

The transference of benefits between the eyes

Does training of express saccades in the dominant eye transfer to the non-dominant eye through the interconnectedness of the abducens nerve?

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Abstract

Saccades have been extensively investigated and have been found to be generated from five places in the brain with the oculomotor center of the brainstem as its pathway to the eyes. Express saccades are low-latency and mostly involuntary saccades which are generated within the superior colliculus. The training of express saccades in one direction can benefit other directions within the same eye. Horizontal saccadic eye movements are performed by the abducens nerve by means of motoneurons. In order to coordinate the eyes, the abducens nerve also sends interneurons to the contralateral eye. With that in mind we hypothesized that by training one eye those benefits might be transferred to the other eye. Nine participants were trained on their dominant eye to perform express saccades and then the dominant and non-dominant eye were tested in the middle and at the end of the study. For the non-dominant eye, saccadic latencies were reduced after training and larger number of express saccades were noticeable. Differences between the dominant and non-dominant eye were not significant. The results therefore show next to complete transfer of training effects from the dominant to the non-dominant. We talk about the need for a reproduction of this study along with possible direction for future studies.

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1. Introduction

The eyes hold a special place of interest to many scientists and clinicians. They hold the potential to reveal the workings of the brain. Furthermore, any ocular abnormalities found with a simple eye scan could lead to improvements in the diagnosis of serious physical and mental illnesses (Leigh & Zee, 2015). Therefore, by researching the eyes one can learn more about the brain. One researcher goes so far as to equate the eyes as a microcosms of the brain seeing as it has “sensory input, motor output and incorporates bits of virtually all the major anatomical structures” (Carpenter, 1994, p. 341). For the two eyes to work in tandem, coordination is required. In Duane Syndrome this coordination is lacking due to a missing or hypoplastic abducens nuclei or nerve (Yüksel, de Xivry, & Lefèvre, 2010) which is responsible for horizontal eye movements (Patestas & Gartner, 2016). With the missing nerve or nuclei, in 78% of cases a unilateral horizontal abduction deficit makes the person unable to move the inflicted eye towards the temple (abduction) (DeRespinis, Caputo, Wagner, & Guo, 1993; as cited by Yüksel, de Xivry, & Lefèvre, 2010). This shows that, much like the two hemispheres of the brain, in order for the eyes to make the same eye movement, at the same time and to the same place, coordination between the eyes is required. In this study we investigated whether because of the coordination of the eyes the benefits of training one eye could be transferred to the other. In order to do this, we discuss types of eye movements, then how they are performed and how they are measured. Finally, we will briefly look at all types of saccades and then focus on express saccades and how they are coordinated between the eyes.

1.1. Types of eye movements

At its simplest all eye movements can be differentiated by eye movements that keep objects on the fovea and shift the gaze to a new stimulus (Leigh & Zee, 2015). In order to keep an object on the fovea we engage in either fixation or smooth pursuit. Fixation is when the eyes fixate on an object (Land, 2011). When we fixate on an object we may assume that our eyes are not moving but in fact there are continual small-scale motions showing irregular drift and tremor along with small saccadic eye movements called microsaccades (Leigh & Zee, 2015; Martinez-Conde, Macknik, & Hubel, 2004). Smooth pursuit is when the eyes follows an object, like a car, to keep it on the fovea. When the eyes perform smooth pursuit they can follow objects that are moving at velocities up to 15°/s. When objects move faster than 15°/s

saccades are interspersed with smooth pursuit until the object is moving faster than 100°/s when saccades take over entirely. Saccadic eye movement happens when the eyes go at high speed to shift our gaze at a new stimulus. A vergence is a special form of eye movement, accommodating for changes in the depth plane of foveal objects, in which the eyes move in opposite direction, either toward the periphery of the eye or together towards the nose to keep an object on the fovea. The reason why vergence eye movements are special is that all eye movements for mammals are conjugate, that is move together in the same direction, except for vergence. When we need to move our head to follow an object or shift our gaze we either use the vestibulo-ocular or the optokinetic reflex to keep the eyes still when the head moves. The vestibulo-ocular reflex handles corrections to the eye when the head moves briefly but the optokinetic reflex handles sustained rotations (Land, 2011).

1.2. The extraocular muscles

The six muscles that control the movements of the eyes are called the extraocular muscles. They are connected through cranial nerves III, IV and VI directly to the brain (Tortora & Nielsen, 2012). The six extraocular muscles come in pairs and rotate the eyes on three axes (x-, y- and z-axis) in any direction. The medial and lateral rectus muscle pair are almost solely responsible for horizontal eye movements and are connected through the abducens nerve (Cranial nerve VI). The superior and inferior rectus muscle pair along with the superior and inferior oblique muscle pair are responsible for both vertical and oblique eye movements with the exact contribution of each pair depending on the position of the eye in the orbit. The superior and inferior rectus muscle pair along with the inferior oblique muscle are connected to the brain through the oculomotor nerve (cranial nerve III) while the superior oblique muscle is connected to the brain through the trochlear nerve (cranial nerve IV). These extraocular muscle pairs work with contractions to move the eyes either through abduction or adduction (towards the temple or towards the nose, respectively) (Kandel & Schwartz, 1985). When a horizontal saccade is made to the left, the medial rectus of the left eyeball and the lateral rectus of the right eyeball contract, whereas the lateral rectus of the left eyeball and the medial rectus of the right eyeball relaxes. With a rightward going saccade this process would be reversed (Tortora & Nielsen, 2012).

1.3. Measurement of eye movements

In order to explain eye movements one needs to know how to measure them. The adult eyeball is a sphere and measures about 2.5 cm with only the anterior one-sixth of the eyeball exposed (Tortora & Nielsen, 2012). Because the eye is a sphere we measure it in degrees, much like the longitudes and latitudes of the Earth and it is traditional to use amplitude as a measure of degrees. Amplitude also conveys information about the size or magnitude of the saccadic eye movement (Jóhannesson, 2014). The velocity of saccades is an important characteristic of them and the peak velocity of a 20° saccade can reach more than 450°/second (Leigh & Zee, 2015). There is an interesting relationship between amplitude and both the velocity and duration of a saccade. This relationship has been named the “main sequence” after the astronomical term of the same name. The duration and peak velocity of saccades increase as the amplitude of the saccades increase (Bahill, Clark & Stark, 1975). This relationship is linear with small saccades but reaches an upper limit where the relationship starts to break down. For peak velocity the correlation is strong up to 20° while for duration it is strong for up to 50° (Leigh & Zee, 2015). However, Jóhannesson and Kristjánsson (2013) found that the asymmetries in the nasal-temporal visual fields led to a violation of the “main sequence”. Peak velocities were higher toward the temporal stimuli, compared to the nasal stimuli, in a monocular presentation. The reason for this difference is still unclear (Jóhannesson & Kristjánsson, 2013). Another measurement needed to understand saccadic eye movements is latency. Saccadic latency is the time from the appearance of the target stimuli to the initiation of a saccade towards that stimuli and can be thought of as reaction time of the eyes (Gilchrist, 2011). The latency of a saccade can be influenced by the properties of its target, such as size and salience (Thoroddsen, 2015).

There have been many unfounded claims about the concept of eye dominance (for an overview see: Mapp, Ono & Barbeito, 2003), whether they involve that eye dominance correlates to hemispheric dominance, that it is egocentric or that there is a single dominant eye for each person. But it seems that no conclusive empirical evidence supports these theories (Mapp et al., 2003). Mapp et al. (2003), however, suggest that the dominant eye should be the eye used for monocular task and therefore has no unique functional role in vision, at least when it comes to monocular studies. There is evidence that support this view. For instance, in some people the dominant eye is the eye they have a habit of using more and other people alternate between situations which eye is the dominant one (Mapp et al., 2003).

1.4. Saccades

In 1879 Louis Émile Javal became the first person to note that, while reading, a person does not perform smooth eye movements but instead performs jerky eye movements which takes the eyes from one place to another. Javal along with Edmund Landolt were the first to use the word saccade to refer to this phenomena (Leigh & Zee, 2015). A saccade can be defined as a quick and jerky movement with speeds of up to $1000^{\circ}/s$ between two fixations points (Wolfe, Kluender, & Levi, 2012). One can clearly see saccades in another person's eyes but never in your own because the brain does not process information between the two fixation points (Campbell & Wurtz, 1978), effectively making a person blind in between them (Land, 2011). Saccades occur at a rate of about three per second (Schiller & Tehovnik, 2001) and allow us to see with the part of the eye with the highest visual acuity, the fovea (Gilchrist, 2011).

As previously mentioned, the fovea has the highest acuity of any part of the eye. Bouma (1970; as cited by Gilchrist, 2011) conducted an experiment demonstrating this. He showed a target letter, either alone or flanked by two other letters at varying eccentricities away from the fovea. When only the target letter was displayed the participants were able to identify the target letter with 100% accuracy at 3° from the fovea but only 50% at 10° . When the target letter was flanked with distractor letters participants were only able to identify the target letter 80% of the time at 1° and 35% at 3° . Correct recognition of this sort of stimuli is therefore essentially impossible without directing the fovea at it. The reason why saccadic eye movements occur so frequently is that saccades are the most expedient way to put stimuli into your fovea (Gilchrist, 2011).

1.4.1. Types of Saccades

Saccades or saccadic eye movements can be thought of as either endogenous or exogenous. When a person reads a sentence it is employing scanning saccades that can be thought of as endogenous (generated inside) while a reflexive saccade, which is triggered by the appearance of a peripheral stimuli, is thought of as exogenous (generated outside) (Sumner, 2011). Exogenous saccadic eye movements are instigated because of peripheral stimuli and generally have a saccadic latency of about 200 ms in standard oculomotor tasks (Becker, 1989; as cited in Edelman, Kristjánsson, & Nakayama, 2007) but the distribution of the latency can be very wide, ranging from around 200 ms and up to 1 second. However trained participants often have shorter latencies and less variance in their distribution (Sumner, 2011).

There are three types of saccadic eye movements, regular saccades, microsaccades, and express saccades. Regular saccades can be subtyped into two categories; prosaccades which have a latency of about 180-220 ms and antisaccades which have a considerably longer latency of about 270-300 ms. Prosaccades are saccades towards a stimulus while antisaccades are saccades of equal amplitude away from the stimulus and the differences between pro- and antisaccades are primarily task related (i.e., dependent on instructions) (Antoniades et al., 2013; Leigh & Zee, 2015). It has been suggested that the longer latency of antisaccades is due to the difficulty in moving the eyes from a stimulus towards nothing (Theeuwes, Kramer, Hahn, & Irwin, 1998). Microsaccades are generated while the eyes fixate on an object (Martinez-Conde, Macknik, & Hubel, 2004) and share many characteristics with regular saccades, except their amplitude can be in the range of 0.02-2° depending on how they are defined (Leigh & Zee, 2015; Rolfs, 2009). Microsaccades occur at a mean frequency of around 1 per second (Rolfs, 2009). Express saccades are usually considered a neurophysiologically distinct type of saccade, characterized and defined operationally by extremely short latencies (Amatya, Gong, & Knox, 2011). Express saccades are primarily reflexive but can be influenced by top-down processes (Edelman, Kristjánsson, & Nakayama, 2007). The latency of express saccades can be adjusted by many factors including task designs. Saccades in the range of 80-120 ms can be considered to be express saccades (Delinte, Gomez, Decostre, Crommelinck, & Roucoux, 2002) and are the focus of this experiment.

1.4.2. Express Saccades

Express saccades were first reported by Saslow (1967; as cited by Kingstone & Klein, 1993) and were thought to be the only truly reflexive saccades. Saslow (1967; as cited by Kingstone & Klein, 1993) also showed that they were more likely to occur within a gap paradigm. The gap paradigm refers to the gap or time interval between the removal of the fixation stimuli and the presentation of the target stimuli. In contrast, an overlap condition refers to the disappearance of the fixation stimulus at the same time as the target stimulus appears. Compared to the overlap condition the gap paradigm significantly reduces saccadic latencies and increases the probability of express saccade production. This reduction in saccadic latencies, with a gap paradigm and increase in production of express saccades, has been dubbed the gap effect. Although the gap paradigm does not always lead to express saccades they are more likely to occur within the gap paradigm (Gezeck, Fischer, & Timmer, 1997). In

spite of this, express saccades can be produced in the overlap conditions. It has been established that rhesus monkeys perform express saccades in overlap conditions and that the generation of express saccades persist even with randomization of the location, time (Boch & Fischer, 1986) and changes in the physical properties of the target stimulus (Schiller & Haushofer, 2005). Importantly, the release from fixation of a stimulus is a prerequisite for the generation of express saccades. Physiological experiments have suggested that when fixation ends the superior colliculus reduces activity of neurons that may inhibit saccadic generation. It is therefore more likely that a gap paradigm is more effective at generating express saccades because of the disengagement of fixation (Munoz & Wurtz, 1992).

As previously stated, the use of a gap paradigm does not guarantee the generation of express saccades. Other factors that increase the likelihood of express saccades include knowing the approximate location of the target (Kurata & Aizawa, 2004), fewer possible target locations (Schiller, Haushofer, & Kendall, 2004) and whether the subject has been trained to make express saccades (Schiller & Haushofer, 2005). This along with similar experiments led to the formation of the motor preparation hypothesis of express saccades which states that the preparation of a saccade to a region is necessary for the generation of express saccades (Dorris, Paré & Munoz, 1997; Paré & Munoz, 1996). Bibi and Edelman (2009) demonstrated that although motor preparation can increase the frequency of express saccades it does not seem to be a necessary precursor. Rather, increased express saccade frequency is more likely due to fixation disengagement. Furthermore, they revealed that training can result in increased express saccade expression and that the impact of training in one direction also appears to generalize to other directions (horizontal, vertical or oblique). That is, by training the saccadic system in any direction can affect saccades made in other directions as well (Bibi & Edelman, 2009). Rohrer and Sparks (1993) revealed that after training, monkeys continued to generate express saccades even when there was a high level of uncertainty about both the location and the time of onset of a peripheral target. They also demonstrated that an express saccade is more likely exogenous rather than endogenous, contradicting the preparation hypothesis, and that the training was not location specific but rather that the location relative to the eyes starting position was trained (Rohrer & Sparks, 1993).

A subpopulation that can be called “express saccades makers” has been identified. This subpopulation generates more prolific express saccades than others, often more than 30%

in overlap conditions where express saccades are normally less than 15% (Biscaldi, Fischer, & Stuhr, 1996). It has also been discovered that there is cultural variation in express saccades. One study demonstrated that 29% of Chinese participants but only 2,9% of Caucasian participants appeared to be express saccade makers (Amatya, Gong, & Knox, 2011). A study by Chua, Boland, & Nisbett (2005) revealed that American participants watched a focal point of a naturalistic scenery while Chinese participants were more likely to watch the background scenery. This study demonstrated that eye movements could differ based on culture and the hypothesis of Chua et al. (2005) is that this happens due to societal differences. East Asians stress societal roles and therefore it is important for them to watch their surroundings for their role in those circumstances. Americans are more independent in social circumstances which allows them to pay less attention to context (Chua et al., 2005). This might be a factor in the fact that east Asians are more likely to be express saccade makers (Amatya et al., 2011). Previously mentioned studies indicate that based on your culture you might be trained by society in a naturalistic setting to make express saccades.

1.4.3. The Anatomy of Saccades

Researchers once believed that the superior colliculus (SC) controlled the production of saccades (Schiller & Tehovnik, 2001). However, an extensive overview performed by Schiller and Tehovnik (2001) revealed that at least five areas of the brain in which play a role in producing saccades of one kind or another. If you stimulate regions in the visual cortex, SC, frontal eye field and parts of the parietal cortex a vector code appears. A vector code is when the amplitude and direction of a saccade depends on the region stimulated. Another coding operation is when parts of the parietal cortex and regions of the medial eye field are stimulated and saccades are created which take the eyes to a particular orbital location. This demonstrates that the expression of saccades is dependent on a diffuse network of brain regions (Schiller & Tehovnik, 2001).

Another misconception was that all cortical signal for the generation of saccades were conveyed through the SC though evidence surfaced to challenge that view. In a lesion study where ablation of the SC was performed on rhesus monkeys it was discovered that even with the removal of the SC the monkeys were still able to make visually guided eye movements (Schiller, True, & Conway, 1979). These findings led to the formulation of the two-stream hypothesis. The two-stream hypothesis states that there are two streams that convey the

information for the generation of saccades to the extraocular muscles. The posterior stream comes from the parietal and occipital lobes and consists of the parietal and visual cortex which then consolidate in the SC before moving onto the brainstem oculomotor center. The anterior stream from the frontal lobe is comprised of the frontal- and medial eye fields and has direct access to the brainstem oculomotor center. From there, both streams convey information to the extraocular muscles (Schiller & Tehovnik, 2001). This hypothesis explains why ablation of the SC does not stop the generation of saccadic eye movements. With additional ablation of the frontal eye fields along with the SC all visually guided saccadic eye movements are eliminated (Schiller et al., 1979).

Saccade generation, from the higher-order of the brain to the initiation of the saccade, can be thought of as both contralateral and ipsilateral. Saccades are initiated at higher-order sites in the contralateral part of the brain and then these orders cross over into the contralateral brainstem by way of a multi-synaptic pathway. Which then means that the generation of saccades occurs ipsilaterally from the oculomotor center of the brainstem (Troost, 1983). This means that for a horizontal leftward saccade the command is initiated in the frontal eye field or the superior colliculus of the right hemisphere and then crosses the corpus callosum in the midbrain and continues to the oculomotor center in the brainstem of the left hemisphere. The final command for a horizontal saccadic eye movement comes ipsilaterally from cranial nerve VI in a region called the paramedian pontine reticular formation. Neurons then fire to indicate that a horizontal saccade should be performed and the neuronal firing then decays to hold its position. This neuronal firing has been named the step and pulse commands (Troost, 1983).

In order to generate a saccade, neurons fire a burst of action potentials (or a pulse) which overcomes the viscous drag of the orbital tissues. Once the eye reaches its final position it is then held in that position by a sustained firing of neurons that produce a fixed contraction of the extraocular muscles (the step) (Cullen & Van Horn, 2011). Within the step command is information about the landing point of the eye and the pulling force, or how much the muscle must contract to overcome the other muscle in its pair and stay in place. The pulse command comprises of information about the velocity of the saccade and about the force needed to overcome the viscosity of the orbit (Sparks, 2002), which can be likened to a space shuttle trying to escape gravity. To escape gravity, you need a certain amount of force but to get to low-earth orbit you don't need as much force as if you're going to high-earth orbit. The step and pulse commands are generated independently as is the horizontal and

vertical pulse commands. The step is generated in the medial vestibular nucleus and the prepositus hypoglossi of the brainstem by a neural network that integrates the velocity signal to derive the position signal (Sparks, 2002). Horizontal eye movements are produced by premotor neurons in the paramedian pontine reticular formation of the pons (Troost, 1983) and in the medulla while vertical eye movements are produced by premotor neurons in the rostral midbrain (Sparks, 2002).

When monkeys fixate on a target a subset of neurons within the SC discharge tonically. These neurons in the rostral pole of the SC can influence the generation of express saccades (Munoz & Wurtz, 1992). Munoz and Wurtz (1992) artificially inhibited these neurons with local injection of an agonist of the neurotransmitter GABA and then the monkeys were less likely to fixate on a target and more likely to generate unwanted visually guided saccades. Many of these unwanted saccades had latencies less than 100 ms and would be considered express saccades. This indicated that not only is the rostral pole of the SC part of the fixation system but also that express saccades can only occur when activity in this fixation system is reduced (Munoz & Wurtz, 1992). Dorris, Paré, and Munoz (1997) investigated the activity of fixation neurons within the gap paradigm. They found out that fixation neurons reduced their discharge in the gap paradigm regardless of saccadic latencies (Dorris et al., 1997). Schiller, Sandell, and Maunsell (1987) performed lesion experiment on both the frontal eye field and the SC. With ablation of the frontal eye field there was no discernible difference except the latencies of saccades were a little bit longer. However, with unilateral ablation of the SC the participants (rhesus monkeys) were unable to generate express saccades. When only the left superior colliculus was ablated the monkeys no longer generated express saccades to the right visual field (Schiller et al., 1987). This shows that the SC is crucial in generating express saccades and that the fixation system needs to reduce its discharge in order to generate express saccades.

1.4.4. The distribution of saccades

The latency distributions of saccadic eye movements are not Gaussian but have been shown to have one, two, three or even four distinct peaks or modes (Gezeck, Fischer, & Timmer, 1997). A bimodal distribution was first shown by Fischer and Boch (1983; as seen in Schiller & Tehovnik, 2001) where two peaks were found in rhesus monkeys. The two peaks showed express saccades around ~100 ms and regular saccades around ~130 ms (Schiller &

Tehovnik, 2001). Gezeck et al. (1996) took 963 data sets which contained 90,927 latencies from 170 participants and found out that the clustering of the modes could be classified into express saccades (90-120 ms), fast regular saccades (135-170 ms) and slow regular saccades (200-220 ms). In support of a multimodal distribution of saccadic latency Gezeck et al. (1996) found out that 87% of the data sets was distributed among the three modes.

Carpenter (2001) suggests that bimodality might in fact be an experimental artifact that does not occur naturally. Carpenter (2001) set up an experiment in which participants undertook a saccadic gap task and the majority showed bimodal distribution with an express and regular saccadic mode. Carpenter (2001) noted that the bimodality seemed to be due to the order of the trials. When the target was on the opposite side of the preceding target the latency of the saccades was faster and therefore more likely to be an express saccade. To further study this phenomenon Carpenter (2001) had participants take part in a two-gap task in which the fixation stimulus disappeared and then the target stimulus appeared either to the right or the left of it for 1 second. After the target stimulus disappeared it reappeared again either to the left or the right of its original position. In this task express saccades were more likely to happen when the target stimulus went in the same direction, that is appeared to the left or right in both situations. This indicates that the oculomotor system might be trying to predict where the next target should be and that saccades in the expected direction have a shorter latency. This indicates that bimodality is therefore a consequence of the way saccadic experiments are conducted (Carpenter, 2001). Schiller & Haushofer (2005) and Kurata & Aizawa (2004) did not, however, find any significant effect of the direction of successive saccades on either express or regular saccades. Kurata and Aizawa theorized that this could have been because the participants in Carpenter's (2001) task anticipated the target location in the forthcoming trial but in their task the participants were trained to perform an instructed gap task and that might have reduced their propensity for anticipation (Kurata & Aizawa, 2004). Schiller and Haushofer (2005) theorized that because their participants trained more than Carpenter's (2001) that they learned to perform the task as an autonomous task and therefore had no need to try and predict the next target location. Schiller, Slocum, Carvey, and Tolia (2004) examined whether express saccades were generated purely under experimental condition or whether they happened in natural viewing conditions. Two rhesus monkeys were shown a variety of naturalistic pictures, a video of monkeys in their natural habitat and a real life laboratory which contained two other monkeys and a few scientists. Schiller, Slocum et

al. (2004) found out that, although the rhesus monkeys generated express saccades commonly under these everyday conditions, overall distribution was unimodal. This experiment further suggested that bi- or multimodal distribution are therefore only obtainable under laboratory conditions (Schiller, Slocum et al., 2004) as Carpenter (2001) had suggested.

1.4.5. The coordination of saccades

The eyes move in accordance with each other regardless of their movement direction. This is achieved by the interconnection of the three cranial nerves, oculomotor, trochlear and abducent (also known as cranial nerve III, IV, and VI respectively), which are connected to the extraocular muscles. These cranial nerves are connected by the medial longitudinal fasciculus so the two eyes can move in unison (Patesta & Gartner, 2016). As mentioned before, the medial and lateral rectus of each eye almost solely produce horizontal movement (Kandel & Schwartz, 1985) but these muscle pairs are controlled by the abducens nerve (VI). When people perform a horizontal saccade the lateral rectus of one side and the medial rectus of the other both contract simultaneously. The abducens nerve does this with two different kinds of neurons inside its nucleus, motoneurons and interneurons. The motoneurons make up 70% of the neurons of the abducens nucleus and project to the ipsilateral lateral rectus. The interneurons make up the rest of the neurons inside the abducens nucleus and project to the contralateral medial rectus by a three-part pathway. First the interneurons project via the contralateral medial longitudinal fasciculus to the contralateral oculomotor nucleus. There, the interneurons synapse with motoneurons of the oculomotor nucleus that project to the medial rectus. Through this three-part pathway the interneurons help coordinate horizontal eye movements in the contralateral eye (Patesta & Gartner, 2016). Further evidence for this coordination, or lack thereof, can be seen in people with Duane Syndrome. Duane Syndrome Type 1 consists of a congenital unilateral horizontal abduction deficit in which people cannot move the afflicted eye towards the nose and may have problems moving it towards the temple. In this syndrome the abducens nerve is missing or hypoplastic which indicates that the abducens nerve is required for the coordination of horizontal eye movements (Yüksel, de Xivry, & Lefèvre, 2010).

1.5. Summary and hypothesis

Express saccades are produced both naturally (Schiller, Slocum et al., 2004) and in laboratory settings, although most likely with the use of a gap paradigm (Carpenter, 2001). With these

experimental conditions bi- or multimodal distributions are often seen for express saccades, short regular saccades and long regular saccades (Gezeck et al., 1996). Saccades can be generated at the higher-order in the SC, frontal, and medial eye fields, parietal cortex and the visual cortex. The order is then sent to the brainstem oculomotor center either by the anterior or the posterior stream depending on where it comes from and the nature of the eye movement (Schiller & Tehovnik, 2001). From the brainstem step and pulse commands are sent towards the cranial nerve responsible for that particular saccadic eye movement (Cullen & Van Horn, 2011). For a horizontal eye movement, the abducens nerve then sends motoneurons to the ipsilateral lateral rectus and interneurons to the contralateral medial rectus so the eyes are coordinated in their horizontal gaze (Patestas & Gartner, 2016).

It is known that gap paradigms increase the likelihood of the generation of express saccades. It is also known that by training express saccades in one direction, the benefits of that training transfer to other directions (Bibi & Edelman, 2009). Given that almost all eye movements are conjugate it is possible that the benefits might carry to the other eye as well, due to the interconnectedness that is required for conjugate eye movement. Horizontal saccadic eye movements are conjugate through interneurons of the abducens nerve (Patestas & Gartner, 2016). The hypothesis is that due to the interconnectedness of horizontal saccadic eye movements the benefits of training express saccades in one eye would be carried over to the other eye. In this study express saccades were trained by using a gap paradigm and two locations (left and right: amplitude = 8°). The dominant eye was trained and the non-dominant eye was observed. We predicted that a greater number of express saccades would be seen after training in the untrained non-dominant eye. It was also anticipated that latencies of saccades in general would be much lower post training.

2. Method

2.1. Participants

Participants were 9 unpaid volunteers (3 were women) who were naïve as to the purpose of this study. Participants were chosen through convenience sampling. All reported normal or corrected to normal vision. Mean age of the participants was 23.78 years, ranging from 22 - 27. All but one participant had a right dominant eye.

2.2. Research Design

This study had a within-subject design, where each participant received the same experimental conditions in all parts of the study. The independent variable of the study was training and probe sessions. Probe sessions assessed saccadic latencies in the dominant and non-dominant eye (the other eye obstructed with an eye-patch) in a horizontal direction before, in the middle of and after training. Training sessions were identical to probe sessions except saccadic latencies were assessed only in the dominant eye. The dependent variable for both training and probe sessions was the latency which was measured in milliseconds and the number of express saccades ($RT = 75\text{-}120\text{ ms}$) made.

2.3. Stimuli

The fixation stimulus was a 1° dot in the center of the screen. The fixation stimulus disappeared after a base gap time of 200 ms which was randomly varied $\pm 10, 20$ or 30 ms around it. The target stimuli were 1° dots which appeared after the fixation stimulus disappeared. The target stimuli appeared randomly either to the left or right on the screen, 8° away from fixation. The RGB value of the screen was [255, 255, 255].

2.4. Equipment

A monocular high-speed video eye tracker from Cambridge Research Systems was used for the experiment, with a sampling refresh rate of 250 Hz (one data point every fourth millisecond). The eye tracker utilizes an infrared camera of the pupil and dual first Purkinje glints to measure eye movement. Infrared light from two diodes are used to create the two corresponding Purkinje images that keep track of the gaze. Each infrared diode is positioned on the opposite side of the infrared camera. By imaging the eye with two infrared illuminations a dark pupil with two bright and horizontally separated Purkinje glints is created. The Purkinje glints will remain bright, compact and constantly separated which gives

the eye allowable eye rotations of up to 40° and creates illumination over the entire eye. Tracking accuracy was between 0.125-0.5° with the horizontal range being $\pm 40^\circ$. Chin and forehead are placed on a chin- and headrest to limit movement although the eye tracker can correct for head movement of up to 8 millimeters (Cambridge Research Systems, 2006). The viewing distance was 58,5 cm.

The experiment was run on a Dell computer with an Intel Core with 2.40 GHz. The working memory was 4 GB and the operating system was a Microsoft Windows 7. A 100 Hz 19" *Hansol* monitor (model: 920D resolution: 1024 x 768 px) was used to display the experiment. The screen had a width of 368 mm and a height of 261 mm.

A custom program was written in Matlab (v. 7.14.0.739, 2012a, 32-bit) for the experiment by Dr. Ómar I. Jóhannesson. Matlab was used to run the experiment, communicate with the eye-tracker and keep track of when the stimuli appeared and disappeared. PsychToolBox was used to display the targets and provide timestamps when they appeared (Brainard 1997; Pelli 1997).

2.5. Procedure

The experiment was run in a sound-proof booth. In order to choose which eye was the dominant eye the participants were asked to point to a distant object (a pen) and close each eye in turn. If the finger did not move when the left eye was closed the right eye was considered to be the dominant eye and vice versa. Participants were then asked to cover the eye, not being tested, with an eyepatch. Participants were asked to fixate on a target in the middle of the monitor and when the target disappeared to move their eyes as quickly and as accurately as possible to the target either on the right or left side. The participants were then asked to make themselves comfortable in their seat and put their head on the chin- and headrest. The eye-tracker was then adjusted to them in relation to their comfortable sitting position and which eye was being tested. Once they announced themselves to be ready the researcher began the experiment.

Before and in the middle of each session an eye calibration was performed. An eye calibration consisted of 9 fixation points (top left, top middle, top right, middle left, middle center, middle right, bottom left, bottom middle and bottom right) with each point being randomly generated one after another on the screen. The participants were asked to be as

accurate as possible while the calibration was being performed. In all there were 18 sessions (with 10 trials in each) which were either probe or training sessions. In the probe sessions, each eye was measured three times, at the beginning, in the middle and at the end. The dominant eye was measured first (probe session 1a, 2a and 3a) and then the non-dominant eye (probe session 1b, 2b and 3b). There were 12 training sessions, 6 before probe sessions 2a and 6 training sessions after probe session 2b (see Figure 1). In the training session only the dominant eye was trained. Both probe and training session had 10 blocks, with each block containing 28 trials. A trial contained an eye movement from the fixation stimulus, in the middle of the screen, towards the target stimulus either to the right or left side and then back towards the middle in preparation for the next trial.

Initially a message appeared stating that participants could quit whenever they wanted by pressing “h” on the keyboard and to press the space bar to continue. The fixation stimuli appeared in the middle of the monitor for 170-230 ms before disappearing. After the fixation stimuli disappeared the target stimuli appeared randomly to either the left or right of the fixation stimuli. If an error was made an error message came up and the participants were required to push the space bar on the keyboard to continue. There were three types of error, when a participant was not looking at the fixation stimulus when it was supposed to appear, when a participant did not look at the target stimuli when they appeared, and when they moved their eyes away from the middle of the screen before the target stimuli appeared. Participants were told that they could take breaks between blocks but asked to try and wait until an eye calibration was performed.

2.6. Statistical Analyses

When a participant accidentally pressed another button than the space bar or “h” the program stopped working. Due to this the program was shut down and restarted. An error in the program did not allow a new session to start numbering blocks in the middle. Therefore, duplicate folders for some blocks in some sessions were created. When that happened a new session was started with the same session number to finish the blocks that were left. Due to this, all duplicate session folders were viewed and the relevant line that indicated the block was changed. The statistical program *RStudio* 0.99.491 (R Core Team, 2015) was used to perform all statistical analyses. First all the relevant text files were brought into a single data frame within *RStudio*. Based upon Bibi and Edelman (2009) all saccades with latencies

smaller than 75 ms were considered to be errors and excluded from the analyses. The mean and standard deviation of saccadic latency for each participant was computed and saccades that were more than 3 standard deviations from the mean were excluded. This constituted 6.9% of the data. A paired *t*-test was performed to test the differences in saccadic latencies in probes 1b and 2b along with 1b and 3b. The same procedure was performed in regards to the number of express saccades. A comparison of each eye in each probe session (a, b and c) was also performed by means of a paired *t*-test. When a *t*-test was performed to check whether express saccades happened more frequently after training only saccades with latencies between 75-120 ms were chosen (based on Delinte et al. 2002).

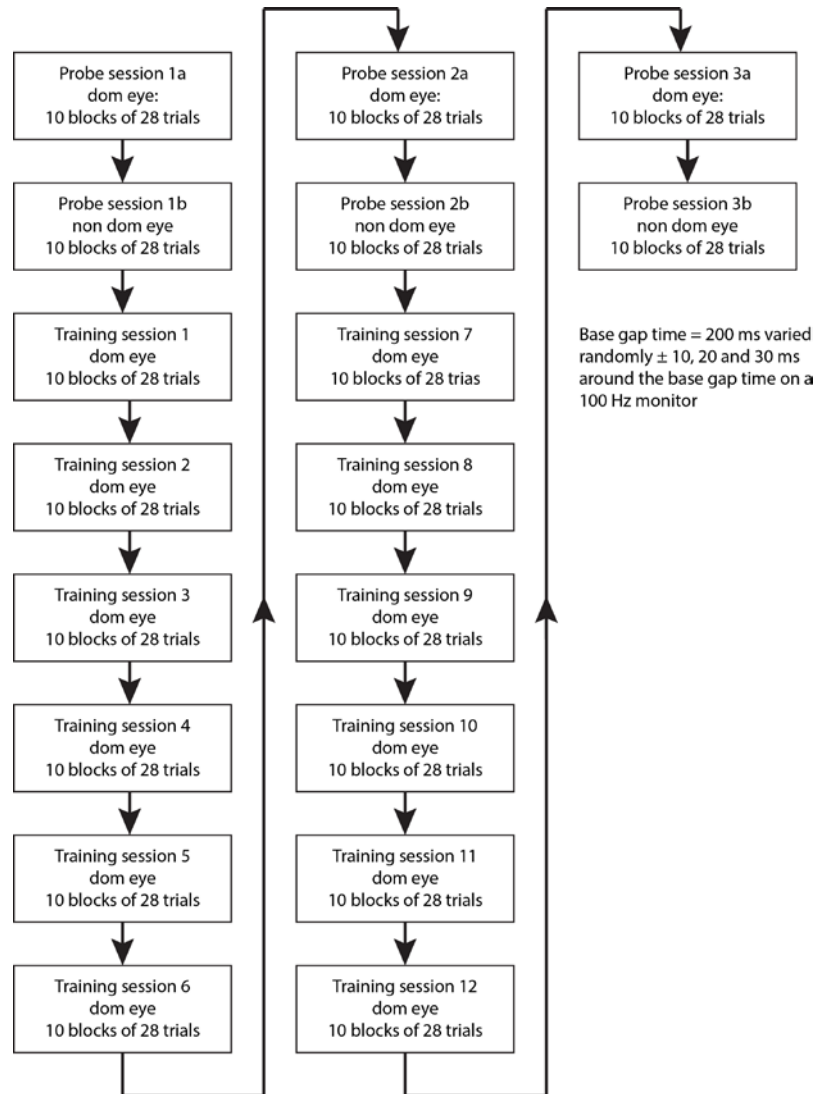


Figure 1. The progression of the experiment from probe session 1a to probe session 3b. Each session consisted of 10 block with 28 trials each block.

3. Results

The difference between mean latency before training (1b) and after training (3b) was significant, $t(8) = 3.74$; $p = 0.0057$. A paired t -test showed a significant difference in mean latency before training (1b) and in the middle of training (2b) $t(8) = 4.2$; $p = 0.003$. As can be seen in Figure 2 there is a clear difference in the mean latency between probing session 1b and 2b along with 1b and 3b. In probe session 1b the mean saccadic latency was 173 ms while probe session 2b had a mean latency of 146 ms and 3b had a mean latency of 140.

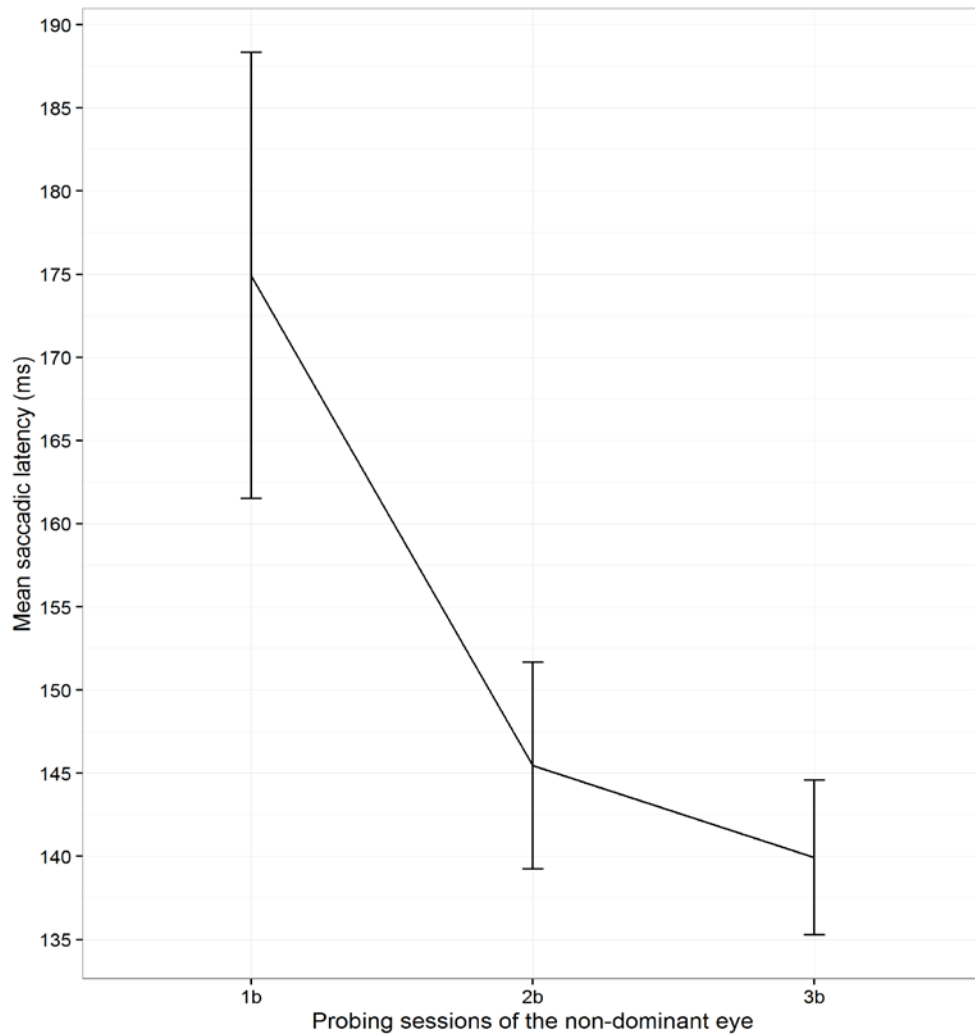


Figure 2. The mean latency (ms) of the three probing sessions of the non-dominant eye with a 95% confidence interval. The latency became shorter with the training in between probe sessions 1b and 2b. This downwards trend continued between probe sessions 2b and 3b.

The difference between the number of express saccades made for probing sessions 1b and 3b was significant $t(8) = -2.64$; $p = 0.03$. The difference between the number of express saccades made for probing sessions 1b and 2b was also significant $t(8) = -2.42$; $p = 0.04$. In Figure 3 the number of express saccades made based on each probe session is shown. The figure shows an upwards trend in the generation of express saccades between probe sessions in both the dominant and non-dominant eye. The difference between probe sessions 1a and 1b is not significant $t(8) = 0.63$; $p = 0.54$. Neither is the difference between probes 2a and 2b along with 3a and 3b significant $t(8) = -0.22$; $p = 0.83$ and $t(8) = -1.07$; $p = 0.32$ respectively.

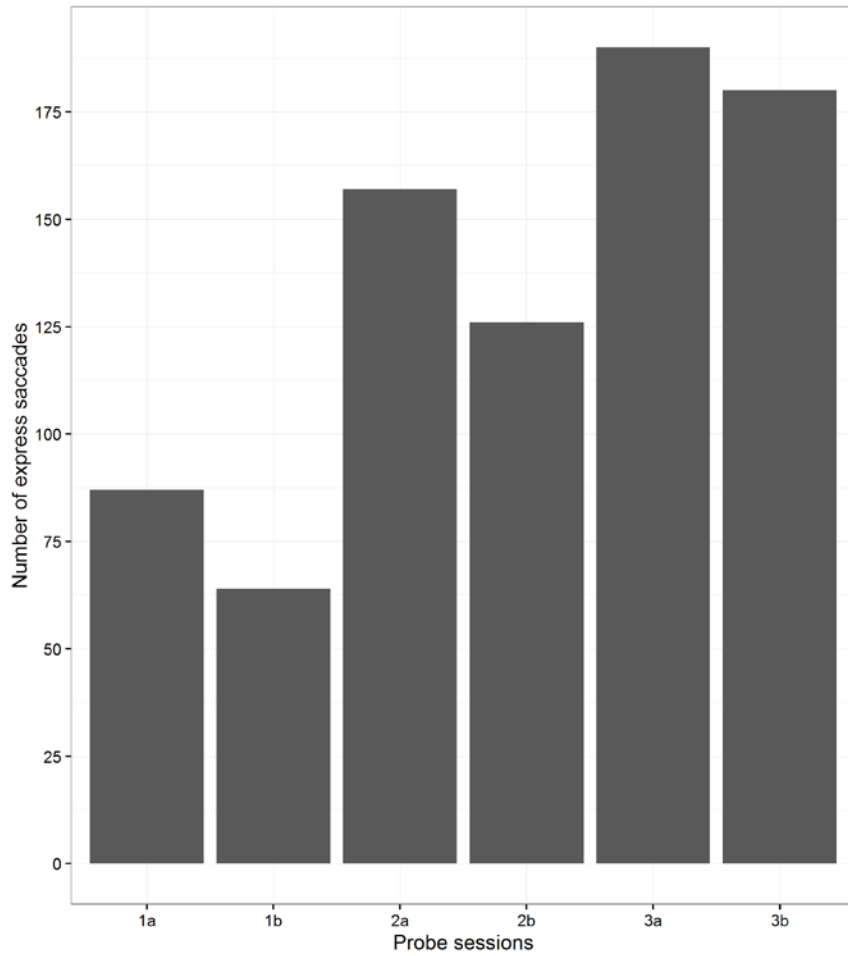


Figure 3. The number of express saccades based on probe sessions with the dominant eye (a) and non-dominant eye (b). An upwards trend is shown with each successive probing session culminating in a relatively small difference between the eyes.

Figure 4 shows a clear trend of the number of express saccades based on the training sessions. The first four training sessions were all below 110 express saccades while the last four training sessions are all above 150 express saccades. Figure 5 demonstrates the probing sessions of the non-dominant eye for all the participants and it appears that not all participants showed the same pattern. Participants 1, 2, 4, 7, and 9 showed clear benefits of the training and a downwards trend of the latency, while participant 3 seems to have lowered his latency minimally. Participant 8 has his lowest latency in probe session 2b while probe session 1b and 3b seem to be on par with each other.

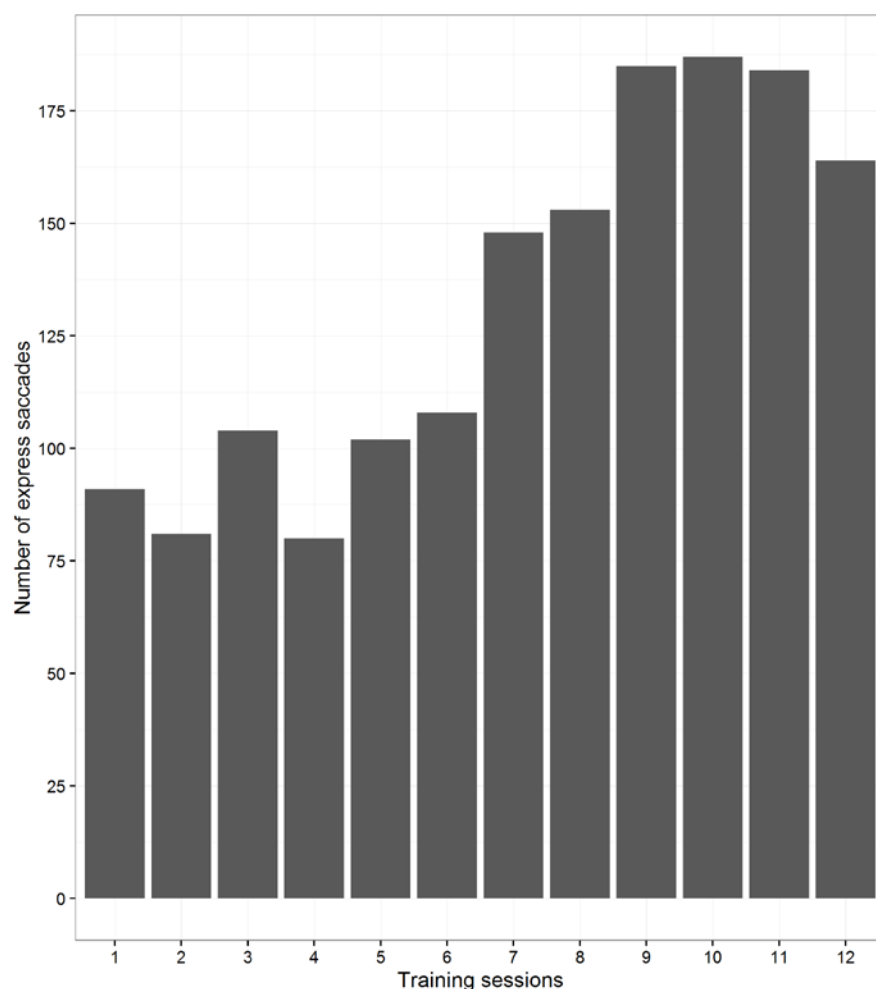


Figure 4. The number of express saccades based upon training sessions. A clear upwards trend of the number of express saccades can be seen.

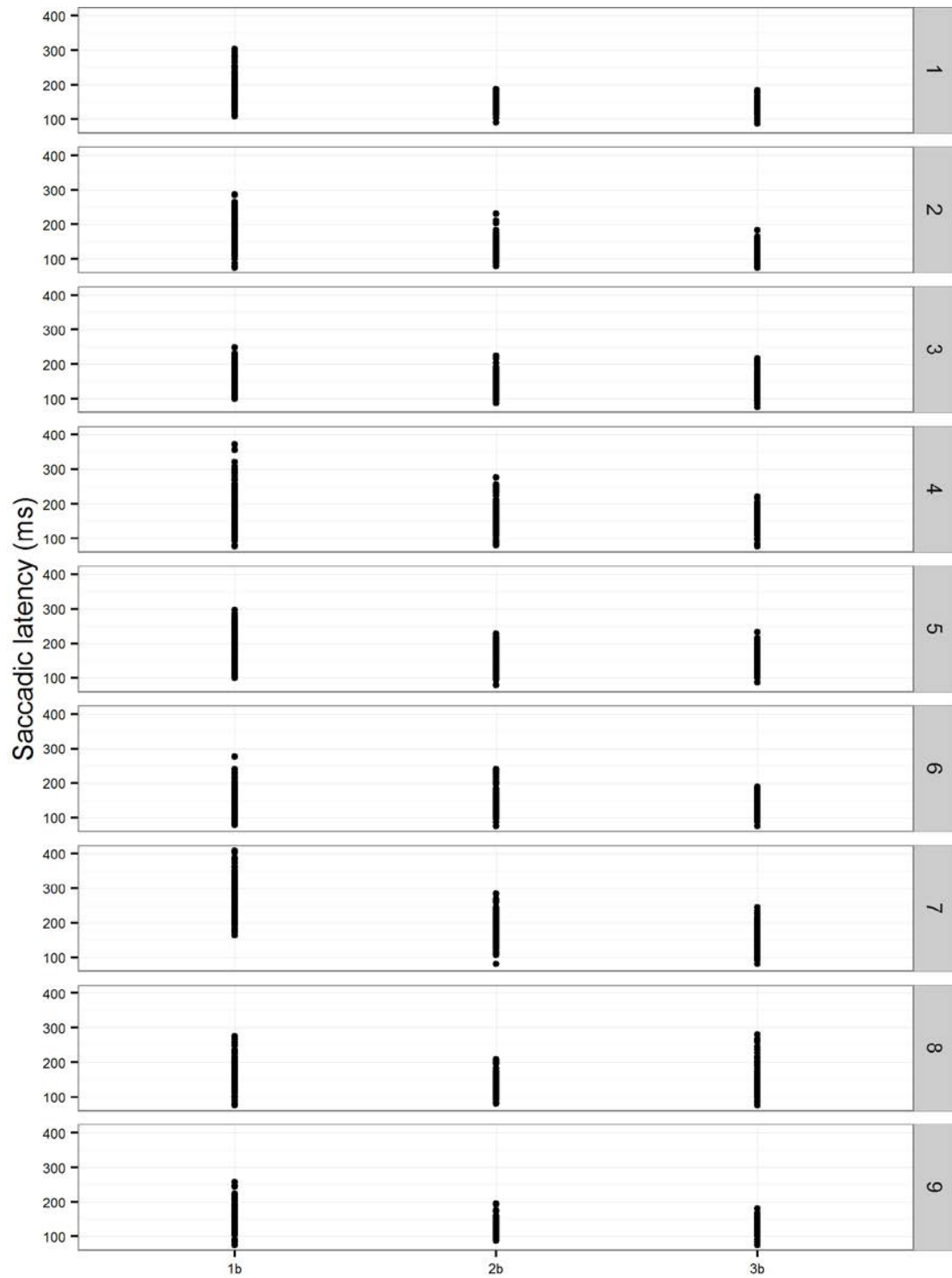


Figure 5. The latency (ms) of each participant based on the probing session of the non-dominant eye. An individual benefit can be seen here. Participants 1, 2, 4, 7 and 9 had clearly lower latencies by the end of the training while participant 3 seems to have only minimally reduced his latency.

4. Discussion

Express saccades have been extensively investigated (see Bibi & Edelman, 2009; Carpenter, 2001; Edelman et al., 2006; Kurata & Aizawa, 2004) and it has been shown that they occur both in natural (Schiller et al., 2004), in laboratory settings (Carpenter, 2001), that they are likely to be exogenous (Rhorer & Sparks, 1993), and can be influenced by top-down processes (Edelman et al., 2007). The transference of benefits between the eyes after training express saccades or any saccades for that matter has not been studied, however. It has been shown that by training express saccades in one direction the benefits of that training can be transferred to the other directions as well (Bibi & Edelman, 2009). It is also known that horizontal eye movements are interconnected through interneurons who connect to the contralateral medial rectus in order to coordinate the eye movements (Patestas & Gartner, 2016).

The purpose of this study was to test whether the training of horizontally made express saccades of the dominant eye would transfer over to the non-dominant eye. The results showed that saccadic latencies were lower in the non-dominant eye both in the middle and at the end of the training. The results also showed that the number of express saccades were more frequent both in the middle and at the end of the training. It can therefore be said that the number of express saccades increased in the non-dominant eye following training, as predicted. It was also established that there were no discernible differences in the number of express saccades between the eyes. This indicates that due to the interconnectedness of conjugate eye movement within the eyes (Patestas & Gartner, 2016) the training of one eye can benefit the other. Since both the saccadic latencies were significantly lower and the number of express saccades significantly higher during the middle of the training this suggests that future research on transference of benefits will not have to go through 12 training sessions. Six training sessions might be adequate to show differences in the non-dominant eye compared to the trained eye when training express saccades.

Carpenter (1994) compared the workings of the eyes to the mechanisms of the brain. With this in mind it is not necessarily surprising that there is a lot of coordination between the eyes. The brain might have hemispheric dominance in many areas like in Broca's area which specializes in speech and Wernicke's area which specializes in language but by utilizing inter-regional interactions coherent behavior can be achieved (Serrien, Ivry, & Swinnen, 2006).

This study shows that the same applies to the eyes. The results demonstrate coherent behavior in the form of moving the same way, at the same time and to the same place and by training one eye the benefits of that training can be transferred by interactions with the other eye. This study also indicates that the eyes do not need to perform the same action in order for both eyes to learn that particular action. By training one eye the benefits of that training can be transferred to the other eye.

As far as we know, this is the first investigation of transfer of benefits between the eyes. In order to confirm this a replication would be needed and it would also be interesting to see whether vertical movements could be transferred between the eyes. We have seen that by training eye movements in one direction the benefits of that training transfer to the other directions (Bibi & Edelman, 2009) but it would also be interesting to see whether the training of one direction in one eye can benefit other directions in the other eye.

5. References

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