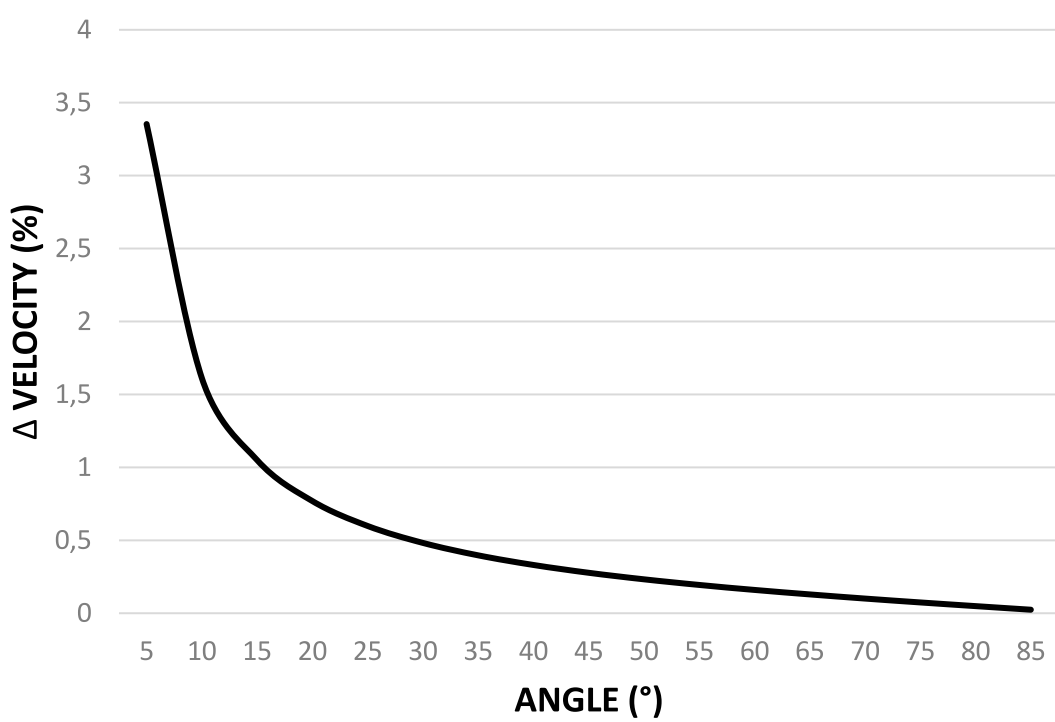

Fig. 5.7. Differences between upper and lower boundaries.

The graph in Figure 5.7 provides information regarding the difference between upper and lower boundaries of the target. It shows that as the throwing angle decreases, errors that the added target area compensates for - increases. Angles lower than 15° compensate for the highest number of errors in the velocity.

Relation between velocity and errors of the angle

Assuming that movements done in high velocity are imprecise and slow movements are more precise (Dean et al., 2007; Howarth et al., 1971), relation between velocity and error of angle of the throw was tested. This was done in order to find whether the strategy of throwing a dart in high velocity will introduce a higher inaccuracy in angle, and, therefore would have a negative effect on precision. The results are provided in Figure 5.8.

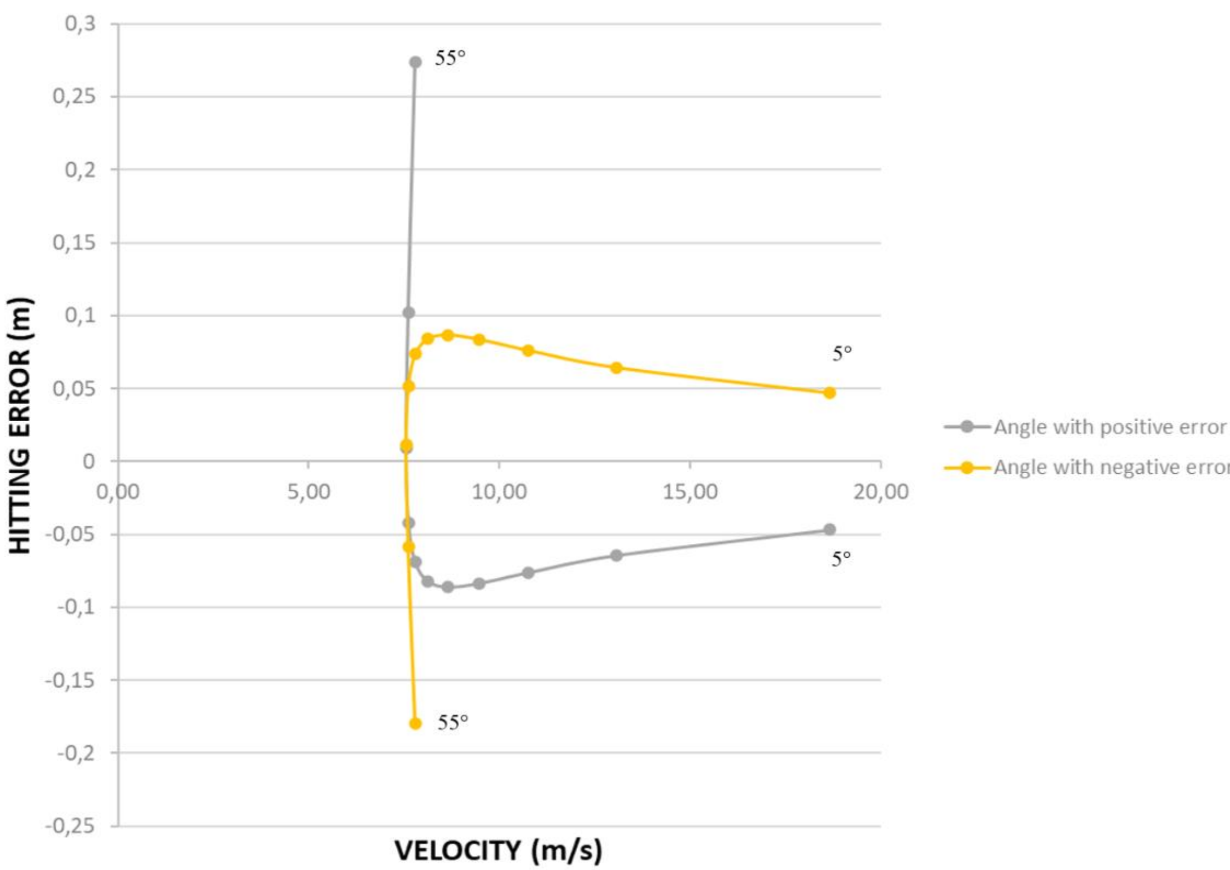

Fig. 5.8. Relation between velocity and error of the angle

The error of the angle was counted by:

$$\Delta\alpha = \alpha \pm \alpha \frac{Vk}{200}, \quad (4)$$

where $\Delta\alpha$ – error of the angle, α – release angle, V – velocity, k – coefficient ($1\frac{s}{m}$).

The graph shows that as the velocity of the throw increases and the angle of the throw decreases, error of hitting the target decrease when angles are below 25°. However, when throwing angles are between 25° and 45°, the error of hitting the target decreases as the velocity decreases. When angles are above 45°, as the throwing velocity and angles of the throw increase, error of hitting the target increase. The results imply that throwing a dart at high velocity and low angles is more precise than throwing at low velocity (unless the throwing angle is 45°).

Compensation of the errors

The errors in the velocity and the angle of the throw arise via different proprioceptors. This would suggest that these errors may be unrelated and errors of the velocity of the throw may affect errors of the angle of the throw either by decreasing their influence on the movement of the dart throw or by increasing it (see Figures 5.9 and 5.10).

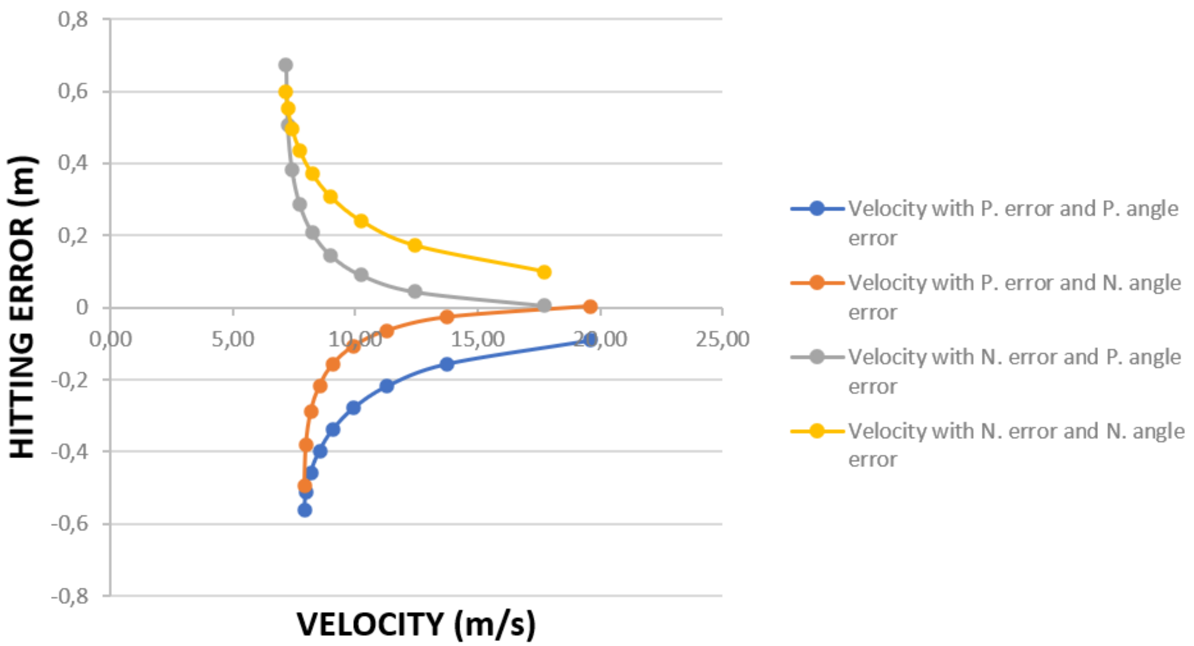

Fig. 5.9. Results of adding errors to the velocity and angle when angles are below 45°.

Figure 5.9 shows the results of changes, which appear when the angles are below 45°. As the velocity increases and the throwing angle decreases - throws become more accurate. This is shown in the graph (Fig. 5.9). When there's a positive error in the velocity and negative error in the angle (orange line) and a negative error in the velocity and positive error in the angle (grey line), the throws are closer to the target than results with the velocity and angle both with negative errors (yellow line) or where both the velocity and angle had positive errors (blue line), respectively. This implies that errors in the velocity and the angle could compensate each other and result in more accurate throws.

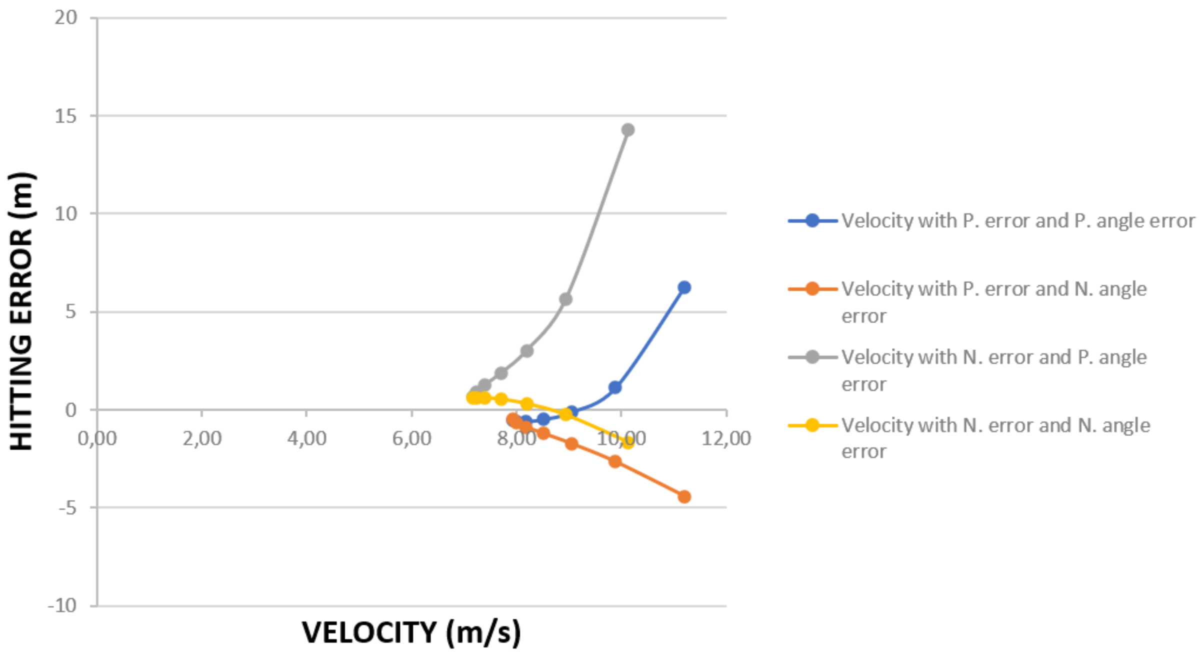

Fig. 5.10. Results of adding errors to the velocity and angle when angles are above.

The graph in Figure 5.10 implies increasing hitting error as the velocity of the throw rises when throwing angles are above 45°. Lines of positive error in the velocity and negative error in the angle (orange line) and negative error in the velocity and positive error in the angle (grey line) are further away from the target than lines of negative error in the velocity and negative error in the angle (yellow line) and positive error in the velocity and positive error in the angle (blue line). This suggests that errors in velocity and throwing angle may strengthen each other when throwing angles are above 45°.

DISCUSSION

In the present study the influence of proprioception on precision of goal directed movements was evaluated. For this reason, a dart throwing model was proposed, where dart landing precision is determined by the velocity and the angle of the throw. Both the velocity and the angle are affected by the imprecision of proprioception, which causes errors in the dart throw. In order to successfully throw a dart, the thrower needs to compensate the imprecision of the proprioception by choosing the most efficient strategy of the dart throw.

The results of this study showed that there are two strategies to throw a dart successfully. One strategy involves throwing a dart at angles below 45° at high velocity and the other – throwing at 45° at low velocity. The former strategy was shown in the present study to be less affected by the errors of proprioception then the latter strategy. While there is an option to throw at angles above 45° and at high velocity, this strategy is significantly affected by error of proprioception. These findings correspond with previous studies where it was found that professional dart players relied on two strategies in their throws: either on pre-planned hand trajectory movement that reaches high speed to compensate timing variability or on reducing timing variability by throwing in lower speed and higher arc (Nasu et al., 2014; Smeets et al., 2002; Tran et al., 2019). While the model in this study does not provide information regarding the changes in the trajectory of the hand, the strategy to throw a dart at high velocity and low angles appear to be superior strategy in order to compensate the errors of the proprioception. However, the research show that professional dart players use both strategies to successfully hit the target (Nasu et al., 2014; Tran et al., 2019). This suggests that professional players learn to compensate velocity errors by changing factors not included in this model, i. e. relying on the releasing time, which in this model only had influence on the angle of the throw.

The boundaries of the target are small as they reach only 3,2 cm in diameter. Successfully hitting such a small target from a distance of 6 meters requires highly trained movement and coordination of body parts. The results of this work imply that added borders of the target mostly help compensate errors of velocity when throws are performed at angles lower than 15°, which would require throwing a dart at high velocity. However, to obtain high velocity throw both upper and lower body parts need to be involved in the throw, which would cause higher errors since all involved body parts would need to be coordinated (Nakagawa et al., 2015; Sevrez & Bourdin, 2015; Tumialis et al., 2020). While the model in this study does not provide information regarding the kinematics of the body of the thrower, it does not seem crucial to add them because professional players learn to compensate variabilities of their body that may influence the performance of the throw (Kudo et al., 2000).

Some authors state that high velocity movements are less precise than slow movements (Dean et al., 2007; Howarth et al., 1971). This corresponds with results in Figure 5.10 where it is shown that angles above 45° at high velocity may cause errors to strengthen each other and result in higher variability. However, according to the graphs in Figures 5.8 and 5.9, throws that are performed at low angles and high velocity are less influenced by the errors of the throwing angle (see Figure 5.8) and throwing a dart at angles below 45° may cause errors of the velocity and errors of the throwing angle compensate each other, which would suggest that imprecision of high velocity movements may not come from imprecision of proprioception but rather from errors in localization and movement planning (van Beers et al., 2004). On the other hand, errors that were added in this model may not necessarily represent errors of proprioceptors as these errors could come from either planning or execution stages, even though errors in execution causes main variability in the movement (van Beers et al., 2004).

CONCLUSIONS

- The precision of hitting the target is the highest when the dart is thrown at low angle and high velocity.
- When the target has boundaries, the highest compensation for errors of the velocity occur at low angles of the throw.
- The highest velocity throws showed the highest precision rates, when testing velocity-dependant margin of error in the throwing angle.

REFERENCES

1. Bagesteiro, L. B., Sarlegna, F. R., & Sainburg, R. L. (2006). Differential influence of vision and proprioception on control of movement distance. *Experimental Brain Research*, *171*(3), 358–370. https://doi.org/10.1007/s00221-005-0272-y
2. Bańkosz, Z., & Szumielewicz, P. (2014). Proprioceptive Ability of Fencing and Table Tennis Practioners. *Human Movement*, *15*. https://doi.org/10.1515/humo-2015-0001
3. Barkley, V., Salomonczyk, D., Cressman, E. K., & Henriques, D. Y. P. (2014). Reach adaptation and proprioceptive recalibration following terminal visual feedback of the hand. *Frontiers in Human Neuroscience*, *8*. https://doi.org/10.3389/fnhum.2014.00705
4. Bellan, V., Gilpin, H. R., Stanton, T. R., Newport, R., Gallace, A., & Moseley, G. L. (2015). Untangling visual and proprioceptive contributions to hand localisation over time. *Experimental Brain Research*, *233*(6), 1689–1701. https://doi.org/10.1007/s00221-015-4242-8
5. Blohm, G., & Crawford, J. D. (2007). Computations for geometrically accurate visually guided reaching in 3-D space. *Journal of Vision*, *7*(5), 4–4. https://doi.org/10.1167/7.5.4
6. Clark, F. J., Burgess, R. C., Chapin, J. W., & Lipscomb, W. T. (1985). Role of intramuscular receptors in the awareness of limb position. *Journal of Neurophysiology*, *54*(6), 1529–1540. https://doi.org/10.1152/jn.1985.54.6.1529
7. Clayton, H. A., Jones, S. A. H., & Henriques, D. Y. P. (2015). Proprioceptive precision is impaired in Ehlers–Danlos syndrome. *SpringerPlus*, *4*. https://doi.org/10.1186/s40064-015-1089-1
8. Collins, D. F., Refshauge, K. M., & Gandevia, S. C. (2000). Sensory integration in the perception of movements at the human metacarpophalangeal joint. *The Journal of Physiology*, *529*(2), 505–515. https://doi.org/10.1111/j.1469-7793.2000.00505.x

9. Collins, D. F., Refshauge, K. M., Todd, G., & Gandevia, S. C. (2005). Cutaneous Receptors Contribute to Kinesthesia at the Index Finger, Elbow, and Knee. *Journal of Neurophysiology*, *94*(3), 1699–1706. https://doi.org/10.1152/jn.00191.2005

10. Dean, M., Wu, S.-W., & Maloney, L. T. (2007). Trading off speed and accuracy in rapid, goal-directed movements. *Journal of Vision*, *7*(5), 10–10. https://doi.org/10.1167/7.5.10

11. Desmurget, M., & Grafton, S. (2000). Desmurget, M. & Grafton, S. Forward modeling allows feedback control for fast reaching movements. Trends Cogn. Sci. 4, 423-431. *Trends in Cognitive Sciences*, *4*, 423–431. https://doi.org/10.1016/S1364-6613(00)01537-0

12. Dessing, J. C., Oostwoud Wijdenes, L., Peper, C. E., & Beek, P. J. (2009). Visuomotor transformation for interception: Catching while fixating. *Experimental Brain Research*, *196*(4), 511–527. https://doi.org/10.1007/s00221-009-1882-6

13. Eduardo Campos, C., Lage, G., Andrade, A., Couto, C., Santos, S., Profeta, V., & Ugrinowitsch, H. (2019). Changes on movement control of dart throwing under distance and target weight constraints. *Journal of Human Sport and Exercise*, *14*. https://doi.org/10.14198/jhse.2019.144.20

14. Ferrell, W. R., Gandevia, S. C., & McCloskey, D. I. (1987). The role of joint receptors in human kinaesthesia when intramuscular receptors cannot contribute. *The Journal of Physiology*, *386*, 63–71.

15. Fuentes, C. T., & Bastian, A. J. (2010). Where Is Your Arm? Variations in Proprioception Across Space and Tasks. *Journal of Neurophysiology*, *103*(1), 164–171. https://doi.org/10.1152/jn.00494.2009

16. Fujiwara, Y., Lee, J., Ishikawa, T., Kakei, S., & Izawa, J. (2017). Diverse coordinate frames on sensorimotor areas in visuomotor transformation. *Scientific Reports*, *7*(1), 14950. https://doi.org/10.1038/s41598-017-14579-3

17. Gazit, Y., Jacob, G., & Grahame, R. (2016). Ehlers–Danlos Syndrome—Hypermobility Type: A Much Neglected Multisystemic Disorder. *Rambam Maimonides Medical Journal*, *7*(4). https://doi.org/10.5041/RMMJ.10261
18. Gu, C., Pruszynski, J. A., Gribble, P. L., & Corneil, B. D. (2017). Done in 100 ms: Path-dependent visuomotor transformation in the human upper limb. *BioRxiv*, 192880. https://doi.org/10.1101/192880
19. Han, J., Waddington, G., Adams, R., Anson, J., & Liu, Y. (2016). Assessing proprioception: A critical review of methods. *Journal of Sport and Health Science*, *5*(1), 80–90. https://doi.org/10.1016/j.jshs.2014.10.004
20. Hansen, R., & Skavenski, A. (1977). Accuracy of eye position information for motor control. *Vision Research*, *17*, 919–926. https://doi.org/10.1016/0042-6989(77)90067-0
21. Howarth, C. I., Beggs, W. D. A., & Bowden, J. M. (1971). The relationship between speed and accuracy of movement aimed at a target. *Acta Psychologica*, *35*(3), 207–218. https://doi.org/10.1016/0001-6918(71)90022-9
22. Izumizaki, M., Tsuge, M., Akai, L., Proske, U., & Homma, I. (2010). The illusion of changed position and movement from vibrating one arm is altered by vision or movement of the other arm. *The Journal of Physiology*, *588*(Pt 15), 2789–2800. https://doi.org/10.1113/jphysiol.2010.192336
23. Jami, L. (1988). [Functional properties of the Golgi tendon organs]. *Archives Internationales De Physiologie Et De Biochimie*, *96*(4), A363-378.
24. Kandel, E. R., Jessell, T. M., Schwartz, J. H., Siegelbaum, S. A., & Hudspeth, A. J. (2013). *Principles of Neural Science, Fifth Edition*. McGraw Hill Professional.
25. Kistemaker, D. A., Van Soest, A. J. K., Wong, J. D., Kurtzer, I., & Gribble, P. L. (2013). Control of position and movement is simplified by combined muscle spindle and Golgi tendon organ

feedback. *Journal of Neurophysiology*, *109*(4), 1126–1139. https://doi.org/10.1152/jn.00751.2012

26. Kuatsjah, E., Khoshnam, M., & Menon, C. (2019). Investigation on the effect of noisy galvanic vestibular stimulation on fine motor skills during a visuomotor task in healthy participants. *PLOS ONE*, *14*(5), e0216214. https://doi.org/10.1371/journal.pone.0216214
27. Kudo, K., Tsutsui, S., Ishikura, T., Ito, T., & Yamamoto, Y. (2000). Compensatory coordination of release parameters in a throwing task. *Journal of Motor Behavior*, *32*(4), 337–345. https://doi.org/10.1080/00222890009601384
28. Kuling, I. A., Brenner, E., & Smeets, J. B. J. (2016). Proprioceptive Localization of the Hand Changes When Skin Stretch around the Elbow Is Manipulated. *Frontiers in Psychology*, *7*. https://doi.org/10.3389/fpsyg.2016.01620
29. Lateiner, J., & Sainburg, R. (2003). Differential contributions of vision and proprioception to movement accuracy. *Experimental Brain Research. Experimentelle Hirnforschung. Expérimentation Cérébrale*, *151*, 446–454. https://doi.org/10.1007/s00221-003-1503-8
30. Leclercq, G., Blohm, G., & Lefèvre, P. (2012). Accurate planning of manual tracking requires a 3D visuomotor transformation of velocity signals. *Journal of Vision*, *12*(5), 6–6. https://doi.org/10.1167/12.5.6
31. Leventhal, E. L., Moore, D. C., Akelman, E., Wolfe, S. W., & Crisco, J. J. (2010). Carpal and forearm kinematics during a simulated hammering task. *The Journal of Hand Surgery*, *35*(7), 1097–1104. https://doi.org/10.1016/j.jhsa.2010.04.021
32. Limanowski, J., & Blankenburg, F. (2016). Integration of Visual and Proprioceptive Limb Position Information in Human Posterior Parietal, Premotor, and Extrastriate Cortex. *Journal of Neuroscience*, *36*(9), 2582–2589. https://doi.org/10.1523/JNEUROSCI.3987-15.2016
33. Loosch, H. Müller. E. (n.d.). *FUNCTIONAL VARIABILITY AND AN EQUIFINAL PATH OF MOVEMENT DURING TARGETED THROWING*. 24.

34. Marini, F., Squeri, V., Morasso, P., & Masia, L. (2016). Wrist Proprioception: Amplitude or Position Coding? *Frontiers in Neurorobotics*, *10*. https://doi.org/10.3389/fnbot.2016.00013

35. Mileusnic, M. P., & Loeb, G. E. (2006). Mathematical Models of Proprioceptors. II. Structure and Function of the Golgi Tendon Organ. *Journal of Neurophysiology*, *96*(4), 1789–1802. https://doi.org/10.1152/jn.00869.2005

36. Monaco, S., Króliczak, G., Quinlan, D. J., Fattori, P., Galletti, C., Goodale, M. A., & Culham, J. C. (2010). Contribution of visual and proprioceptive information to the precision of reaching movements. *Experimental Brain Research*, *202*(1), 15–32. https://doi.org/10.1007/s00221-009-2106-9

37. Moscatelli, A., Bianchi, M., Ciotti, S., Bettelani, G. C., Parise, C. V., Lacquaniti, F., & Bicchi, A. (2019). Touch as an auxiliary proprioceptive cue for movement control. *Science Advances*, *5*(6). https://doi.org/10.1126/sciadv.aaw3121

38. Nakagawa, J., An, Q., Ishikawa, Y., Oka, H., Takakusaki, K., Yamakawa, H., Yamashita, A., & Asama, H. (2015). Analysis of Human Motor Skill in Dart Throwing Motion at Different Distance. *SICE Journal of Control, Measurement, and System Integration*, *8*(1), 79–85. https://doi.org/10.9746/jcmsi.8.79

39. Nasu, D., Matsuo, T., & Kadota, K. (2014). Two types of motor strategy for accurate dart throwing. *PloS One*, *9*(2), e88536. https://doi.org/10.1371/journal.pone.0088536

40. Neggers, S. F., & Bekkering, H. (1999). Integration of visual and somatosensory target information in goal-directed eye and arm movements. *Experimental Brain Research*, *125*(1), 97–107.

41. Newton, R. A. (1982). Joint Receptor Contributions to Reflexive and Kinesthetic Responses. *Physical Therapy*, *62*(1), 22–29. https://doi.org/10.1093/ptj/62.1.22

42. Prochazka, A. (2015). Sensory control of normal movement and of movement aided by neural prostheses. *Journal of Anatomy*, *227*(2), 167–177. https://doi.org/10.1111/joa.12311

43. Proske, U., & Gandevia, S. C. (2012). The Proprioceptive Senses: Their Roles in Signaling Body Shape, Body Position and Movement, and Muscle Force. *Physiological Reviews*, *92*(4), 1651–1697. https://doi.org/10.1152/physrev.00048.2011

44. Proske, Uwe. (2015). The role of muscle proprioceptors in human limb position sense: A hypothesis. *Journal of Anatomy*, *227*(2), 178–183. https://doi.org/10.1111/joa.12289

45. Rienhoff, R., Hopwood, M., Fischer, L., Strauss, B., Baker, J., & Schorer, J. (2013). Transfer of motor and perceptual skills from basketball to darts. *Frontiers in Psychology*, *4*. https://doi.org/10.3389/fpsyg.2013.00593

46. Sainburg, R. L., Lateiner, J. E., Latash, M. L., & Bagesteiro, L. B. (2003). Effects of Altering Initial Position on Movement Direction and Extent. *Journal of Neurophysiology*, *89*(1), 401–415. https://doi.org/10.1152/jn.00243.2002

47. Sarlegna, F. R., & Sainburg, R. L. (2009). The Roles of Vision and Proprioception in the Planning of Reaching Movements. *Advances in Experimental Medicine and Biology*, *629*, 317–335. https://doi.org/10.1007/978-0-387-77064-2_16

48. Sevrez, V., & Bourdin, C. (2015). On the Role of Proprioception in Making Free Throws in Basketball. *Research Quarterly for Exercise and Sport*, *86*(3), 274–280. https://doi.org/10.1080/02701367.2015.1012578

49. Smeets, J. B. J., Frens, M. A., & Brenner, E. (2002). Throwing darts: Timing is not the limiting factor. *Experimental Brain Research*, *144*(2), 268–274. https://doi.org/10.1007/s00221-002-1072-2

50. Smirnov, A. S., Alikovskaia, T. A., Ermakov, P. N., Khoroshikh, P. P., Fadeev, K. A., Sergievich, A. A., Tumialis, A. V., & Golokhvast, K. S. (2019). Dart Throwing with the Open and Closed Eyes: Kinematic Analysis. *Computational and Mathematical Methods in Medicine*, *2019*. https://doi.org/10.1155/2019/4217491

51. Sober, S. J., & Sabes, P. N. (2003). Multisensory Integration during Motor Planning. *Journal of Neuroscience*, *23*(18), 6982–6992. https://doi.org/10.1523/JNEUROSCI.23-18-06982.2003

52. Tamei, T., Obayashi, C., & Shibata, T. (2011). Throwing darts utilizes the interaction torque of the elbow joint. *Conference Proceedings: ... Annual International Conference of the IEEE Engineering in Medicine and Biology Society. IEEE Engineering in Medicine and Biology Society. Annual Conference*, *2011*, 1283–1286. https://doi.org/10.1109/IEMBS.2011.6090302

53. Thorp, E. B., Kording, K. P., & Mussa-Ivaldi, F. A. (2017). Using noise to shape motor learning. *Journal of Neurophysiology*, *117*(2), 728–737. https://doi.org/10.1152/jn.00493.2016

54. Touzalin-Chretien, P., Ehrler, S., & Dufour, A. (2010). Dominance of Vision over Proprioception on Motor Programming: Evidence from ERP. *Cerebral Cortex*, *20*(8), 2007–2016. https://doi.org/10.1093/cercor/bhp271

55. Tran, B. N., Yano, S., & Kondo, T. (2019). Coordination of human movements resulting in motor strategies exploited by skilled players during a throwing task. *PLOS ONE*, *14*(10), e0223837. https://doi.org/10.1371/journal.pone.0223837

56. Tsay, A., Savage, G., Allen, T. J., & Proske, U. (2014). Limb position sense, proprioceptive drift and muscle thixotropy at the human elbow joint. *The Journal of Physiology*, *592*(Pt 12), 2679. https://doi.org/10.1113/jphysiol.2013.269365

57. Tumialis, A., Smirnov, A., Fadeev, K., Alikovskaia, T., Khoroshikh, P., Sergievich, A., & Golokhvast, K. (2020). Motor Program Transformation of Throwing Dart from the Third-Person Perspective. *Brain Sciences*, *10*(1). https://doi.org/10.3390/brainsci10010055

58. van Beers, R. J., Baraduc, P., & Wolpert, D. M. (2002). Role of uncertainty in sensorimotor control. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *357*(1424), 1137–1145. https://doi.org/10.1098/rstb.2002.1101

59. van Beers, R. J., Haggard, P., & Wolpert, D. M. (2004). The Role of Execution Noise in Movement Variability. *Journal of Neurophysiology*, *91*(2), 1050–1063. https://doi.org/10.1152/jn.00652.2003

60. Vardakastani, V., Bell, H., Mee, S., Brigstocke, G., & Kedgley, A. E. (2018). Clinical measurement of the dart throwing motion of the wrist: Variability, accuracy and correction. *Journal of Hand Surgery (European Volume)*, *43*(7), 723–731. https://doi.org/10.1177/1753193418773329

61. *WDF Rules – WDF*. (n.d.). Retrieved May 5, 2020, from https://www.dartswdf.com/rules/

VILNIAUS UNIVERSITETAS
GYVYBĖS MOKSLŲ CENTRAS
BIOMOKSLŲ INSTITUTAS

Egidijus Linkevičius

Magistro baigiamasis darbas

PROPRIOCEPTORIŲ ĮTAKA Į TIKSLĄ NUKREIPTŲ RANKOS JUDESIŲ TIKSLUMUI

SANTRAUKA

Proprioceptoriai teikia esminę informaciją, reikalingą sąveikai su aplinka. Vis dėlto proprioceptinė informacija yra sugadinama nervinės sistemos triukšmų ir tokiu būdu padaro proprioceptorius netiksliais. Netiksliai suvoktos kūno dalys gali sukelti klaidų vėlesnėse judesio sugeneravimo stadijose ir privesti prie judesių netikslumo. Tačiau CNS išmoksta kompensuoti propriocepcijos netikslumus ir privesti prie tikslių judesių.

Šio darbo tikslas – įvertinti proprioceptorių įtaką smiginio strėlyčių metimo judesių tikslumui.

Šiame darbe buvo sukurtas smiginio strėlyčių mėtymo modelis, siekiant įvertinti propriocepcijos netikslumo įtaką judesių tikslumui ir smiginio strėlyčių mėtymo strategijas, skirtas kompensuoti propriocepcijos netikslumą. Rezultatai parodė, kad egzistuoja dvi smiginio strėlyčių mėtymo strategijos: metimas 45° kampu mažu greičiu arba metimas mažesniu negu 45° kampu dideliu greičiu. Pastaroji strategija yra mažiausiai paveikiama propriocepcijos paklaidų.

Gautos išvados: 1) pataikymo taiklumas yra didžiausias, kai smiginio strėlytė metama mažu kampu dideliu greičiu; 2) didžiausia greičio paklaidos kompensacija įvyksta prie mažų kampų, kai taikinys turi ribas; 3) didžiausio greičio metimai pasižymėjo didžiausiu tikslumu, kai buvo tiriama nuo greičio priklausoma kampo paklaida.

VILNIUS UNIVERSITY

LIFE SCIENCES CENTER

INSTITUTE OF BIOSCIENCES

Egidijus Linkevičius

Master thesis

THE INFLUENCE OF PROPRIOCEPTION ON PRECISION OF GOAL-DIRECTED ARM MOVEMENTS

SUMMARY

Proprioception provides essential information for interacting with the environment. However, the proprioceptive information is corrupted by the noise from the nervous system, making proprioceptors imprecise. The imprecise perception of the body limbs can cause errors in later stages of movement generation and lead to imprecise movements. However, CNS learns to compensate the impreciseness of proprioception and result in precise movements.

The aim of this study is to evaluate the influence of proprioception on precision of arm movements in dart throwing.

In this study, a dart throwing model was proposed in order to evaluate the influence of imprecision of proprioception on the precision of the movements and to evaluate the dart throwing strategies to compensate the impreciseness of proprioception. The results show that there are two strategies to throw a dart precisely: throw at 45° angle and low velocity or throw at lower than 45° angle and high velocity. The latter is the least effected by errors of proprioception.

In conclusion: 1) the precision of hitting the target is the highest when the dart is thrown at low angle and high velocity; 2) when the target has boundaries, the highest compensation for errors of the velocity occur at low angles of the throw; 3) the highest velocity throws showed the highest precision rates, when testing velocity-dependant margin of error in the throwing angle.