

CAROLINA MURD

Mechanisms of processing
visual motion information:
Psychophysical, bioelectrical and
transcranial magnetic stimulation
investigations



DISSERTATIONES PSYCHOLOGICAE UNIVERSITATIS TARTUENSIS

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LIST OF ORIGINAL PUBLICATIONS

This dissertation is based on the following original publications, further referred to by respective Roman numerals:

- I Bachmann, T., **Murd, C.**, & Põder, E. (2012). Flash-lag effect: complicating motion extrapolation of the moving reference-stimulus paradoxically augments the effect. *Psychological Research*, 76, 654–666.
- II Kreegipuu, K., **Murd, C.**, & Allik, J. (2006). Detection of colour changes in a moving object. *Vision Research*, 46(11), 1848–1855.
- III **Murd, C.**, Kreegipuu, K., & Allik, J. (2009). Detection of colour change in moving objects: Temporal order judgment and reaction time analysis. *Perception*, 38 (11), 1649–1662.
- IV **Murd, C.**, Kreegipuu, K., Kuldkepp, N., Raidvee, A., Tamm, M., & Allik, J. (*accepted*). Visual evoked potentials to change in colouration of a moving bar. *Frontiers in Human Neuroscience*.
- V **Murd, C.**, & Bachmann, T. (2011). Spatially localized motion aftereffect disappears faster from awareness when selectively attended to according to its direction. *Vision Research*, 51(10), 1157–1162.
- VI **Murd, C.**, Einberg, A., & Bachmann, T. (2012). Repetitive TMS over V5/MT shortens the duration of spatially localized motion aftereffect: The effects of pulse intensity and stimulation hemisphere. *Vision Research*, 68, 59–64.

The author of the present dissertation contributed to these publications as follows:

- In Studies **I** and **II**: participated in developing the study concept and data collection, carried out data analyses and participated in writing the manuscript.
- In Study **III** and **IV**: participated in conducting the experiments and data collection, carried out data analyses and wrote the manuscript as the main author.
- In Study **V**: participated in conducting the experiment and data collection, carried out data analyses and participated in writing the manuscript.
- In Study **VI**: participated in formulating the research hypothesis, collecting data, analysing data and writing the manuscript.

Principal aims of the studies are to:

- Study I: introduce a new experimental setup for flash-lag effect (FLE) design and investigate whether the motion extrapolation mechanism is crucial for FLE.
- Study II: test whether the presence of motion information influences the perception of other features of the moving object, indicating to the (in)dependency in processing different features.
- Study III: control whether the effect of velocity found in Study II is universal and appears also in tasks where different setups or stimuli are used.
- Study IV: replicate the simple reaction time setup used in Study II and in addition measure visual evoked potentials in order to study how the effect of velocity on the detection of colour change shows up at the cortical level of perception.
- Study V: test whether motion processing mechanisms responsible for static motion after-effect are facilitated or inhibited by the spatial selective attention and use motion perception mechanisms as a means to explore relations between attention and awareness.
- Study VI: study involvement of the middle temporal cortical area (V5/MT) in the attention-sensitive motion after-effect by causally modulating the functional state of this area by repetitive transcranial magnetic stimulation (rTMS).

INTRODUCTION

Perception of motion is one of the most important functions of our visual system. The ability of the visual system to process and use the information provided by motion enables us to cope with the dynamic environment. Even more importantly – perceptual analysis of motion helps us to adapt to the environment and survive in it. Therefore, we can say that the capacity of visual motion analysis is vital. From the first person perspective it would be quite unimaginable to live without being able to ‘see’ motion.

But what makes this ability so amazing – and, for a researcher, a lot more mind-poking – is the fact that it does not work quite ‘online’. The representation of the environmental variables that our brain has constructed based on the perceived information, is actually out of date when compared to the currently existing physical reality. This applies particularly well to motion perception.

In physics, motion is defined as a change in the spatial position of an object over time. Despite the perceptual lag of the mental representation, when performing an act based on this representation (e.g., catching a ball or getting out of its way), we are able to predict the future reality adequately in most of the circumstances. This indicates that our brains perform computations and draw predictions based on these computations that ensure an adequate response. A variety of research traditions have a common aim to figure out these exact computations and predictions rules by using motion signals. Some typical experimental paradigms used for this purpose are as follows: comparing processing of moving versus stationary objects (e.g. flash-lag effect, reaction time to stationary versus moving stimuli), motion aftereffect, and apparent motion. The present dissertation was also motivated by the interest in the perception of motion as it unfolds in different stimulation contexts and in differences in the perception of moving objects compared to stationary objects. An attempt to capitalize on the methodological resources provided by the variety of experimental paradigms of motion perception has led to formulation of the generic purpose of the present dissertation – to contribute to the understanding of the perception of motion from both the psychophysical and neuroscientific perspective and bearing in mind the variety of sensory-perceptual contexts the motion perception unfolds.

I. MOTION PERCEPTION

I.I. Encoding motion information in the visual system

Nowadays, it is generally accepted that the middle temporal visual area (MT/V5; Zeki, 1974) is specialized prevailingly for processing motion information. The direction- and speed-selectivity of MT/V5 neurons has been demonstrated in body of studies (Maunsell & Van Essen, 1983; Rees, Friston, & Koch, 2000; Tootell, Reppas, Dale, Look, Sereno, Malach, Brady, & Rosen, 1995; Van Essen, Maunsell, & Bixby, 1981).

But the V5/MT is not the only mechanism in the brain or in the whole visual system that detects and encodes motion. Direction-selectivity of motion analysis is already present in the retina (Barlow & Hill, 1963). There are M cells in the retina from where the information of motion is projected to lateral geniculate nucleus (LGN; layers 1–2) and from LGN to primary visual area V1 via the magnocellular pathway. The other major neural pathway connecting the retina and visual cortex (via LGN; layers 3–6) is the parvocellular pathway. The M cells and parvocellular P cells in the retina differ by their sensitivity to wavelengths, contrast, signal transfer speed, and acuity (Kaplan & Shapley, 1982). The P cells in the retina respond (differently) to different wavelengths, indicating that they carry the information about colour (Hubel & Wiesel, 1972; Livingstone & Hubel, 1988). M cells (in the retina and LGN) are relatively insensitive to chromatic contrast, but highly sensitive to luminance contrast. Since the magnocellular axon has a larger diameter than the parvocellular axon, it transmits the electrical signal faster. The magnocellular neurons have been shown to have about 10-20 milliseconds shorter central response latencies than the parvocellular neurons; the latter also do not show any direction-selectivity (Munk, Nowak, Girard, Chouinlamountri, & Bullier 1995; Nowak, Munk, Girard, & Bullier, 1995; Maunsell, Ghose, Assad, McAdams, Boudreau, & Noerager, 1999). The M cells receive their input from many photoreceptors and have large spatial summation capacity. On the other hand, P cells receive their input from fewer cells and have smaller spatial summation capacity.

There is also a third visual pathway from the retina to the V1 – the koniocellular pathway. While the parvocellular pathway has been considered mainly as a contributor to the signal analysis in the red-green colour vision, koniocellular pathway seems to get its input from S-cones in the retina and some K cells respond to colour (blue-ON cells). Many K cells are found to be intermediate between P and M cells in their temporal and spatial properties (Solomon, White, & Martin, 1999). However, the role of the koniocellular pathway is not quite clear. Namely, it is not purely ‘colour’ pathway, it has been found to be sensitive to stimuli moving at high temporal frequency. Morand and her colleagues (Morand, Thut, de Peralta, Clarke, Khateb, Landis, & Michel, 2000) have found that in some moving stimuli koniocellular pathway appears to cause an earlier activation in cortex than magnocellular pathway.

The information from V1 is passed on by two main routes – the ventral and the dorsal stream (Goodale & Milner, 1992). The ventral stream (also named the “what” or perceptual pathway), which receives both magno- and parvocellular inputs, projects its fibers to the extrastriate cortex areas and to inferotemporal cortex. The ventral stream has been associated with object recognition. The dorsal stream (“where”/“how” or action pathway), receiving mostly magnocellular input, projects to posterior parietal cortex. It has been associated with movement for action and processing of motion (V5/MT).

Another aspect worth mentioning here is that additionally to the retinocortical pathways there is a route from the retina to superior colliculus (SC) that sends information to pulvinar, which in turn sends signals to parietal cortex (by-passing V1). This route has been associated with the control of eye movements and spatial attention (Shipp, 2004). There are also some neurons in the koniocellular pathway that innervate extrastriate areas – among others V5/MT – without projecting through V1 (Hendry & Reid, 2000; Sincich, Park, Wohlgemuth, & Horton, 2004). Of course, there is considerable amount of inter- and feedback-connections between different areas, which indicates that the distinction between the dorsal and the ventral stream and between within-stream areas, and establishing their specialization, is rather relative. This only proves that information processing paths in visual system are indeed complex and by no means yet fully mapped.

I.2. Making a decision based on sensory motion-processing

Most of the time the sensory perception results in some sort of an action – saccadic eye movements, grasping, oral reports, or more complex combination of actions. This kind of performance is usually a result of processing sensory information and based on this information making a decision about action execution (Hommel, Müsseler, Aschersleben, & Prinz, 2001). The assumptions about involvement and processing characteristics of the sensory stage of information processing are often made based on the performed action. This is essentially what the standard psychophysics does – analysing how the values of varying sensory input (stimulus) affect the corresponding subjective experience or behaviour and drawing conclusions about the perceptual processes behind the outcome which itself is based on the performance. Technological development and interdisciplinary research has made it possible to shed some light to the neural sensory processes and different stages of information processing (perception, decision-making and formulation of motor response) on which psycho-physical behavioural regularities are founded. This aspect of research is what Fechner termed “inner psychophysics” regarding it not to have less of a value than the traditional behavioural aspect of psychophysics or “outer psychophysics” has (Scheerer, 1987). Considerable amount of research has been done with different methods, such as electroencephalography (EEG), functional

magnetic resonance imaging (fMRI), transcranial magnetic stimulation (TMS) and many others. This research has provided an invaluable contribution to mapping the neural activity onto corresponding mental and behavioural effects and ascertaining the role of different brain areas during information processing. Among other results, this approach has also given a glimpse at the role of certain brain areas involved in formulating a decision based on sensory information (Gold & Shadlen, 2003; Mulder, Wagenmakers, Ratcliff, Boekel, & Forstmann, 2012; Roitman & Shadlen, 2002; Shadlen & Newsome, 2001).

For example, Newsome, Britten and Movshon (1989) demonstrated in a study on monkeys that activation in motion direction sensitive area (V5/MT) predicts the decision that is about to be made. Roitman & Shadlen (2002) found shorter reaction times (RT) and stronger stimulus motion to be correlated with steeper rise of the activity of neurons in lateral intraparietal area (LIP, the analogue of the area intraparietal sulcus in humans, IPS) in macaques, suggesting that intraparietal sulcus (IPS) is involved in integrating sensory information from MT and formulating a decision based on the accumulating evidence for specific behavioural response. Frontal brain areas, such as frontal eye field (FEF), have been also found to have changes in activation in correlation with the activity of area MT when a decision about motion direction has to be made (Kim & Shadlen, 1999).

However, these modulating processes are even more varied and not unidirectional – our intentions and motivations influence our perception. The influence of attention on the perception of motion has been repeatedly demonstrated already in psychophysical studies (Allen, & Ledgeway, 2003; Alais & Blake, 1999). The fMRI and micro-stimulation studies have shown that the activity of MT can vary remarkably depending on whether motion is attended or not (Beauchamp, Cox, & DeYoe, 1997; O'Craven, Rosen, Kwong, Treisman, & Savoy, 1997; Rees, Frith, & Lavie, 1997; Treue & Maunsell, 1996, 1999). For example, O'Craven and colleagues presented their subject with a display that consisted of both stationary and moving stimuli. Subjects were instructed to attend alternately to moving or stationary stimuli. They found that the activity of area MT was reduced when stationary stimuli were selectively attended and the activation increased as moving stimuli were attended. As the display did not change, this result illustrates the attentional effect on perception. They also had another important finding – when stationary stimuli were attended in a control display where moving stimuli were absent, the activity of MT was even more reduced than in the main condition where moving stimuli were present but not attended. These results demonstrate nicely that even when motion information is irrelevant, it is not easily ignored by sensory systems and that attention is an important variable in motion perception.

Therefore, – as the whole process from the retinal stimulation to action is complex, involving different stages of information processing, decision building, performing an act and having influences which are mutually modulatory, – it is advisable to use different methods and paradigms measuring different stages and aspects of this process of motion perception. The following

investigations, on which the present dissertation is based on, were driven by this belief, concentrated on several aspects and used different research techniques to study the perception of motion.

2. THE PERCEPTION OF MOVING AND STATIONARY OBJECTS

2.1. Flash-lag effect

For more than half a century, beginning with studies by Hazelhoff and Wiersma (1924), Metzger (1932), MacKay's article in Nature in 1958, and re-introduced by Nijhawan in 1994, the flash-lag effect (FLE) paradigm has been one of the most popular paradigms for investigating the perception of moving objects as compared to the perception of static objects. This phenomenon supposedly reflects how our visual system compensates for or overcomes the inevitable perceptual delays in order to make perception more veridical in space and time. It has been shown that when a briefly flashed static target is presented in a physical alignment with a moving target, they appear to be misaligned so that the position of the moving target is assessed to be ahead along the moving trajectory. Over the years quite many theories have tried to explain how exactly this kind of misperception takes place and these theories have been updated along the way as new research methods, additional aspects of the phenomenon and findings about information processing have been found. Despite that the exact mechanism of this phenomenon is yet unknown, all theories assume that the stimuli compared in the context of the FLE (a briefly flashing versus a moving stimulus) are processed differently. A brief overview of the most popular theories would be as follows.

Extrapolation/prediction theory

According to the extrapolation/prediction theory (Nijhawan, 1994; 2008; Maus & Nijhawan, 2008) the visual system makes predictions and overcomes the processing delay of the moving stimulus by extrapolating it virtually into the future position. But since the brief stationary object is not including any clues about the possible future position (which is thus unpredictable), the visual system does not perform an operation of extrapolation and “predicts” the same static position.

Latency-difference theory

The latency-difference theory (Whitney & Murakami, 1998) assumes that moving objects are processed faster than brief stationary objects by the visual system. Therefore, when information about the positions of objects is being perceived, the flashed static object appears to be located at the perceptual position lagging behind the position of the moving object because the latter is signalled faster.

Attention shifting theory

The attention shifting theory (Baldo & Klein, 1995) assumes that the appearing flash engages attention, shifting attention to the stimuli takes time, and at the time when attention is fully engaged (and is necessary for perception) the

moving object provides positional information from a new, spatially advanced position. As a result, when the subsequent positions of the flashed stationary and the moving object are evaluated by the attentive perception, the positions seem misaligned.

Postdiction theory

According to the postdiction theory (Eagleman & Sejnowski, 2000), visual awareness is postdictive – the gathering of different features of the object takes time, and thus their delayed perception which has to “wait” until the slowest processed features are added to the forming percept is a function of the events taking place after the flash. But the formed percept (including the advanced position of the moving object) is attributed back to the time of flash.

Perceptual retouch theory

The perceptual retouch theory (Bachmann, 1999; Bachmann, Luiga, Pöder, & Kálev, 2003; Bachmann, 2007) claims that perception involves two distinct processes. The faster process using primary afferent pathways includes specific information about object’s features, but is not sufficient for conscious perception; the slower thalamo-cortical process is a non-specific activation necessary for modulating specific contents up to conscious perception. The FLE occurs because the slow process “finds” specific information of the moving object specifying an advanced spatial position, but the flashed object position is “found” from the sensory memory indicating the unchanged position. Furthermore, because the moving object represents a stream of stimulation, the preceding signals of the stream can ignite the action of the slow mechanism for the later in-stream signals which become facilitated. Thus, the advanced position of the moving stimulus is communicated for perception faster than the position of the stationary flash, for which there has been no preceding signals that would have facilitated processing.

Updating theory

The updating theory (Kanai, Carlson, Verstraten, & Walsh, 2009) suggests that by the time the flash as a new object appears and formation of its representation starts, the moving object has been visible for a while, which means that there already is a mental representation of the moving object and its updating (position updating) takes less time than building up a new representation for the flash as a new object.

Some of these theories have tried to explain the mislocalization of the moving object by lower-level, some by higher-level processing mechanisms.

Using the FLE as a model case of perception involving dynamic events, we asked whether the lower or higher level mechanisms are responsible for the FLE; for this, we ran several experiments (**Study I**). In the different experimental setups we used two oppositely moving (mutually approaching / meeting / departing) stimuli where the reference-moving stimulus was marked with a

certain colour and the briefly flashed static stimulus had to be compared to that. If lower-level motion-coding mechanisms that are tuned to opponent motion vectors and therefore mutually inhibitory, would be conducting an extrapolation or prediction, then the presence of opposite moving vectors should nullify the FLE. Even if it is assumed that two parallel independent extrapolations/ predictions are made based on the two stimuli moving in opposite directions, it should lead to the decrease of the FLE magnitude. The perceptual retouch theory on the other hand would predict the FLE increase in presence of two opposite moving stimuli. This is because the opposite-to-reference moving stimulus might act as a sort of prime for the position of the reference-stimulus. The priming stimulation would prepare the slow activation ahead in time and the specific signals of the moving reference stimulus should be perceived faster, thus increasing the FLE magnitude.

In Experiment 1, in the main condition the opposite moving stimuli approached each other and met in the central part of the screen; thereafter, only the reference stimulus kept moving after the meeting-point was crossed. We also had a control condition (a FLE display otherwise identical to that of the main condition, but only with one moving stimulus). The results showed that in the presence of two opposite motion vectors, the FLE magnitude increased compared to the control condition (**Study I**, Figure 2.). This means that when the flashed object was presented before the moving reference-object arrived at the meeting-point it nevertheless became perceptually aligned (in spatial dimension) with the moving reference-object. (The status of the reference object was known since the beginning of each trial.) When the flashed object was presented exactly at the moment when the moving stimuli arrived at the meeting-point, the FLE emerged. In the control condition where the opposite-to-reference moving stimulus was absent, the FLE was smaller. To be sure that this magnitude rise in the FLE was not induced by the abrupt offset or by differences in sensory memory for motion of the opposite-to-reference stimulus, we conducted a second experiment. In Experiment 2, in one condition the opposite-to-reference stimulus kept moving after the flash (continuous opposite motion). In another condition, we slightly shifted the trajectory of the opposite-to-reference stimulus up so that when it met the reference-stimulus they did not overlap spatially anymore (adjacent opposite motion condition); as soon as the moving stimuli became aligned the stimulus moving opposite to the reference was switched off. The results of the two experiments taken together were as follows: when the different opposite-motion conditions (the main condition in Experiment 1 and both conditions of Experiment 2) were compared to the control condition (one moving stimulus, Experiment 1) the FLE was significantly stronger in all of the opposite-motion conditions (when measured as mean values of the point of subjective alignment; p-values varying between .003 and .005). This indicates that the increase of the FLE magnitude in Experiment 1 in the opposite-motion condition was not caused by abrupt offset of the stimulus moving oppositely to the reference or by ‘merging’ of the moving stimuli when they started to overlap. (The latter event would have

possibly caused the real considerable advancement of the front edge of the moving stimulus and produced the flash-lag as an artefact.)

This indicates that the lower-level mechanisms that work according to the principle of mutual inhibition of the opponent neural mechanisms (expected to nullify or reduce the FLE) are not responsible for the FLE. Thus, the FLE may be based either on higher-level motion analysing mechanisms or on mechanisms independent of the sensory system specifically dedicated to motion analysis. Furthermore, the above described results suggest that the FLE may not be the best paradigm to explore basic motion-perception mechanisms.

2.2. Processing different features of the dynamic object

The speed of perceptual processing of different stimuli and their attributes varies considerably. Consequently, this poses quite difficult computational problems for the visual system and limitations for human observers in the tasks requiring rapid evaluations and responding. For example, it has been pointed out by the retouch theory (Bachmann, 1999, 2007) and updating theory (Kanai et al., 2009) that in the FLE paradigm subjects are asked to compare the characteristics of an on-going stimulation for which the perceptual representation is just updated, and a new stimulus for which the perceptual representation has yet to be formed from the very beginning. It is worth reminding here that creating a representation of a new object takes more time than updating a representation of an old object. Essentially, we are dealing with a task of perceptual comparison where stimulus objects that are more or less completely perceptually updated have to be evaluated according to their spatial positional information. However, the perceptual evaluation of objects in motion is by no means limited to relative estimation of their spatial positions. Attributes such as size, shape, and colour are also bound to moving objects. Therefore, it is essential to know how the values of these attributes have an effect on motion detection and vice versa – how motion may have an effect on perceiving these other attributes.

There is a solid body of research using various experimental designs for displaying stimulation so that it allows comparisons between different features of the objects. In studies where colour change and motion direction change have been compared (Moutoussis & Zeki, 1997; Zeki & Bartels, 1998; Arnold, Clifford, & Wenderoth, 2001; Holcombe & Cavanagh, 2008), the main common result indicates that colour has a perceptual advantage compared to change in motion direction. Typically, in order to perceive a change in motion direction and change in colour as simultaneous, the change in motion direction has to precede colour change. What causes this effect? Some researchers attribute this to the involvement of magno- and parvocellular pathways and specialized areas MT/V5 and V4 that primarily carry, respectively, the information about (respectively) motion and colour (Zeki, Watson, Lück, Friston, Kennard, & Frackowiak, 1991; Moutoussis & Zeki, 1997; Zeki & Bartels,

1998), with differences in time constants characterizing the action of these pathways. Yet, there is a considerable amount of findings suggesting that these separate (or rather distinguished) pathways are actually quite interactive (see **Study II** later on; Dobkins & Albright, 1993; Cicerone, Hoffman, Gowdy, & Kim, 1995; Monnier & Shevell, 2004; Werner, 2007).

In most of the studies where a temporal advantage of perception of colour over the perception of motion was found, and separate processing of these attributes suggested, a task of comparison between these two changes has been used. But what if we put this assumed independence (between processing of colour and motion information) to test and analyse perception separately with the stationary and moving stimuli (thereby using so-called absolute evaluations) and ask an observer to detect the same event (colour change) in these stimuli separately? If features such as colour and motion were processed separately, then in a setup where motion is actually an irrelevant/secondary feature due to the task demands, one should find no difference in the times needed to detect change in colouration in stationary and moving stimuli.

Simple reaction time task

To test whether the presence or absence of motion information affects the detection of some other event happening to the same object, we conducted a simple reaction time (RT) experiment (**Study II**, Experiment 1). A single moving bar (having one of five possible velocities between 5.9 and 35 deg/s) or a stationary bar changed their colour or luminance (depending on the experimental block in hand). The change took place in the middle third part of the screen. The observers were asked to respond – as quickly as they detected the change – by pressing a response key at the keyboard. The results showed that the mean RT to the colour and luminance changes differed significantly – the mean RTs were shorter for luminance change. However, in case of both types of the changes – colour and luminance – there was an identical significant main effect of velocity. Namely, the mean RTs for detecting a change decreased with the increase of the velocity of the moving stimulus. Except for the slowest velocity (5.9 deg/s), the RTs for the colour/luminance change of the moving stimulus were shorter than for the colour/luminance change in stationary stimuli (values of difference varied up to 70 ms). This finding clearly indicates that different features or qualities of the same object are not independently processed. However, the exact mechanism of the effect of velocity remained unclear. We do not know whether the presence of motion ‘runs’ the information about change through processing stages more quickly or does the motion act as a some sort of spatial and/or temporal cue that helps to raise the observers readiness to respond. Indeed, it has been shown that the increase of spatial probability of stimuli appearance is accompanied by the decrease in simple RTs. Carreiro and colleagues (Carreiro, Haddard, & Baldo, 2003) manipulated the probability of the target to appear in one or another hemifield and found that simple RTs were shorter when the target appeared in the hemifield which was favoured in the experimental block in hand. However, another interesting aspect

by these authors found is that the fact whether the participants were informed about the exact proportion of instances in which the target will appear in one or another hemifield did not have any effect on the RTs. This indicates that – at least in a simple task – participants adapt to the experimental setup very quickly.

We also found a trend for the RTs to become shorter as the stimulus reached closer to the end point of the possible area of the colour change (i.e., the end of the middle third section of the screen). The observers knew that the colour of the bar changed in every trial and quickly learned the boundaries of the area where the colour change took place. However, since the spatial location of the colour change in stationary stimulus had the same spatial probability (the colour change took place where the stationary stimulus was presented) the motion could have acted as a spatiotemporal cue.

To have a better control over the possible cues we conducted another experiment (**Study II**, Experiment 2) where the spatial position of the colour change was fixed (the spatial probability was therefore invariant), but the probability of the change was manipulated in different blocks of trials. The results showed that both, the probability of the change as well as the velocity had an effect on the mean RTs of colour change – the RT decreased with increase in change probability and velocity. There was no interaction between these two factors, which indicates that although probability of the appearance of expected event does have an effect on RTs (as it has been shown already by Gordon, 1967; Näätänen, 1972; Mattes, Ulrich, & Miller 2002) this does not eliminate nor exhaustively explain the effect of velocity on the detection of colour change.

Temporal order judgments

The previously described results of perception of colour seemingly having a temporal advantage over perception of motion were mostly gathered on a comparative basis, where subjects were asked to compare and decide the temporal order of two changes, colour versus motion direction change (Moutoussis & Zeki, 1997; Arnold et al., 2001, Holcombe & Cavanagh, 2008). We do not know whether the effect emerges mainly in comparative tasks assessing within-object changes. Therefore, in **Study III** (Experiment 1) we decided to put to the test the same stimulus as was used in **Study II** – the colour change of a moving versus stationary stimulus – but this time the task required a comparison of the change in visual stimulus with a brief auditory signal. It means that we used a temporal order judgement (TOJ) task. However, we did not find any main effect of velocity of the colour changing stimulus on the point of subjective equality (PSE) of occurrence between the colour change and auditory signal. If the effect of velocity would have been universal ('motion helps to detect the colour change faster in whatever conditions'), the expected results would have shown an effect of velocity on the values of PSE. However, despite the fact that in this case our subjects were not instructed to give quick responses (which was required in the simple RT task in **Study II**) and speed was assessed indirectly

by the category of answers, we also measured answer times (time from the physical colour change to the moment when the response about the temporal order of events was produced). These answer times revealed a similar effect of velocity that we had found in **Study II** – answer times decreased with an increase of velocity of the colour changing stimulus.

Yet, in this experiment we had also the problem mentioned earlier when discussing the FLE: when we are comparing a brief auditory signal and a colour change in a stimulus that has been present for a while before the event takes place we are, once again, comparing a new object to an event in an old object. Therefore we conducted another experiment (Experiment 2, **Study III**) where two equivalent events exemplified by two colour changes were compared to each other. The display consisted of two rectangular areas filled with sinusoidal spatial distribution of luminance (i.e., gratings) depicted as stationary or in motion. The two gratings to be compared had different velocities. If the increase of velocity accelerates the processing of the colour change, it must be expected that the PSEs favour the colour change of the faster moving grating over the colour change of the slower moving or stationary grating. However, this prediction did not hold. According to the PSE values, the colour change of the faster moving grating did not have any advantage compared to the colour change of the slower moving or stationary grating. Therefore, the effect of velocity found in **Study II** might be attributable to the type of the task.

Simple reaction time versus temporal-order judgment

In **Study III** (Experiment 1) the temporal order judgments did not show the expected dependency on the stimulus velocity, but the time needed to give the judgment showed velocity-dependent decrease. Similar discrepancy has been found by Aschersleben and Müsseler (1999). They found RTs to be shorter for the onset of moving object compared to the onset of stationary objects. However, as in our experiment the advantage of moving stimuli versus stationary stimuli was absent the subjects were asked to judge the temporal order of visual stimulus onset and onset of an auditory signal. It has been suggested that this kind of discrepancy between RT and TOJ results might be due to the difference in decision-making routines in the tasks of simple reaction time and temporal-order judgment (Kanai et al., 2009; Nishida & Johnston, 2002) or that two different decision criteria are applied on the same internal representation (Aschersleben & Müsseler, 1999; Cardoso-Leite, Gorea, Mamassian, 2007; Sternberg & Knoll, 1973).

Stimulus difference

There is one parameter-related factor that might possibly cause the effect of facilitation in the condition where single moving object is presented. Namely, the faster velocity may cause a motion blur, which filters out the high spatial frequencies and the decision is then made based on lower spatial frequency information. According to previous studies (Breitmeyer, 1975; Gish, Shulman, Sheehy, & Leibowitz, 1986; Greenlee & Breitmeyer, 1989; Plainis & Murray,

2000; Vassilev & Mitov, 1976) simple RT decreases with decreasing spatial frequency. This is what we found when manipulating the spatial frequency of the single moving stimulus (**Study II**, Experiment 3) – overall mean RTs were shorter for the stimulus with lower spatial frequency. However, this did not eliminate the effect of velocity – the RTs also decreased with increase of velocity for both stimuli of lower and higher spatial frequency.

As briefly mentioned earlier, in Experiment 1 (**Study III**) we found that answering times were shorter for the colour change of the faster moving stimulus, indicating that the decision about temporal order of the events was made quicker. But in Experiment 2 (**Study III**) while comparing colour changes of two gratings we did not find similar effect, which made us consider that maybe the lack of velocity-dependency in this experiment was not only due to the task-difference, but also due to the stimulus-difference. Indeed, when our subjects were asked to detect a colour change in a stationary or moving grating (**Study III**, Experiment 3) that moved inside a fixed window and it was not possible to predict the end of the motion trajectory or the possible spatial location or time of the colour change, the effect of velocity was the opposite – the RTs were slightly increased with the increase of velocity indicating that it was a bit harder to detect the colour change of the faster moving grating.

The stimulus-dependent (single moving bar versus moving grating) velocity effect on the detection of colour change seems to be due to the three-system theory of motion perception – the existence of the first-, second- and third-order motion system (Lu & Sperling, 1995; 2001). According to the notion of involvement of this tripartite system, the moving grating is presumably mainly analysed by lower-order systems, while single moving object translating over space is analysed by higher-order motion tracking system which is able to integrate information along the movement trajectory.

In a situation where stimulus motion does not give any spatial and/or temporal cue about the colour-change event, the presence of movement is rather a disruptive factor. Indeed, a recent TOJ study by Brenner & Smeets (2010) has found that despite of the fact that subjects often rely on the illusory motion (as a cue about the succession of events) between two spatially closely located stimuli changing colour, task-irrelevant motion of the colour-changing stimuli impairs the accuracy of the temporal order judgements.

Visual evoked potentials

However, while the research presented in this dissertation has – up to this point – revealed a variety of psychophysical factors and regularities involved in the effect of facilitation it is still not clear what the underlying mechanisms might be. Thus it was advisable to see whether visual evoked potentials (VEPs) might reveal some more specific evidence about the origin of the effect of velocity found in **Study II**. In **Study IV** we used the same experimental setup as in **Study II** (Experiment 1) and supplemented it with measurement of VEPs. The RTs nicely replicated the results found in **Study II** – mean RTs to colour changes decreased as the object moved faster. Some previous studies on VEPs

accompanying motion perception have revealed weaker amplitudes of certain VEP components (P1, P2 and N2) with motion onset of a slow moving stimulus when compared to fast moving stimulus (e.g. McKeeffry, 2001). But if we suggest that (faster) moving stimulus attracts more attention compared to a static stimulus, we may expect VEPs to show attention-specific differences. VEP component N1 has been found to show attention-related stronger amplitude (Beer, & Röder, 2004; Luck, Hillyard, Mouloua, Woldorff, Clark, & Hawkins, 1994). Contrary to what was expected, based on the RT results and the mentioned VEP studies, VEPs of colour change in the conditions of moving and stationary stimuli showed the reversed velocity-dependency – the faster was the stimulus moving, the smaller were the amplitudes of VEPs to the colour change. As an exception, the amplitude of N1 did not show the same regularity. Taken together, the results on the effects of VEPs put in doubt any strong attention dependency of the influence of velocity on the temporal parameters of the subjects' responses.

However, the RTs show strong motion-dependency and motion information processing has been considered to “travel” through the magnocellular pathway and dorsal stream which have been considered to be dominantly related to preparation for action. It has also been demonstrated that sensitivity of VEPs to magno- and parvocellular input is different and that VEPs reflect the action of parvocellular input better (Foxe, Strugstad, Sehatpour, Molholm, Pasieka, Schroeder & McCourt, 2008). In this context our results seem to agree with the view that human visual system has indeed the functionally distinct (but highly interactive) streams, each specialized for different stimulus attributes.

3. ILLUSORY MOTION

3.1. Motion aftereffect

The motion aftereffect (MAE), also known as a Waterfall illusion, is another prominent motion perception related phenomenon, already described by Aristotle (Ross, 1931). When after being exposed, for some time, to movement in one direction the movement stops, we tend to perceive movement in the opposite direction to the one we had been adapted to. This means that we are perceiving motion when there is no retinal movement or position change in the real physical object or visual background that we are observing. MAE studies have had an important role in investigating the mechanisms encoding motion information.

The most common explanation of this illusion has been that it is caused by neural fatigue. There are ON/OFF ganglion cells in the retina (functioning as motion-detectors) that are activated by certain direction of movement (Barlow & Hill, 1963; Barlow, Hill, & Levick, 1964). When the real motion stops, the activation level of this active detector has become dropped under the baseline level as it is fatigued. This means that the detectors sensitive to the movement in the opposite direction are now a bit more excited due to the imbalance in the normally balanced mutual inhibitory relation between the units. However, more recent studies suggest that neural fatigue in lower level motion processing is not the exhaustive cause of the MAE and higher-level motion processing mechanisms (V5/MT) reveal adaptation also (Campana, Maniglia, & Pavan, 2013; Tootell et al., 1995). Tootell and colleagues (1995) found strongest activity rise in MT during MAE, compared to areas V2, V3a, but no activation change in area V1.

For many reasons it is inevitable that involvement and the effects of attention are definitely relevant in considering motion perception as it has been already described previously (see O’Craven et al., 1997). Moreover, due to the multi-aspect nature of virtually all displays used in studying the mutual effects of stimuli features including motion, the effect of dividing or focusing attention may be substantially involved in determining the behavioural outcomes. To begin with, it should be parsimonious to approach this issue by using the kinds of motion experience as “pure” as possible in order to minimise experimental confounds. For this purpose, MAE seemed to be a proper paradigm. In this dissertation the effects of attention on MAE are explored.

Role of attention in motion aftereffect

In MAE studies attending the moving (adapting) stimulus has resulted in longer duration of MAE (Chaudhuri, 1990; Rees et al., 1997). However, we have previously found a reverse effect of attention when we asked our subjects to attend to colour afterimages (Bachmann & Murd, 2010) – the decay of the attended afterimage was quicker compared to the unattended afterimages presented at the same time. To find out whether selectively attending to motion

aftereffect results in a similar influence of attention, we conducted an experiment (**Study V**). In the experiment subjects were presented with four sine-wave gratings moving in different directions. After the adapting stimuli had induced the aftereffect, subjects were asked to keep their gaze fixated while monitoring the MAEs without a selective-attentional instruction or selectively attending to a MAE drifting in certain direction. In the monitoring conditions subjects were asked to report which MAE among the four alternatives decayed first and in the selective attention condition whether the attended MAE faded first compared to the alternative MAEs. We found spatial selective attention to have inhibitive effect on the duration of perceiving the motion aftereffect. When a certain direction of MAE was attended, it appeared to fade earlier than its unattended alternatives. Apparently, attention has opposite effects on MAE depending on where the attention is selectively directed. Attending the “pure” motion sensing (in the absence of real input) shortens the duration of MAE (**Study V**). This opposite effect of attention is a bit puzzling. According to the abovementioned inhibitory logic suggested to underlie the MAE, we would have assumed an enhancing effect of attention on the activity of neurons processing the attended direction. If we instead assume that selective attention is exhausting the resources for firing for these neurons (e.g., possibly the supply of necessary neurotransmitters), our findings in **Study V** are partly explained. However, whether this effect of attention on motion awareness is mediated by higher-order feature-invariant mechanisms of modulation of the effects of sensory processing or lower-order cortical mechanisms specific for certain features of sensory processing is not clear. Let us remember that the inhibiting effect of attention was noticed for colour aftereffect also (Bachmann & Murd, 2010). It is necessary to have a more precise experimental control selectively on the dedicated motion-analysing units in the brain.

Transcranial magnetic stimulation studies on static MAE

Transcranial magnetic stimulation (TMS) has been widely used for mapping the functions of brain areas, as it enables to create temporary “virtual lesions” (Barker, Jalinous, & Freeston, 1985; Murd, Luiga, Kreegipuu, & Bachmann, 2010; Pascual-Leone, Bartres-Faz, & Keenan, 1999; Ridding & Rothwell, 2007). It has also been used to assess the role of different visual areas in causing the motion perception in general and MAE in particular. Theorét and his colleagues showed that stimulating MT during the perception of static MAE causes the aftereffect to decay quicker (Theorét, Kobayashi, Di Capua, & Pascual-Leone, 2002). Campana and colleagues (2013) have also shown the effect of stimulation of V5/MT, but additionally demonstrated that TMS targeting areas V2/V3 decreased the duration of the static MAE as well.

However, in most of the works where the causal involvement of V5/MT in motion perception has been investigated with TMS, the display has consisted of a single area capturing motion without any competing stimuli with motion signals. Therefore we do not know whether these effects of TMS would be similar when two opposite adapting motion vectors are present. We also do not

know whether TMS might cause similar disruption in perception of MAE as selective attention did and whether the adverse effect of attention on motion sensing might be linked to the area V5/MT. Consequently, an experiment is necessary where competing motion signals are presented from different spatial locations and the stimulation setup should be compatible to the one used in the experiment exploring the attentional effects on motion sensing. Another important aspect of this kind of setup is that using a comparative evaluation based assessment of MAE duration is less arbitrary than trial-by-trial based assessment because the MAE does not have an abrupt and clear offset. Driven by these considerations, we conducted a repetitive TMS (rTMS) experiment (**Study VI**), using basically the same stimuli as in **Study V**, except that instead of four we now used two adapting stimuli presented on either sides of fixation and moving in opposite directions (upward and downward). We applied rTMS either to the right or left V5/MT immediately after the offset of adapting stimuli and asked subjects to manually report which of the two alternative MAEs faded first. We also used high and low stimulation intensities as it has been previously shown that high and low intensity TMS might have different effects (Ruff, Blakenburg, Bjoertomt, Bestmann, Weiskopf, & Driver, 2009; Schwarzkopf, Silvanto, & Rees, 2011). The results (**Study V**) showed that the stimulus presented contralaterally to the stimulation site (right or left V5/MT) tended to decay first. This rTMS effect was stronger for the right hemisphere stimulation (causing more “left MAE decayed first” responses) and in the low intensity TMS condition. TMS-induced stronger changes in the activation of right hemisphere have been demonstrated earlier (Muggleton, Postma, Moutso-poulou, Nimmo-Smith, Marcel, & Walsh, 2006; Ruff et al., 2009) and considered to be due to the right hemisphere specialization in producing causal effects on visual perception (Ruff et al., 2009). The finding that despite of the presence of opposite motion vectors the contralateral TMS effect on spatially localized MAEs is not nullified indicates that MAE perception has location-specific nature. As the TMS effects in **Study VI** were similar to the attentional effects found in **Study V**, we suggest that the effect of selective attention might be mediated by higher level mechanisms (V5/MT), the activity of which can be modulated by top-down attention.

CONCLUSIONS

To summarize the results of the empirical part of the dissertation, the main findings were as follows:

- 1) The flash-lag effect (FLE) increases when an object moving in the opposite direction to the target object is presented on the display (**Study I**). This does not support the theory that FLE is being caused by low level mutually inhibitory mechanisms. This also shows that FLE may not be the appropriate method for studying motion-perception mechanisms *per se* unless the influence of other factors such as proactive priming is controlled or factored out.
- 2) The presence of motion information influences the detection of other features of the moving object. The time needed to detect colour or luminance change decreases with the increase of velocity of the single moving object (**Study II, IV**). This effect was found to appear even when the probability of colour change or the spatial frequency of the stimulus were manipulated (**Study II**).
- 3) However, the above-mentioned enhancing effect of motion appears to be task- and stimulus-dependent (**Study III**). This indicates to the different representation (or to different stages of the same representation) of the stimulus required for detecting an event and judging the temporal order of events.
- 4) The visual evoked potentials (VEPs) of colour change did not correlate with reaction times (RTs), and this might be due to the two methods reflecting different processing mechanisms (**Study VI**).
- 5) Motion perception can be strongly influenced by selective attention, however as our results in MAE study (**Study V**) indicate, the direction of the attentional effect highly depends on the type of experimental task vis-à-vis stimulus type and on the temporal characteristics.
- 6) The stimulation of human visual area V5/MT results in a similar effect (**Study VI**) as was found in (**Study V**) concerning the influence of selective attention. However, the results revealed hemispheric asymmetry of the effect. Because of this asymmetry, future research should consider the possibility that functional lateralization may be involved in the motion effects and that the fronto-parietal attention system (**Study VI**, Corbetta & Shulman, 2002; Ruff et al., 2009) may be implicated as well. Therefore, experimental designs should beware of the possible laterality- and laterally unbalanced attentional effects.

In conclusion, motion perception is a highly integrative process manifesting in different phenomena and is based on different psychological and neurophysiological processes in the complex multilevel visual-cognitive system. Yet, despite the complexity of the visual motion perception we know certain brain mechanisms necessary for sensing motion which at the same time are susceptible to the effects from other cognitive processes. Although the quite

long history of research has confirmed this picture in general, new studies like this one, piece by piece, add empirical evidence allowing to know the regularities of motion perception increasingly in a more detail and more completely. While over the decades researchers have tried to map the exact mechanisms underlying many of the motion-related phenomena in an incremental fashion, the complete and exhaustive picture of the mechanisms of motion perception has still not been achieved. I do hope that the present work has helped to add some additional useful nuances to the dynamic picture of the psychological and neural science of motion analysis. Hopefully, this picture has moved a bit closer to what can be called a “complete theoretical picture of motion perception”.

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SUMMARY IN ESTONIAN

Visuaalse liikumisinformatsiooni töötlusmehhanismid: Psühhofüüsikalised, bioelektrilised ja transkraniaalse magnetstimulatsiooni uurimused

Väitekiri kästitleb liikumisinformatsiooni töötlemist ajus. Psühhofüüsikaliste, bioelektrilise (EEG) ning transkraniaalse magnetstimulatsiooni (TMS) meetoditel uuritakse väitekirja aluseks olevates uurimustes (**Uurimused I–VI**) kolme peamisse teemasse kuuluvaid tajunähtusi. Esmalt uuritakse, millist uut informatsiooni annab uudse katsedisainiga sähvatuse mahajäämuse fenomeni (*flash-lag effect, FLE*) eksperiment nimetatud fenomeni aluseks olevate liikumisinformatsiooni töötlevate protsesside kohta (**Uurimus I**). Teiseks käsitletakse seda, kuidas mõjutab liikumine liikuva objekti teiste omaduste (antud uurimus-töödes värv) muutuse tajumist, milline see mõju on ning mis tingimustel see ilmneb, kasutades lihtsa reaktsiooniaja (*reaction time, RT*), ajalise järgnevuse hindamise (*temporal order judgement, TOJ*) ning bioelektriliste visuaalselt evotseeritud potentsiaalide (*visual evoked potentials, VEP*) mõõtmise meetodeid (**Uurimused II, III ja IV**). Kolmandaks käsitletavaks teemaks on selektiivse tähelepanu mõju liikumisinformatsiooni töötluusele liikumise järelefekti (*motion after-effect*) fenomeni puhul (**Uurimus V**) ning milline on nägemispoolkonna V5/MT roll tähelepanu-tundliku liikumise järelefekti tekkimisel (**Uurimus VI**), manipuleerides nimetatud piirkonna funktsioneerimist transkraniaalse magnetstimulatsiooni korduvimpulsside abil (*repetitive transcranial magnetic stimulation, rTMS*).

Antud väitekirja peamised tulemused on järgmised:

1. Kahe vastastikkuse vektori kasutamine sähvatuse mahajäämuse katses liikuva objekti lokaliseerimisviga ei elimineeri, vaid suurendab nimetatud viga. Antud tulemus seega ei toeta teooriat, mille kohaselt põhjustavad lokaliseerimisviga madalamata taseme vastastikkuse pärssimise põhimõttel töötavad mehhanismid (**Uurimus I**).
2. Liikuva objekti värvimuutuse avastamiseks kulub vähem aega. Manuaalsed reaktsiooniajad värvimuutusele on kiirustundlikud – mida kiiremini object liigub, seda kiiremad on reaktsiooniajad muutuse avastamisele (**Uurimused II ja IV**), ning efekt ei sõltunud värvimuutuse toimumise tõenäosusest ega stiimulite ruumilisest sagedusest (**Uurimus II**).
3. Selline liikumise ja liikumiskiiruse mõju aga sõltub lähteülesandest (stiimuli avastamine või stiimulite ajalise järekorra raporteerimine) ning sellest, millised on liikuva stiimuli füüsилisted omadused (kas tegemist on üksikobjekti või heleduslaotusega) (**Uurimus III**).
4. Visuaalselt evotseeritud potentsiaalid värvimuutusele aga ei kajasta reaktsiooniaegades näidatud liikumistundlikkust (**Uurimus VI**). Antud tulemus võib viidata sellele, et kaks meetodit peegeldavad erinevaid töötlusmehha-nisme ajus.

5. Tähelepanu suunamine liikumisele mõjutab olulisel määral liikumise tajumist. See mõju sõltub aga eksperimendiinstruktsioonist ja tähelepanu suunamise ajalistest karakteristikutest (**Uurimus V**).
6. Nägemispiirkonna V5/MT stimuleerimine liikumise järelefekti katses (**Uurimus VI**) annab sarnaseid tulemusi selektiivse tähelepanu suunamisega (**Uurimus V**) – mõlemad kutuvad esile liikumise järelefekti kiiremat kustumist teadvusest. Antud uurimuses (**Uurimus VI**) ilmnes ka rTMSi poolkeraliselt erinev mõju järelefekti kustumisele, mis viitab võimalikule funktsionaalsele lateralisatsioonile; ühtlasi on see järgnevate eksperimentide seisukohalt oluline leid.

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