





## **AIRE RAIDVEE**

Pooling of elementary motion, colour, and  
orientation signals into global perception



TARTU UNIVERSITY PRESS

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Dissertation is accepted for the commencement of the degree of Doctor of Philosophy (in Psychology) on January 13, 2012 by the Council of the Faculty of Social Sciences and Education, University of Tartu.

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Commencement: February 17, 2012

Publication of this thesis is granted by the Department of Psychology, University of Tartu and by the Doctoral School of Behavioural, Social and Health Sciences created under the auspices of European Union Social Fund



European Union  
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ISSN 1024–3291

ISBN 978–9949–19–937–2 (trükis)

ISBN 978–9949–19–938–9 (PDF)

Autoriõigus: Aire Raidvee, 2012

Tartu Ülikooli Kirjastus

[www.tyk.ee](http://www.tyk.ee)

Tellimus nr 10

# CONTENTS

LIST OF ORIGINAL PUBLICATIONS .....	6
INTRODUCTION.....	8
Elementary motion detector .....	9
Pooling of elementary motion signals into global perception .....	12
Bernoullian psychophysical model.....	13
Ideal observer analysis .....	17
Repeated tagging as an aspect of mental architecture .....	18
CONCLUSIONS.....	21
ACKNOWLEDGEMENTS .....	23
REFERENCES .....	24
SUMMARY IN ESTONIAN .....	28
PUBLICATIONS .....	31

## LIST OF ORIGINAL PUBLICATIONS

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

- I** **Raidvee, A.**, Averin, K., Kreegipuu, K., & Allik, J. (2011). Pooling elementary motion signals into perception of global motion direction. *Vision Research*, *51*(17), 1949–1957.
- II** Kuldkepp, N., Kreegipuu, K., **Raidvee, A.**, & Allik, J. (2011). Reaction time to motion onset and magnitude estimation of velocity in the presence of background motion. *Vision Research*, *51*(11), 1254–1261.
- III** **Raidvee, A.**, Kurjama, K., Pölder, A., & Allik, J. (2012). Discrimination of numerical proportions defined by colour or orientation. *Journal of Vision* (submitted).
- IV** **Raidvee, A.**, Averin, K., & Allik, J. (2012). Visibility versus accountability in pooling local motion signals into global motion direction. *Attention, Perception & Psychophysics* (submitted).
- V** **Raidvee, A.**, Pölder, A., & Allik, J. (2012). A new approach for assessment of mental architecture: Repeated tagging. *PLoS ONE*, *7*(1): e29667.

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

- in studies III, IV and V: formulating the research questions;
- in studies I, III, IV and V: creating research designs, programming the experiments, supervising the data collection, developing mathematical approaches; carrying out data analyses, and writing manuscripts;
- in study II: programming the experiments, writing segments of the manuscript, carrying out some of the data analyses;
- in studies I, and IV: carrying out the data collection.

Principal aims of the studies:

- simplification of the Random Dot Motion (*RDM*) displays to a degree which allows the application of the *Ideal Observer Model (IOM)* with as few postulated assumptions as possible, to the problem of pooling local motion vectors into a perception of the global motion direction (**Study I**);
- devising an equally accurate deterministic Bernoullian measurement model as an alternative to the Thurstonian stochastic discrimination model and relating the parameter of the Bernoulli binomial model to the description of empirical psychometric functions (**Study I**);
- estimating the effect of background on motion detection, and thus the relativity principle in the perception of motion (**Study II**);
- relating the parameters of the Bernoulli hypergeometric model to the description of empirical psychometric function (**Study III**);
- proposing a new approach for quantifying the distinction between visible and accountable visual information (**Study IV**);
- testing and falsifying the Common Fate principle in discrimination of numerical proportions (**Study IV**);
- introducing a new probabilistic approach for the assessment of mental architecture that would not suffer from potential model mimicking (as the reaction-time based approaches would), specifically for establishing whether the same visual element can be counted only once or repeatedly several times on subsequent time moments (**Study V**).

## INTRODUCTION

While the first observations about motion perception go back to the ancient times, probably one of the first who considered a composite percept of direction as comprising of elementary vectors was a Moravian physicist and psychologist Ernst Mach (Mach, 1896/1959; Malone, 2009). Usually the perception of motion was understood as a higher-order cognitive process, the result of some kind of unconscious inferences. Sigmund Exner, another brilliant researcher who worked in Vienna, discovered that two very closely placed electric sparks could produce a vivid impression of motion even though they were not spatially separable (Exner, 1876). He came to an inevitable conclusion that motion perception is an elementary sensation, not a derivative of some more elementary perceptions of space and time. These demonstrations of irreducibility of motion perception paved the way to the fundamental status that motion perception acquired in the Gestalt movement. Like his predecessors, Max Wertheimer (1923) described motion as composed of elementary motion vectors which are perceived as a resulting vector sum (the latter itself not contained in the stimulus). Another among the early approaches was a series of experiments by Hans Wallach (Wallach, 1935). Wallach started out with the study of how the direction of elementary forms was perceived through apertures of different shapes. He showed that an “infinite” line (i.e. a line with endpoints outside of aperture) is always seen as moving perpendicularly to its orientation, when in fact it could be moving in any other non-perpendicular direction as well. From elementary forms, Wallach moved on to more complex stimuli – line gratings and patterns, and showed similar effects in these, probably the most famous of which is the “Barberpole illusion” [as also noticed by (Guilford, 1929)] describing the phenomenon of a line grating that is perceived as moving in the direction of the aperture’s longer axis. Nevertheless, Wallach concluded that the perceptual change in the direction of the line or grating must be caused by an interaction between the local motion vectors and the aperture borders (for the motion vector normal of the line or grating is constant) – an observation laying ground to much of the current work on the aperture problem (Angelaki, Shaikh, Green, & Dickman, 2004; Born & Bradley, 2005; Lorenceau & Shiffrar, 1992).

However, the integration of motion information based on recognizable forms and stimulus singularities seems to be a special case of motion perception. In many ecologically valid cases the visual field is not structured and motion information can be extracted even when there are no individuated visual elements available. The Random Dot Motion (*RDM*) displays are free from many problems that are intrinsic to, for example, gratings and plaids. Historically, random dot stimuli were devised and created by Béla Julesz with the purpose to get rid of identifiable parts and to observe the operation of binocular vision or motion perception in their most elementary forms (Julesz, 1971). In this respect *RDM* displays are even more ambiguous than plaids and gratings since every element can be potentially paired with all other identical elements that are presented at

$\Delta t$  time later. Since elements in the *RDM* displays are specified only by their position in space and time, it is relatively easy to create the required amount of various elementary motion vectors in all possible configurations. Certainly, *RDM* displays are miles away from ecologically valid images but compared with the classical stroboscopic presentation of two bars in the Wertheimer's classical experiments it is a substantial progress. However, it is important to realize that different types of motion stimuli are suitable for the study of different perceptual mechanisms (Zanker, 1994).

Like other visual attributes it is vigorously debated whether motion is perceived by a singular or multiple mechanisms. For example, it was proposed that there are two different mechanisms for the perception of the first-order (i.e. luminance modulation based) and second-order (contrast modulation based) motion perception. Even though models suggesting a common mechanism for both types exist (Benton, Johnston, McOwan, & Victor, 2001; Johnston, McOwan, & Buxton, 1992), data on order-specific disorders of motion perception (Greenlee & Smith, 1997; Vaina & Cowey, 1996; Vaina, Soloviev, Bienfang, & Cowey, 2000) as well as neuroimaging data (Ashida, Lingnau, Wall, & Smith, 2007; Vaina & Soloviev, 2004) suggest that first- and second-order motion perception is carried out by different pathways, neuroanatomically. Psychophysical studies have shown that the two types of motion are processed independently at least in the early stages (Nishida, Ledgeway, & Edwards, 1997) or even up to and including the stage where global motion signals are extracted (Edwards & Badcock, 1995). However, the nomenclature of mechanisms may be not exhausted by the division into the first- and second-order mechanisms. It is very likely that at least one additional mechanism is required to complete the list of motion processing mechanisms (Lu & Sperling, 1995, 1996; Zanker, 1994).

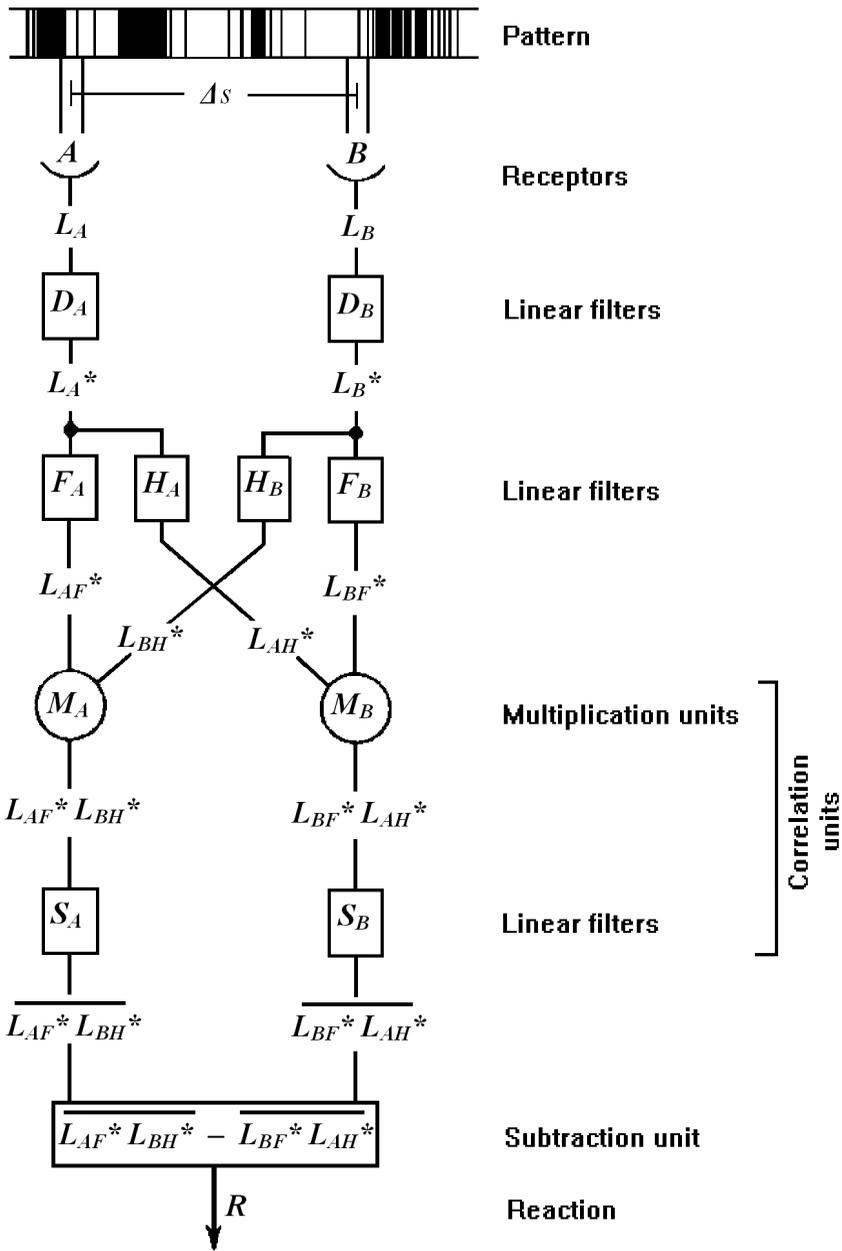
## Elementary motion detector

It seems to be inevitable that motion perception starts with a large array of elementary motion encoders which register motion information in one restricted region of the visual field. Properties of these local motion analyzers – elementary motion detectors – are relatively well understood. These detectors seem to be based on the same principle of correlational analysis across all species from beetles to human vision (Adelson & Bergen, 1985; Reichardt, 1959). Their properties were formally described firstly by Werner Reichardt and Bernhard Hassenstein who devised an ingenious experiment with a beetle *Chlorophanus* (Hassenstein & Reichardt, 1951). They made use of the beetle's optokinetic response – it would always follow the perceived direction of the visual surround in order to compensate for its perceived deviation from the track. By the experimental results they devised a correlational model of a motion detector that has become to be called the 'Hassenstein-Reichardt model' or simply the 'Reichardt detector' (Hassenstein & Reichardt, 1951).

The working principle of the detector (as depicted in Figure 1) is straightforward: it is based on delaying and mutual comparison (multiplication) of the inputs into two different locations of a directionally selective unit's receptive field (one input corresponds to one photoreceptor or receptive field). First, the signal from one photoreceptor is delayed ( $H_A$  or  $H_B$ ) by a low-pass filter so that it could interact with the undelayed part of the signal from the second input ( $F_A$  or  $F_B$ , that comes in at a slightly different time moment compared to the first signal). Next, the two signals are multiplied ( $M_A$  and  $M_B$ ). All this is performed in a mirror-symmetrical fashion thus leading to two multiplication products, which are compared against each other with the sign of the output reflecting the perceived direction of the motion.

This simple delay-and-multiply scheme led to several counterintuitive predictions which have nevertheless been confirmed by experimental results during the following decades (Barlow & Levick, 1965; Borst, 2000; Hassenstein & Reichardt, 1951; Reichardt, 1961; Reichardt, 1962). The model is also exceptionally universal across species. An increasing amount of evidence shows that the computational mechanisms underlying motion detection are basically similar in invertebrates as well as vertebrates, including man (Borst & Egelhaaf, 1989). Later theoretical studies have revealed that motion can only be detected by a neural network capable of nonlinear operations (e.g., multiplication) – ultimately leading to the conclusion that apart from reasonable reservations, any motion analyzer has to be mathematically equivalent to the Reichardt type detectors (Poggio & Reichardt, 1973).

The nature of the elementary motion detector leads to the fact that motion can be perceived even without any real displacement by mere fluctuations in the luminosity at two disparate visual locations (Allik & Pulver, 1994, 1995; Johansson, 1950). There lies an explanation for the mechanism of various visual illusions: if the sign of the contrast of one of the input signal is changed, the perceived motion direction would be inverted as well, despite the fact that the stimulus could have remained stationary. At least in primates, the contrast polarity appears to be coded by two anatomically distinct systems, called ON- and OFF-channels of the visual system (Schiller, Sandell, & Maunsell, 1986). The ON-channel codes incremental, whereas the OFF-channel codes decremental luminance values, thus, the former becomes hyperpolarized in response to illumination onset or increase, whereas the latter becomes depolarized, resulting in inversion of the receptor signal. Therefore, if the polarity of contrast is changed at one input, the perceived direction would be reverted – a principle confirmed by discovery of the reverse phi motion (Anstis, 1970). If the image in the first frame is replaced, in the second frame, by the same image that has been shifted rightwards, a vivid impression of movement occurs in the shift direction. Yet, when the image in the second frame was replaced by its negative, the perceived motion direction is opposite to the actual displacement. The reversed phi also demonstrates the existence of the cross-talk across the ON- and OFF-channels.



**Figure 1.** Schematic description of Reichardt motion detector (reproduced from Reichardt, 1961).

## Pooling of elementary motion signals into global perception

What is considerably less understood is how local motion signals from different positions in the visual field are combined together into the global motion impression. As it was already said, both psychological and neurophysiological data indicate that motion is initially recorded in parallel by arrays of elementary motion detectors (Burr, 2003) and is probably analyzed simultaneously at multiple spatial scales (Morgan, 1992; Movshon, Adelson, Gizzi, & Newsome, 1986). Many visual tasks require estimation of global information which is attributable to a larger area or the whole object. In any case, either the information in the scene is fragmented (discrete) or not, there are typically only a limited number of areas which motion characteristics are relevant for the observer. The latter argument is further supported by the finding by Morgan (1992) that the size of the spatial filter preceding motion detection and required to explain the empirical data is similar in size compared to the receptive field of neurons in the primate magnocellular pathway that has been considered as the branch of visual system “specialized” on motion. Even though other findings have undermined the vital role of magnocellular pathway in motion (Merigan, Byrne, & Maunsell, 1991), the pooling mechanism for integrating local motion signals into a global percept is presumably bound to exist: hence, there must be a mechanism which pools together elementary motion signals across a certain area and time interval and attributes the result to this area.

The principles of pooling of visual motion signals are not very well understood in spite of a considerable number of works that have been carried out on this topic. Physiological studies seem to indicate that, in primates, motion pooling is most likely executed by motion-sensitive neurons in the middle-temporal (MT) cortex (Pack & Born, 2001), known as V5 in humans. Many neurones in V5 are sensitive to all aspects of the input, both the global pattern motion and the local noise components (Braddick & Qian, 2001). Although physiological studies have indicated the approximate locations where motion pooling could take place in the brain, they have contributed very little into the knowledge about computations that are underlying motion pooling. For example, all textbooks like to stress the relative character of motion perception. Well-known phenomena like induced motion seem to stress that motion of some area is always judged relative to the background or neighbourhood which serves as a frame of reference. Nevertheless, this may not always be the correct approach. **Study II** demonstrated that the background of a test area plays a relatively minor role when it concerned noticing the motion onset. The background had a noticeable effect only if the test area was very small and there was no space between the test and surrounding background moving either in the same or opposite direction with the test stimulus. The most interesting is that the relative direction of the background had a negligible effect. The relativity principle which seems to play an important role in the higher-order perceptual phe-

nomena was absent when it concerned simple detection of motion onset. Instead of enhancement, the relative disparity between velocities of the test and background motion made the detection of the test motion if anything then more difficult. Irrespective of whether the background moved in the same or opposite direction, it prolonged the time needed for the detection of motion onset.

What is known about mechanism of pooling of motion signals? Several rules have been proposed for how pooling is performed. It is known that a random dot pattern appears to drift in the direction close to the vector sum of the dots' motion directions (Williams & Sekuler, 1984), in the direction of the most dominant direction when other directional signals become weak (Zohary, Scase, & Braddick, 1996; Webb, Ledgeway, & McGraw, 2007), or in the direction of the largest information entropy (Gilden, Hiris, & Blake, 1995). Other studies have looked at the effects of elementary motion signal density, number, and duration on the tolerance to noise (Eagle & Rogers, 1997; Frederickson, Verstraten, & Van de Grind, 1994; Todd & Norman, 1995) but there is limited knowledge about the efficacy of local motion information pooling on global direction perception.

## **Bernoullian psychophysical model**

A common mistake made by many researchers is to draw schemes with hypothetical information flows and without elements that carry out actual measurements. Every measurement executed by a physical or biological device has its fundamental limitations meaning that a measured physical attribute can be represented in internal states of an organism only as a fuzzy image of that attribute. During the first century of psychophysics, Thurstonian models of internal discrimination process (Thurstone, 1927) have been virtually the only analytic tools that were in the possession of researchers. As it was noted by Robert Duncan Luce – Thurstonian model of random internal representations is the “essence of simplicity” and nobody has ever seriously succeeded in challenging it (Luce, 1977). The basic idea of Thurstonian models is that the stimulus attributes are projected onto the continuum of psychological states. Due to noise in this internal representation, the image of internal positions on which the external attribute is projected is blurred. Internal images of the two sufficiently similar stimuli are overlapping. The overlap of these two images explains discriminability between these two stimuli. More specifically, a Thurstonian representation for a function of two stimuli (with stochastically independent random images and deterministic decision rules) is a model in which the two stimuli are mapped into their perceptual images as two independent random variables, which, as assumed by Thurstone, are normally distributed but this need not be the case, as alternative distributions have been considered (Dzhafarov, 2003a).

However, Thurstonian model is a convenient mathematical construction for which speaks its utility rather than empirical evidence. Even theoretically, Thurstonian model has problems since it cannot handle some plausible experimental outcomes. Specifically, Thurstonian model cannot explain, in principle, properties of some “well-behaved” discrimination functions that are typically observed and expected in behavioural experiments (Dzhafarov, 2003a, 2003b).

Usually, psychophysics deals with continuous physical variables such as luminance or loudness. However, in many cases stimuli can be enumerated and represented by integers. Even light consists of discrete quanta which can be counted, in principle at least. In many cases, for example in *RDM* displays, stimuli consist of a number of identical elements or events. It is immediately clear that Thurstone’s model may not be the best language to describe situations where the solution of the task requires estimation of the relative number of elements or events in the stimulus. Especially when the number of pooled or counted elements is small, the idea of internal fuzzy images is not the best one. It seems not to be inevitable that the observer uses a continuum of internal states to represent a small number of events that can be enumerated.

In all of the described cases the Bernoullian models formulated in **Studies I, III, IV** and **V** provide a more “natural” and conceptually more transparent description of the experimental situation. It seems that all such situations can be represented by a classical Bernoulli’s urn model which was devised by Jacob Bernoulli in his posthumous *Ars conjectandi* (1683/1713). This was developed as an idealized mental exercise in which some objects or concepts of real interest (such as people, event outcomes, visual objects, etc.) are represented as coloured balls or pebbles which are drawn, one after another, randomly from the urn and their colour is noted. The central idea of this model is that the decision is not based on all but only a fraction of elements which the observer is able to take into account or pay attention to. It is assumed (but not excluded) that the observer is not able to take into account all  $N$  elements presented in each trial. Instead of that she or he randomly selects a limited number of  $K \subset N$  elements which are inspected and which properties, for example colour or motion direction, are determined. Knowing the actual proportion between the two types of elements between which the observer was asked to discriminate, it is easy to calculate (on the basis of either binomial or hypergeometric distributions) the number of elements ( $K$ ) that is required to achieve the discrimination performance observed empirically.

The exact formulas for calculating the value of  $K$  corresponding to empirical response probabilities are slightly different for binomial and hypergeometric response models. The probabilities of a certain response for odd and even  $K$  according to the binomial model are given by equations (1) and (2):

$$P_{\text{bin}\{K \text{ is odd}\}} = \sum_{i=1+\lfloor \frac{K}{2} \rfloor}^K \binom{K}{i} p^i (1-p)^{K-i}, \quad K = 2k-1 \quad (1)$$

$$P_{\text{bin}\{K \text{ is even}\}} = \sum_{i=1+\frac{K}{2}}^K \binom{K}{i} p^i (1-p)^{K-i} + 0.5 \binom{K}{\frac{K}{2}} p^{\frac{K}{2}} (1-p)^{\frac{K}{2}}, \quad K = 2k \quad (2)$$

where

- $k$  is any positive natural number;
- $p$  is the proportion of a certain type of elements to the total number of elements (either  $N_A/(N_A+N_B)$  or  $N_B/(N_A+N_B)$ ), depending on the experimental definition;
- $K$  is the number of elements taken into account in the decision process.

The probabilities of a certain response for odd and even  $K$  according to the hyper-geometric model are given by equations (3) and (4):

$$P_{\text{hyp}\{K \text{ is odd}\}} = \sum_{i=1+\lfloor \frac{K}{2} \rfloor}^K \frac{\binom{N_A}{i} \binom{N_B}{K-i}}{\binom{N}{K}}, \quad K = 2k-1 \quad (3)$$

$$P_{\text{hyp}\{K \text{ is even}\}} = \sum_{i=1+\frac{K}{2}}^K \frac{\binom{N_A}{i} \binom{N_B}{K-i}}{\binom{N}{K}} + 0.5 \frac{\binom{N_A}{\frac{K}{2}} \binom{N_B}{\frac{K}{2}}}{\binom{N}{K}}, \quad K = 2k \quad (4)$$

where

- $k$  is any positive natural number;
- $N_A$  is the number of type  $A$  elements in the stimulus;
- $N_B$  is the number of type  $B$  elements in the stimulus;
- $N$  is the total number of elements in the stimulus ( $N = N_A + N_B$ );
- $K$  is the number of elements taken into account in the decision process.

For practical purposes, it is enough to consider either odd or even values of  $K$  only as the probabilities given by a pair of equations (either those for the binomial model or for the hypergeometric model) are equal, given equal values for  $k$  (**Studies I and V**).

If the Thurstonian model was called the “essence of simplicity” then the Bernoulli’s urn model deserves this title even more. Indeed, there is not even a

need to assume an internal fuzzy representation. The human observer is able to determine attributes of all registered elements accurately. The only uncertainty is the selection of a supposedly limited number of elements from the total number of elements presented in each trial. According to the Bernoullian model, all internal representations are accurate. What is random is the selection of the restricted number of elements that are taken into account for formulating an answer in each experimental trial.

Interestingly, as it turned out in terms of descriptions of the empirical psychometric functions, Thurstonian and Bernoullian models are formally equivalent. Any given empirical psychometric function which can be approximated sufficiently well with a cumulative Gaussian function, corresponds to a Thurstonian and a Bernoullian model. In **Study I**, cumulative normal function was fitted to empirical psychometric functions. The parameter of the Bernoulli binomial model described by equations (1) and (2), namely the length of Bernoulli series  $K$ , is directly related to the slope of the respective psychometric function ( $\sigma$ ) via a simple equation:

$$K = \frac{1}{4\sigma^2} - 0.7542 \quad (5)$$

Thus, in an experimental setup reducible to proportion discrimination of discrete sets, it is always possible, for every Thurstonian (at least Case V) model, to find a respective Bernoullian model. The stimulus need not be limited to two sets only as the Bernoullian model could easily be extended to polytomous case via the multinomial or multivariate hypergeometric distributions. Multidimensional models, where elements are discriminated on the basis of not just one attribute (e.g., colour or orientation) but rather two or more attributes (e.g., size together with location) are mathematically conceivable as well. On the basis of the psychometric function alone it is impossible to decide which of the two models – Thurstonian or Bernoullian – provides a biologically more adequate description. Nevertheless, the description given by the Bernoullian model would provide a more simple description with a smaller number of underlying and more transparent assumptions.

When the Bernoulli approach was applied to pooling of motion (**Studies I and IV**), colour and orientation (**Studies III and V**) signals, it turned out that the number of elements taken into account in the decisions about global motion direction remains constant over the range of 12–800 elements. At variance from motion, the number of accounted elements  $K$  increases disproportionately with the growth of the total number of elements  $N$  provided that two sets of elements are distinguished either by colour or orientation (**Study III**). One possible explanation is that with the increase of the total number of elements the probability of binding elements with similar attributes into chunks also increases (cf. Allen, Baddeley, & Hitch, 2006). This implies the possibility that instead of separate elements the observer is able to count doublets, triplets and so forth of

elements all sharing the same perceptual quality. If it is true then it automatically means that colour has higher potential of chunking than orientation. However, currently these considerations remain speculative until new experimental schemes are invented to prove or disprove them.

## Ideal observer analysis

The Ideal Observer Analysis (*IOA*) is one of the most powerful tools invented for the analysis of human perception. Its ground was laid in a classic work by Rose (1948) and popularized by the Signal Detection Theory formulated by Tanner and Birdsall in 1958 (Tanner & Birdsall, 1958). The *IOA* approach helps researchers to gain knowledge about the nature of the steps involved in information processing, being one of the central principles leading the way in modern research. Out of all the quantitative theories applied in vision research, *IOA* has been one of the most fundamental (Geisler, 2011).

An ideal observer is a theoretical device able to base its decisions upon absolutely every piece of information present in the stimulus, i.e. it can apply all the available information without any loss. The performance of an ideal observer is limited only by the physical availability, not by accessibility, of information contained in the stimulus. Therefore, by the ideal observer, the maximal theoretical performance is given. A concept that is part and parcel in the *IOA* is efficiency, usually denoted by  $\eta$  and defined as the ratio of the amounts of information that are needed by the ideal and the real observer, respectively, to perform in similar situations (Burgess, 1999). By analyzing the difference between real and ideal observers, one can understand a lot about the way information is coded by a real observer. Less than perfect efficiencies reflect losses in the information on some stages of information processing. Beside providing a quantitative approach for comparing the real observer's performance across different tasks and conditions (Gold, Abbey, Tjan, & Kersten, 2009), the *IOA* also provides the badly needed metrics for the human performance.

Unfortunately, many researchers have disturbed the original idea of the *IOA*. The performance of an observer is often compared not with the absolute physical limits [e.g., quantum noise (Rose, 1948)] but with models built on the basis of some arbitrary decisions and properties.

Not all psychometrical models are naturally compatible with the *IOA* approach. For example, the application of the *IOA* to the Thurstone's model is somewhat problematic. The *IOA* practically denies Thurstone's model assuming that the internal discrimination process does not have any variance. The variance of the discrimination process must be zero, or, in the case of discrete objects, smaller than the distance between two neighbouring units. In the Bernoullian model, the definition of the ideal observer model is straightforward – an ideal device can take into account all elements and is able to

discriminate the smallest difference that is the one element difference irrespective of the total number of elements.

The application of the Bernoullian model together with the *IOA* analysis to motion pooling resulted with surprising results. Despite of popular beliefs about efficiency of the motion perception (which main purpose is survival of an organism), the human observer turned out to be surprisingly inaccurate in discrimination of proportion between two spatially overlapping sets of randomly distributed elements moving in two opposite directions (**Study I**). Even small corrections to these limitations (**Study IV**) cannot deny that from all available information the observer is using only a small fraction for making decisions about the global motion direction. It is interesting that the observer is not literally blind to all these elements he or she is ignoring when the task is to tell the global motion direction. When the exact same stimulus is used for making inferences about the number of moving elements and with no regard of their actual motion direction, then a considerable fraction of these elements (up to 70%) are used to make the decision. Thus, a considerable number of moving elements which are visible when it concerns numerosity task dispossess qualities that are required for pooling local motion information (“motion blindness”).

What is the mechanism of this motion blindness? Since the direction of each motion element can be determined with a near absolute certainty if presented in isolation, this means that the extraction of available motion information is distracted by other elements present on the screen. In this respect the situation is very similar to other well-studied experimental conditions (attentional blink, crowding, dual task etc.) where a strong sensory signal cannot be noticed when processing is diverted by some other events (Andrews, Watson, Humphreys, & Braithwaite, 2011; Kanai, Walsh, & Tseng, 2010). Unfortunately, we have very little information about spatial, temporal or other limits of this form of motion blindness.

## **Repeated tagging as an aspect of mental architecture**

The way mental processes are organized – their architecture – has been one of the main concerns for both psychologists and neuroscientists (cf. Townsend, Fific, & Neufeld, 2007). The question of whether people perform perceptual and mental operations in parallel or in series has been pivotal in many of these pursuits (Dzhafarov, Schweickert, & Sung, 2004; Townsend, 1990; Townsend & Wenger, 2004). However, it is surprising that the serial versus parallel debate has almost entirely escaped the numerosity discrimination accuracy problem. It is possible that even the most fundamental principle of numeration – the one-to-one correspondence between items and counting tags in the process of transformation of every item from the to-be-counted category to the already-counted category – cannot always be obeyed (cf. Gelman & Gallistel, 1978). Percep-

tually it may be difficult to assign only one counting tag to every object with the purpose of preventing the same object from being counted twice. When the searched objects lack a clear structure it may be difficult to keep track of which object is already counted and which is still on the waiting list. Since something can be counted twice only at two separate time moments, the violation of the one-to-one principle is simultaneously an indication that at least some of the mental operations are executed in a serial order, one after another.

Returning to the Bernoulli's urn problem, every probability textbook teaches that balls or pebbles once extracted can or cannot be returned to the urn, which leads to two distinct probability distributions for the number of balls of a given colour: the binomial and hypergeometric distributions, respectively. These two different replacement schemes, however, have an important application to the problem of mental architecture. Provided that Bernoulli's urn model describes sufficiently accurately what happens in the perception of numerical differences, the scheme of sampling with replacement (leading to the binomial response model) implies that there is no tagging of which elements are already counted and which are not: the same element can, in principle, be inspected more than once. Consequently, if empirically determined psychometric functions for numerical discriminations between two sets of items are better described by binomial rather than hypergeometric response model, it would provide evidence that some of these elements are inspected twice or more times which, understandably, can only be done at two or more different time moments.

**Study V** shows that in perceptual tasks that can be solved more automatically and spontaneously, like discriminations based on colour, the observers have a tendency to keep track of elements that have already been counted. By contrast, in tasks like discrimination based on orientation that require more deliberation and scrutinizing of each element, the observers tend to confuse which elements have already been counted and which have not. Although the accurate tagging of the counted elements does not necessarily mean that the processing is executed in parallel, lack of the one-to-one tagging implies that at least some elements are processed serially, one after another. Thus, this study provided a strong proof that in a considerable number of trials, human observer counted the same element twice or more times which, as it was said already, can only be done at different time moments.

However, it seems that the avoidance of repeated counting of elements is not a rigid part of mental architecture but rather a flexible strategy that can be changed and, if necessary, learned. This conclusion is supported by the fact that no single theoretical model involving or prohibiting repeated tagging was able to provide a satisfactory explanation for most of the empirical psychometric functions. The best fit was found when predictions of different theoretical models were combined. This implies that the observers do not adhere to only one strategy even during one experimental session.

It remains to be demonstrated, to what degree the concept of repeated counting (consequently serial processing) is applicable for motion pooling. A

very low efficiency of motion pooling (in the best case, 20% of all elements) makes testing of this conjecture if not problematic then complicated. If only a small number of elements are taken into account it is also not very likely that some of these elements are counted repeatedly. It is a task for future studies to demonstrate whether the repeated counting is specific to a selected number of visual attributes (e.g., orientation) or is it common to many visual attributes including motion pooling.

## CONCLUSIONS

Many previous studies have presumed, explicitly or tacitly, that in forming of the global motion percept, all elementary motion signals present in the stimulus are pooled together. As the results of the **Studies I** and **IV** indicated this is not always the case. It is clear that the efficiency of taking stimulus elements into account is dependent upon particular physical parameters of the stimulus – density, contrast, spatial range etc. – to name a few. Apart from the finding that humans are perceptually limited in the given task of motion discrimination, an approach of estimating observer's efficiency in a straightforward fashion that is also highly comparable across different tasks and based on Bernoulli's urn model, is proposed. Motion perception seems to share, at least in certain conditions, the fate of many other visual attributes where from a large amount of available information only a small fraction is actually used in making decisions about global perception.

The results from **Study II** showed that in estimating the motion of a particular target area, only the immediate neighbourhood is effective, whereas the global percept is not explained by the summation or contrast of motion vectors in the immediate surrounding. Together with this finding and the fact that pooling of the motion signals was not more efficient in case the motion signals were made orthogonal (**Study I**), it is concluded that the limited efficiency is not an outcome of local motion inhibition.

**Study IV** demonstrated that the efficiency of using available visual information depends on the visual task. In the motion direction discrimination task the decisions were based on taking 21% of moving elements into account while from exactly the same display 74% of all elements were used when it concerned the discrimination of the number of moving elements irrespective of their direction. Also, it was evident that the common fate of the signals – moving coherently in one direction – did not improve the numerosity discrimination task. A sharp contrast between outcomes of these two tasks – motion and numerosity discrimination – allowed proposing an operationalization for the distinction between visible and accountable information.

In all situations where stimuli consist of discrete quantifiable elements, the Bernoulli's urn model has obvious advantages before the classical Thurstonian model which requires a continuum of internal states and a fuzzy projection of external attributes onto it. Alternatively to the classical Thurstonian model of discriminational processes, in Bernoullian models the randomness lies not in the internal representations of the stimuli, but in the sampling of the elements out from the total number of elements in the display. Nevertheless, it was shown that the Bernoullian model is formally equivalent to the Thurstonian discrimination model in terms of the description of empirically obtained psychometric function (**Studies I** and **III**). Although it is impossible to discriminate Bernoullian and Thurstonian models on the basis of their formal fit to empirical

data, the Bernoullian model seems to be relatively simpler and more easily falsifiable.

Finally, it was shown (**Study V**) that if an empirically determined psychometric function for numerical discriminations between two sets of items is better described by binomial rather than hypergeometric response model, it would provide evidence that some of these elements are inspected twice or more times which, understandably, can be done only at two or more different time moments. This new method for identifying one neglected aspects of the mental architecture – avoiding repeated tagging – provided a strong proof that in a considerable number of trials human observer counted the same element twice or more times which can only be done at different time moments, that is serially.

## ACKNOWLEDGEMENTS

I am deeply grateful to my supervisor Prof. Jüri Allik for sharing his wisdom, as well as for inspiration, encouragement and his contagious enthusiasm! This cooperation has been a joy that has propelled me a lot.

I also want to thank Aavo Luuk for his warm support and for the fact that he was the first to introduce me to the realms of mathematical psychology.

I am really thankful to Prof. Ehtibar Dzhafarov for all his kindness and invaluable comments on the manuscript.

I wish to thank all my colleagues from Tiigi Street and from our experimental lab for good company, especially Nele Kuldkepp, Kairi Kreegipuu, Kristiina Averin, Agne Põlder and Kristin Kurjama, whose help in preparation of the thesis has been indispensable!

Last, but certainly not least, my warmest thanks go to my dear family and friends for lasting support and recreation.

This research was supported by grants from the Estonian Ministry of Science and Education (SF0180029s08) and the Estonian Science Foundation (#ETF8231). We are thankful to our subjects for patience and endurance.

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## SUMMARY IN ESTONIAN

### Elementaarsete liikumis-, värvi- ja orientatsioonisignaali summeerimine terviklikuks tajuks

Enamik senistest uurimustest on eksplitsiitselt või implitsiitselt eeldanud, et globaalse liikumismulje kujunemisse on kaasatud kõik stiimulis esindatud elementaarsignaalid. Samas näitavad **uurimuste I ja IV** tulemused, et see eeldus ei pea alati paika, vaid inimeste taju on konkreetsetes liikumissuuna eristamise ülesandes üsna piiratud. On ilmne, et stiimuli elementide arvessevõtmise efektiivsus sõltub konkreetsetest füüsilistest stiimuli parameetritest, näiteks tihedusest, kontrastist, ruumilisest ulatusest jt. Lisaks tulemusele taju piiratusest esitatakse töös konkreetne ja läbipaistev Bernoulli urnimudelil põhinev meetod hindamiseks reaalse vaatleja efektiivsust ideaalse vaatleja suhtes, mis võimaldab võrrelda sooritust erinevate ülesannete lõikes.

**Uurimuse II** tulemused viitavad, et piiratud ala liikumise hindamist mõjutab vaid selle vahetu lähiümbus, samas kui terviktaju ei ole seletatav lähiümbruse liikumisvektorite summeerimise ega kontrastiefektidega. Arvestades lisaks ka asjaolu, et ortogonaalsete signaalide summeerimine ei olnud efektiivsem kui vastassuunaliste signaalidega summeerimine (**uurimus I**), võib järeldada, et piiratud efektiivsus ei ole seletatav liikumissignaali lokaalse vastastikuse pidurdamisega.

**Uurimus IV** näitas, et olemasoleva visuaalse info kasutamise efektiivsus sõltub konkreetsest ülesandest. Liikumissuundade eristamise ülesandes võeti vastamisel arvesse 21% elementidest, samas identse kuva puhul suutsid vaatlejad haarata 74% elementidest juhul, kui ülesandeks oli hinnata elementide suhtelist arvukust sõltumata nende liikumissuundadest. Ilmnes ka, et nn "ühise saatuse" printsiip ei parandanud suhtelise arvukuse eristust. Identse kuva, kuid erinevate ülesannete puhul ilmnenuid sooritusefektiivsuste drastiline erinevus võimaldab operatsionaliseerida nähtava ja arvesse-võetava informatsiooni eristamise.

Olukordades, kus stiimulid koosnevad diskreetsetest ja kvantifitseeritavatest elementidest, on Bernoulli mudelil traditsioonilise Thurstone'i mudeli ees mitmed väga selged eelised. Klassikalise mudeli üheks eelduseks on sisemiste seisundite kontinuum, millele projitseeritakse välise atribuutide hägusad, stohhastilised representatsioonid. Erinevalt klassikalisest Thurstone'i eristusprotsesside mudelist asetub Bernoulli mudelite puhul juhuslikkuse komponent mitte stiimuli sisemistes representatsioonides, vaid elementide alamhulga valikus kuvatud elementide koguhulgast. Samas, empiirilise psühhomeetrialse funktsiooni kirjelduse tasandil on Bernoulli ja Thurstone'i mudelid formaalselt absoluutselt ekvivalentsed (**uurimused I ja III**). Kuigi Bernoulli ja Thurstone'i mudelid ei ole formaalse sobituse alusel eristatavad ning sellest lähtuvalt puuduvad esialgu argumendid nende adekvaatsuse ja bioloogilise tõepära võrdlevaks hindamiseks, on Bernoulli mudel matemaatiliselt minimalistikum ning lihtsamini falsifitseeritav.

**Uurimuse V** raames jõuti järeldusele, et kui suhtelise arvukuse hindamise täpsust kajastav empiiriline psühhomeetriiline funktsioon on paremini kirjeldatav binomiaalse kui hüpergeomeetrialse vastusmudeliga, viitab see üheselt, et teatud osa stiimulelementidest inspekteeritakse korduvalt, mis on võimalik ainult kahel või enamal ajahetkel (väljastatud on olukord, kus paralleelne töötlusmudel imiteeriks seriaalset). Pakutud meetod võimaldab uurida mentaalse arhitektuuri üht seni vähest tähelepanu pälvinud

aspekti – elementide korduvat loendamist – ning selle rakendamine on viinud kaalukate tõenditeni, mis viitavad, et teatud hulgal vaatluskordadest segistab inimene juba loendatud ning veel loendamata elemendid, võttes üht ja sama elementi arvesse korduvalt, mis saab sündida vaid seriaalselt.

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