DISSERTATIONES PSYCHOLOGICAE UNIVERSITATIS TARTUENSIS

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AIRE RAIDVEE

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

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CONTENTS

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., Põlder, 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.**, Põlder, 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 Oberver 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

Δt 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.

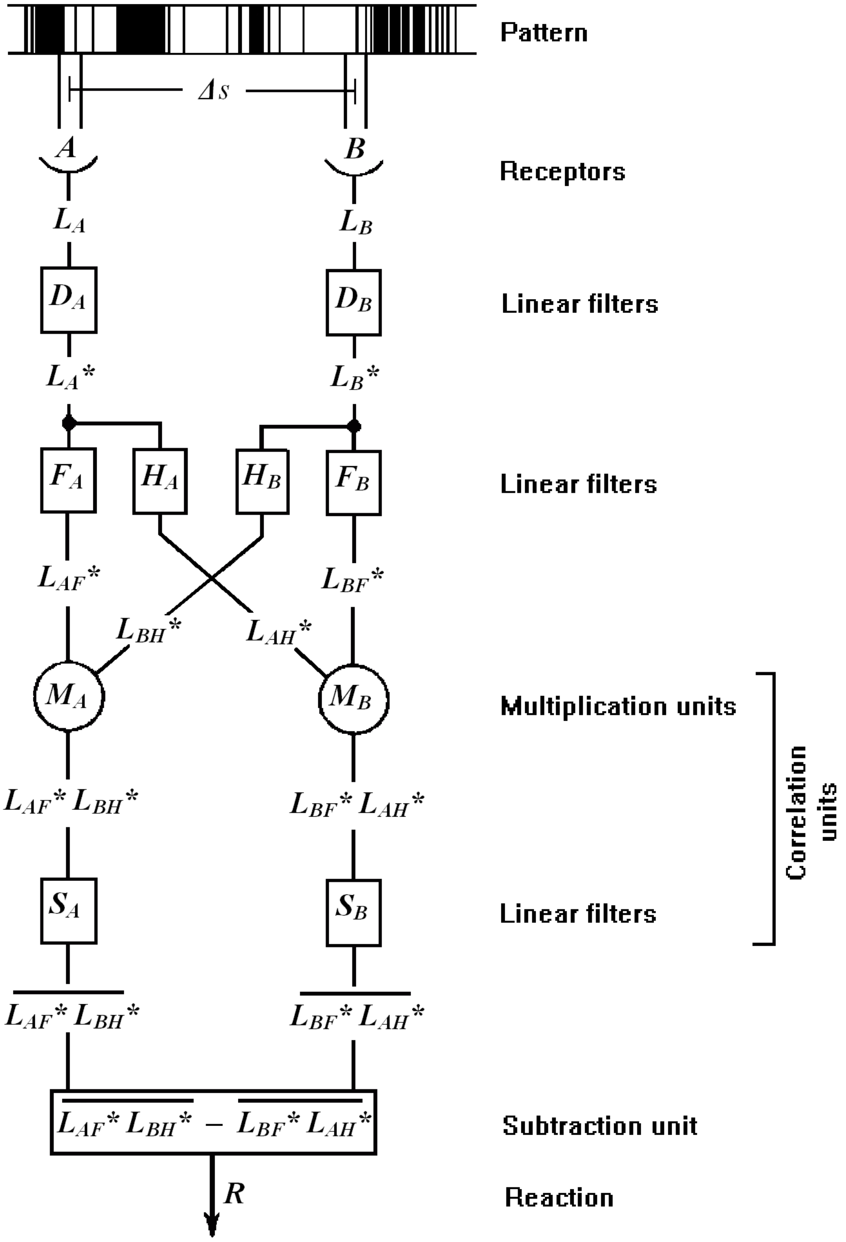

Figure 1. Schematic description of Reichardt motion detector (reproduced from Reichardt, 1961).

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 phenomena 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; Fredericksen, 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).

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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* (1968/1713). 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):

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

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

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):

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

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

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 (σ) via a simple equation:

$$K = \frac{1}{4\sigma^2} - 0.7542 \tag{5}$$

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 η 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

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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). Perceptually 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 discriminal 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

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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.

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SUMMARY IN ESTONIAN

Elementaarsete liikumis-, värvi- ja orientatsioonisignaalide 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 konkreetses 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 hindamaks 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 lähiümbrus, 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 liikumissignaalide 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 ilmnenud 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 kontiinum, millele projitseeritakse väliste 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 psühhomeetrilise 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 minimalistlikum ning lihtsamini falsifitseeritav.

Uurimuse V raames jõuti järeldusele, et kui suhtelise arvukuse hindamise täpsust kajastav empiiriline psühhomeetriline funktsioon on paremini kirjeldatav binomiaalse kui hüpergeomeetrilise vastusmudeliga, viitab see üheselt, et teatud osa stiimulelementidest inspekteeritakse korduvalt, mis on võimalik ainult kahel või enamal ajahetkel (välistatud 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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I

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Pooling elementary motion signals into perception of global motion direction

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ABSTRACT

Six observers were asked to indicate in which of two opposite directions, to the right or to the left, an entire display appeared to move, based on the proportion of right *vs* leftward motion elements, each of which was distinctly visible. The performance of each observer was described by Thurstone's discriminative processes and Bernoulli trial models which described empirical psychometric functions equally well. Although formally it was impossible to discriminate between these two models, treating observer as a counting device which measures a randomly selected subsample of all available motion elements had certain advantages. According to the Bernoulli trial model decisions about the global motion direction in a range of 12–800 elements were based on taking into account about 4 ± 2 random moving dot elements. This small number is not due to cancellation of the opposite motion vectors since the motion direction recognition performance did not improve after the compared motion directions were made orthogonal. This may indicate that the motion pooling mechanism studied in our experiment is strongly limited in capacity.

1. Introduction

It is generally agreed that elementary motion signals are processed by a large array of bilocal Reichardt detectors (Adelson & Bergen, 1985; Reichardt, 1961; Van Santen & Sperling, 1984, 1985; Watson & Ahumada, 1985), devices which perceive the correlation between time-varying luminance modulations at two disparate retinal locations, resulting in several seemingly counterintuitive phenomena: motion can be seen in stimuli containing no spatially displaced elements (Allik & Pulver, 1994, 1995; Johansson, 1950) and contrast reversal in one of the input luminance functions results in reversal of the direction of perceived motion (Anstis, 1970). In a sufficiently small area, local motion signals are pooled together into a composite perception which corresponds to a vector sum of individual components (Allik, 1992a; Allik & Pulver, 1995; Watanabe & Kikuchi, 2006). There is also evidence that elementary motion signals can be recruited along the trajectory of a moving object (Krekelberg & Lappe, 1999; Verghese, Watamaniuk, McKee, & Grzywacz, 1999; Watamaniuk, McKee, & Grzywacz, 1995) but there are obvious limitations to this recruitment since motion in random dot kinematograms is perceived almost identically when some of the elements travel along extended trajectories as when trajectories are interrupted and transferred to a new set of elements in the next frame (Allik & Dzhafarov, 1984; Scase, Braddick, & Raymond, 1996). In general, elementary motion detectors appear to operate locally and are not substantially influenced by other more distant motion coding elements (Dzhafarov, Sekuler, & Allik, 1993).

It is much less understood how a global motion direction ascribed to an extended area is processed from a large number of elementary motion signals contained within an area. 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 (Webb, Ledgeway, & McGraw, 2007; Zohary, Scase, & Braddick, 1996), 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; Fredericksen, 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.

Most studies have assumed that all or at least the majority of local motion signals are used in the processing of global motion direction. However, from the study of other visual functions, we know that many perceptual decisions are based on a limited amount of information, often only a small fraction of all potentially available information (Barlow & Lal, 1980; Burgess, 1984). This may mean that not all elementary motion signals are taken into account in decisions about global motion but, rather, only a limited subset of them. When an ideal observer analysis (Barlow & Lal, 1980; Burgess, Wagner, Jennings, & Barlow, 1981; Geisler, 1989)

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was applied to motion detection and discrimination tasks, estimated efficiencies were in the order of 1–2% (Gold, Tadin, Cook, & Blake, 2008; Simpson, Falkenberg, & Manahilov, 2003). The same research methodology applied to the problem of elementary motion signal pooling revealed that the largest limiting factor in the detection of global motion is correspondence noise: each spatially identifiable element has many potential corresponding elements towards which it can displace in subsequent time-frames (Barlow & Tripathy, 1997). It was proposed that, since the human visual system evolved to be able to integrate many directions of motion into a percept of global flow, pooling of elementary motion vectors is performed with high efficiency and an average effectiveness around 35% (Watamaniuk, 1993). Barlow and Tripathy (1997) found the highest efficiency in coarsely quantified stimuli: as high as 44% of the upper theoretical limit. Dakin and his colleagues (2005) also found similar percentage of the total number of elements in the display that determines global direction discrimination.

All previous applications of the ideal observer methodology to the pooling of elementary motion signals have used rather complex random dot motion displays which require rather elaborate assumptions for the construction of an ideal decision mechanism. For example, it is necessary to define correspondence rules for elements in successive frames, areas of spatial, and periods of temporal integration (Barlow & Tripathy, 1997; Dakin, Mareschal, & Bex, 2005; Watamaniuk, 1993). The main purpose of this study is to simplify motion displays to the degree in which the application of the ideal observer analysis would be as simple as possible, with the minimum number of postulated assumptions. In order to achieve this goal, it was necessary to solve several problems, such as how to eliminate the correspondence problem. Typical random dot motion displays contain the whole 360° spectrum of movement directions, which serve as the noise relative to which a coherent motion in one specified direction must be detected (Barlow & Tripathy, 1997; Williams & Sekuler, 1984). Although coherence thresholds show individual variation, it is typically in less than 10% of elements moving in a particular direction among all other directions that global coherent motion is sufficient enough to be perceived, among both human observers and trained monkeys (Britten, Shadlen, Newsome, & Movshon, 1992). One way in which to overcome the correspondence problem is to eliminate its main source – the noise or motion signals in all possible directions except the two opposite motion directions between which the observer is asked to discriminate. Another solution is to separate each elementary motion signal from all other motion elements by an inhibitory radius *R*, prohibiting them from being closer to each other than the critical distance *R*. It is established that only shortest motion vectors have significant contribution to the global motion impression (Allik, 1992a; Allik & Dzhafarov, 1984). It is also necessary for each motion element to be presented alone in order to be clearly visible and for its motion direction to be identified with near 100% certainty. This kind of random dot motion display containing only elements moving in one of either of two opposite directions with the observer's task to identify in which of these two directions the perceived global motion is more dominant closely resembles Reichardt's classical experiment with a beetle whose optomotor reactions were recorded at the junctions of an endless Y-maze (Reichardt, 1961).

A schematic depiction of the basic experimental idea is shown in Fig. 1A. Filled dots represent the spatial location of an element in the first frame at time t_1 and empty dots the same element in a slightly displaced position in the second frame after a short interstimulus interval at time t_2. Thus, a proportion of elements, N_R, move to the right (●○) and the remainder of elements, N_L, move to the left (○●). It is expected that the observer's probability of choosing the answer "R" ("Moving right") increases with the increase of the proportion of rightward moving elements compared to the total number of elements: $N_R/(N_R + N_L)$. The steepness of the choice probability function indicates the precision with which the numbers of rightward and leftward motion elements are summed and these two sums compared with each other. The probability of choosing the "R" answer is expected to exceed the probability of choosing the "L" answer as soon the number of rightward moving elements surpasses the number of leftward moving elements, $N_R > N_L$. Since an ideal observer is able to take into account all elements presented in a random dot motion (RDM) display, she is expected to notice even the smallest (one element) difference between rightward, N_R, and leftward, N_L, moving elements. It is also logical to presume that in the case of $N_R = N_L$, both directions would be chosen randomly with equal probability. Unlike an ideal device, however, a human observer usually needs a much larger disparity between the number of rightward and leftward moving elements to make a reliable distinction between the two competing motion directions. In quantitative terms, the precision of motion discrimination can be expressed by the slope of the cumulative psychometric function which increases proportionately to the ratio $N_R/(N_R + N_L)$. Provided that the empirical psychometric function is sufficiently close to the cumulative normal distribution, the precision of direction discrimination can be characterized by the standard deviation (σ) of the normal distribution.

According to a standard psychophysical model, the number of right- and leftward motion elements are represented as two random variables ("images") on a continuum of internal states expressing a subjective degree of perceived motion either in the right- or leftward direction (Thurstone, 1927). If an internal representation of the number of rightward moving elements exceeds an internal representation of the number of leftward moving elements then the rightward direction is chosen by the observer as an answer. It is rather obvious that if the number of rightward, N_R, and leftward, N_L, moving elements is approximately equal then the two random internal representations of these two numbers overlap substantially and the probability of the correct discrimination of proportions of the moving elements is close to the chance level. With the increase of the disparity between N_R and N_L their internal "images" start to depart from one another leading to a more confident discrimination of moving elements. Assuming that

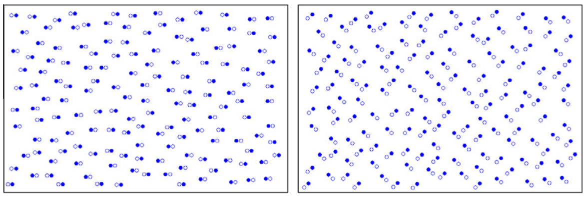

Fig. 1. Schematic view of the experimental design in Study 1 (A, left) and Study 2 (B, right).

these two random variables are independent and can be represented sufficiently well by two normal distributions with an equal standard deviation (the Case V in the Thurstone system) we can come to a conclusion that the slope of this psychometric function (σ) characterizes the standard deviation of what Thurstone called the *discriminal deviation* or *dispersion* (Thurstone, 1927). For example, let us suppose that on a display, 40 elements move to the left and 60 elements move to the right. Fig. 2 demonstrates hypothetical internal representations (random "images") of these two groups of elements moving in the opposite directions. Provided that these two internal "images" are rather smeared and both have a standard deviation equal to approximately 12.7 elements ($\sigma' = N \cdot \sigma/\sqrt{2}$, given that $\sigma = 0.18$ as in case of observer KA, see Fig. 3), the correct motion direction with the larger number of elements ("R") will be chosen in 86.7% of trials. Thus, in 13.3% of cases the wrong answer ("L") will be given in spite of twenty extra elements moving in the opposite direction. Almost by definition, an ideal observer has the discriminal deviation equal to zero which guarantees that she can differentiate the proportions correctly in case of only one extra element in either direction.

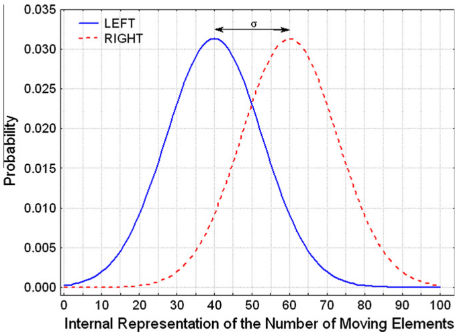

Fig. 2. Schematic view of the Thurstonian discriminal deviation processes.

However, it is also possible to analyse data in terms of the amount of information used. Assuming that a real observer is making decisions about global motion direction not on the basis of the full amount of information available on the display but on a smaller sample of moving elements, the situation becomes formally equivalent to a Bernoulli trial, in which the selection of either a rightward or leftward moving element is completely random. As an extreme case, it is even possible that the observer randomly picks up a single element and on the basis of its direction decides about the movement of the whole display. Provided that the observer is randomly selecting out N' elements from a considerably larger number of motion elements N, her choice probabilities are based on the proportion of the rightward N'_R and leftward N'_L moving elements: if the number of the rightward moving elements N'_R exceeds the number of the leftward moving elements N'_L ($N'_R > N'_L$) then the rightward direction is chosen as an answer; if the number of elements moving in the opposite directions happens to be equal ($N'_R = N'_L$) then the choice between two response categories is random with equal probability (assuming there is no response bias). Obviously, with any increase in the sample size N', the probability of making an accurate choice becomes closer to one, independent of the actual proportion between N_R and N_L (except for the case of $N_R = N_L$), and finally, when the sample contains all elements ($N' = N$) the correct choice will be made whenever $N_R \neq N_L$.

Thus, from the proportion of elements moving to the right N_R compared to those moving to the left N_L, one can easily compute the probability of choosing the right answer ("R") for a given N' using either cumulative binomial (the same element can be counted in multiple instances) or hypergeometric distributions (each element is counted only once). There is a simple relationship between the slope of the approximating psychometric function σ and the size of a randomly selected subset of elements N', which could give a virtually identical psychometric function (provided

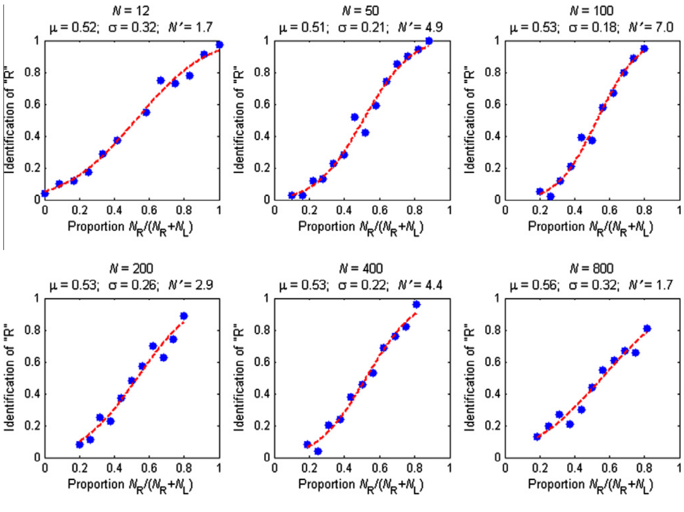

Fig. 3. Psychometric functions from Study 1 for the observer KA dependent of the number of motion elements.

that the selection of N' elements is based on the binomial distribution):

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

The relationship would make responses identical for $N' = 2j$ and $N' = 2j - 1$ (where j is any positive natural number) which is derived from the unbiased property of the counting device. One obvious advantage of normal approximation is that the estimated size of the binomial series N' is not confined to only positive natural numbers. On each and every single trial there could be only one fixed subset of elements N' on the basis of which the observer's decisions were made. It is possible, however, that this number varies from trial to trial and the summary estimate N' is an average across many trials. For example, fractions (e.g. $N' = 100.5$) could be interpreted as a mixture of the binomial series of different lengths (e.g. in 50% cases $N' = 100$ and in the remaining 50% cases $N' = 101$). Details of derivation are given in Appendix A.

We have two at least formally indistinguishable descriptions – in terms of the Thurstone's law of comparative judgement and in terms of series of Bernoulli trials – which could be equally applied to the description of empirical psychometric functions. Besides the description of the pooling of elementary motion signals we are also interested in establishing which of these descriptions gives a better explanation of the observed data.

2. Study 1

2.1. Methods

2.1.1. Participants

There were six participants, four women and two men, with normal or corrected to normal visual acuity and no reported history of visual disorders. Their ages ranged from 19 to 27 and four of them had no prior experience with psychophysical experiments.

2.1.2. Apparatus

Stimuli were generated using a Cambridge Research Systems ViSaGe image generator driven by a Pentium computer. Stimuli were displayed on a Mitsubishi Diamond Pro 2070SB 22″ (active display area 20″) monitor operating at a refresh rate 140 Hz with a spatial resolution of 1024 × 769 pixels.

2.1.3. Stimuli

The stimuli were presented according to the scheme presented in Fig. 1A at a viewing distance of 170 cm on a rectangular area extending horizontally 12.9° and vertically 9.7° with a constant monochromatic luminance of 60 cd/m^2. Each stimulus consisted of two subsequent frames containing 12, 50, 100, 200, 400, or 800 motion elements around a central fixation point. The duration of each frame was 100 ms and the interframe interval was 30 ms. Each moving element was a dot 3′ in diameter and 120 cd/m^2 in luminance surrounded by an inhibitory area with a radius of 30′, in cases of 12 and 50 elements, and 12′, in cases of 100, 200, 400, and 800 elements, which prohibited other elements from being closer than 27′ or 8′, respectively. Within each series of experiments, the total number of motion elements was kept constant but the proportion between elements moving to the right N_R and to the left N_L was varied. Motion was created by the horizontal displacement of each dot in the second frame 9′ to the right or left from where it had appeared in the first frame. The calculated velocity of the transition was 5°/s which guaranteed it's near optimal visibility.

2.1.4. Procedure

In each trial the observer was instructed to indicate in which direction, to the right or to the left, the whole pattern appeared to move by pressing one of two buttons. The proportion of rightward moving elements $N_R/(N_R + N_L)$ was determined randomly during the experimental session and varied at 12 levels for $N = 12$; 14 levels for $N = 50$; and 11 levels for either 100, 200, 400 or 800 elements. The condition of $N_R = N_L$ was not included. Each condition, corresponding to the total number of moving elements N and the proportion of the rightward moving elements $N_R/(N_R + N_L)$, was replicated in each series 20 times and each series was repeated five times to gain 100 responses per stimulus condition.

2.2. Results and discussion

Fig. 3 shows the psychometric functions of one participant, KA, in identifying the rightward global motion direction in random dot patterns containing $N = 12$, 50, 100, 200, 400, or 800 motion elements, as a function of the proportion of the rightward motion elements $N_R/(N_R + N_L)$. Continuous curves demonstrate cumulative normal distributions, with the respective means (μ) and standard deviations (σ) providing the best least square approximation to these empirical psychometric functions. The goodness of fit was satisfactory since the proportion of the explained variance was at least 93.3%. On the basis of the slopes of the psychometric functions (σ), it is easy to find the length of the Bernoulli trials N' which produce psychometric functions of the same shape (Eq. (1)). For example, the moving dot patterns with the smallest ($N = 12$) and the largest ($N = 800$) number of elements were both characterized by a psychometric function with $\sigma = 0.32$. This means that according to the Bernoulli trial model, the observer seems to have randomly selected about $N' = 2.44$ motion elements and on the basis of these decided which of the two global motion directions, to the right or to the left, to choose. In the first case, it is about 20.3% of all available motion elements but only 0.3% of the 800 motion elements in the most numerous random dot pattern. In terms of the Thurstonian model the standard deviation of the psychometric function $\sigma = 0.32$ with only 12 elements means that the internal representations have standard deviations equal to $\sigma' = 12 \cdot 0.32/\sqrt{2} = 2.72$ elements. In the presence of even a small number of elements moving in the opposite directions the internal representation of moving elements becomes surprisingly imprecise: for example six elements are often perceived as movements caused by 3 or 9 elements.

The best performance ($\sigma = 0.18$) was with the stimulus containing $N = 100$ elements, where the decision was made on the basis of about five ($N' = 4.96$) randomly selected elements. If we express the best performance of the observer KA not in terms of proportions but absolute number of elements, the internal representation will be rather blurry with a standard deviation equal to about 12.7 elements as it is shown in Fig. 2. This means that the observer is expected to make a few mistakes even if the proportion of moving elements is 20–80. The global motion direction identification was the poorest with $N = 12$ elements out of which only 1.63 elements were used on average to make decisions. In the worst case, the number of counted elements was even less than one ($N' < 1$) indicating that on a certain number of trials the answer was based on pure guessing. It is important to notice that even with such poor efficiency do the psychometric functions asymptotically reach sufficiently close to the minimum (zero) and the maximum (one) values. This is not that the coherent unidirectional motion cannot be seen. It only takes a lot of elements moving in one direction to surpass elements moving in the opposite direction.

Summary results of all six participants are presented in Table 1. The average percentage of explained variance across all 36

Table 1
Parameters of the best approximation and the estimated number of elements on which decisions about global motion direction are based in Study 1.

Observer		Number of motion elements (N)					
		12	50	100	200	400	800
KA	μ[a]	0.52	0.51	0.53	0.53	0.53	0.56
	σ[b]	0.32	0.21	0.18	0.26	0.22	0.32
	σ (95%CI)	0.28–0.35	0.18–0.24	0.15–0.21	0.21–0.31	0.19–0.25	0.26–0.38
	N'[c]	1.69	4.91	6.96	2.94	4.41	1.69
	N' (95%CI)	1.29–2.43	3.59–6.96	4.91–10.36	1.85–4.91	3.25–6.17	0.98–2.94
	JND	1.92	5.25	9.00	26.00	44.00	128.00
	%EV[d]	98.9	98.2	98.8	96.8	98.7	96.3
MT	μ	0.52	0.44	0.35	0.46	0.47	0.48
	σ	0.39	0.37	0.43	0.33	0.32	0.20
	σ (95%CI)	0.32–0.45	0.31–0.42	0.34–0.51	0.25–0.41	0.26–0.38	0.19–0.22
	N'	0.89	1.07	0.60	1.54	1.69	5.50
	N' (95%CI)	0.48–1.69	0.66–1.85	0.21–1.41	0.73–3.25	0.98–2.94	4.41–6.17
	JND	2.34	9.25	21.50	33.00	64.00	80.00
	%EV	97.1	96.6	95.1	93.3	96.0	99.7
KK	μ	0.59	0.52	0.50	0.49	0.52	0.51
	σ	0.35	0.19	0.21	0.22	0.20	0.20
	σ (95%CI)	0.29–0.40	0.16–0.22	0.19–0.24	0.19–0.24	0.18–0.21	0.15–0.24
	N'	1.29	6.17	4.91	4.41	5.50	5.50
	N' (95%CI)	0.81–2.22	4.41–9.01	3.59–6.17	3.59–6.17	4.91–6.96	3.59–10.36
	JND	2.10	4.75	10.50	22.00	40.00	80.00
	%EV	97.7	98.9	99.1	99.0	99.7	96.9
PT	μ	0.51	0.51	0.53	0.5	0.53	0.50
	σ	0.38	0.30	0.26	0.22	0.31	0.51
	σ (95%CI)	0.34–0.41	0.27–0.32	0.22–0.31	0.19–0.26	0.28–0.34	0.41–0.61
	N'	0.98	2.02	2.94	4.41	1.85	0.21
	N' (95%CI)	0.73–1.41	1.69–2.68	1.85–4.41	2.94–6.17	1.41–2.43	0–0.73
	JND	2.28	7.50	13.00	22.00	62.00	204.00
	%EV	99.1	99.0	97.2	97.9	98.9	95.0
MA	μ	0.51	0.47	0.48	0.43	0.47	0.42
	σ	0.32	0.24	0.23	0.18	0.22	0.25
	σ (95%CI)	0.28–0.36	0.22–0.27	0.20–0.26	0.15–0.22	0.19–0.25	0.22–0.28
	N'	1.69	3.59	3.97	6.96	4.41	3.25
	N' (95%CI)	1.17–2.43	2.68–4.41	2.94–5.5	4.41–10.36	3.25–6.17	2.43–4.41
	JND	1.92	6.00	11.50	18.00	44.00	100.00
	%EV	99.0	99.1	98.7	97.7	98.3	98.9
LE	μ	0.50	0.46	0.44	0.39	0.44	0.44
	σ	0.25	0.16	0.15	0.18	0.22	0.20
	σ (95%CI)	0.22–0.27	0.15–0.18	0.13–0.17	0.15–0.21	0.20–0.24	0.17–0.23
	N'	3.25	9.01	10.36	6.96	4.41	5.50
	N' (95%CI)	2.68–4.41	6.96–10.36	7.9–14.04	4.91–10.36	3.59–5.5	3.97–7.9
	JND	1.50	4.00	7.50	18.00	44.00	80.00
	%EV	99.4	99.7	99.1	98.4	99.4	98.5

[a] μ = mean of the approximated psychometric function.
[b] σ = standard deviation (slope) of the psychometric function.
[c] N' = the estimated number of elements on which the decision about global motion direction is based on.
[d] %EV = percentage of explained variance.

psychometric functions was 98.1%, with a standard deviation of 1.5% and a minimum of 93.3%. Thus, on average, only 1.9% of the total variance remained unexplained with the best fitting psychometric function. The estimated length of the Bernoulli trials N' which could reproduce a psychometric function with a specific standard deviation σ varied from extremely low, $N' = 0.21$ (denoting random guessing on at least four of five trials), to moderately high, $N' = 10.36$. The average number of elements counted in deciding the global motion direction across all 36 conditions was 3.82 with a standard deviation equal to 2.43. After rounding these figures, it would be fair to say that according to the Bernoulli trial model an average human observer is able to count 4 ± 2 random moving dot elements when making decisions about global motion direction. The statistical efficiency (N'/N) varied from 27.1% to 0.03%, with an average of 5.2%.

There was no clear relationship between the number of motion elements and the effective usage of these for motion direction identification. Observer KK performed the best at 50 motion elements, whereas observers KA and LE performed the best at 100; observers PT and MA at 200; and observer MT at 800 elements. Across all six observers, performance was the best at 100 motion elements, from which only about 5 on average were used to make decisions about the global motion direction. Nevertheless, the total number of motion elements seemed to play a relatively minor role in the efficiency of pooling elementary motion signals.

Can the shape of psychometric functions be explained by density of moving elements? Not likely so. Although the density of moving elements was not a target of the direct experimental manipulation, the range of its variation was more than 66 times. For example, with $N = 12$ moving elements there were on average 0.096 but with $N = 800$ moving elements approximately 6.39 elements per each 1° by 1° square of visual angle. Nevertheless, the slopes of psychometric functions changed only very little.

It is also possible to analyse the obtained psychometric functions in terms of the Thurstone's law of comparative judgement. For example, we can express the internal discriminative dispersion in terms of the Just Noticeable Difference (*JND*) – that is, the difference in the number of leftward and rightward moving elements that is required by subjects to correctly discriminate motion direction in 84.1% of the cases. All calculated *JND* values are shown in

Table 1. Inspecting Table 1 it is easy to see that *JND* is increasing with the total number of moving elements. For instance, the observer KA needed on average 1.92 element difference to discriminate reliably motion directions in displays containing $N = 12$ elements but she required 128 elements to discriminate among $N = 800$ moving elements moving in the opposite directions. Since the argument of the psychometric functions was expressed as the proportion of moving elements $N_R/(N_R + N_L)$, the estimated slope of the psychometric function is directly proportional to the Weber fraction. The fact that the observer counted approximately an equal number 4 ± 2 moving elements implies automatically that the Weber fraction remains relatively constant with the increase of the number of moving elements. It is useful to remind that it is not necessarily so for all visual attributes. For example, for the numerosity discrimination, *JND* is a power function, not a constant, of the number of elements with the exponent close to 0.7 (Allik & Tuulmets, 1991).

This may seem puzzling that the observers in this experiment were able to count on average only 4 ± 2 moving elements. One likely explanation is that observers' performance was so poor since most of the local motion signals are cancelled by nearby motion in the opposite direction. As a result, these two local movement vectors pointing in opposite directions nullify each other and no motion information is available from this region (Allik, 1992a, 1992b; Allik & Pulver, 1995). However, the cancelling of opposite motion signals is expected to increase with the density of motion signals. A display containing 800 motion elements should elicit much more mutual motion cancelling than a display containing only 12 elements, since every element almost certainly has in its vicinity another element moving in the opposite direction. Nevertheless, actual data speak about the opposite tendency: decisions about global motion direction tend to be slightly more accurate with larger numbers of motion elements. One way how to escape the cancelling of opposite motion directions is to change the angle between two populations of moving dots. Orthogonal movement directions are known to be processed by independent mechanisms (Levinson & Sekuler, 1975) and if the low processing capacity is caused by the cancellation of opposite motion directions then one can expect much higher counting number in discrimination between two populations of moving dots separated by 90° angle in their direction.

3. Study 2

3.1. Methods

3.1.1. Participants

There were three participants with normal or corrected to normal visual acuity and no reported history of visual disorders. Two of them participated also in the first experiment.

3.1.2. Apparatus

Apparatus was identical to the first experiment.

3.1.3. Stimuli

A schematic representation of the basic stimulus configuration is shown in Fig. 1B. The stimuli were identical to the first experiment except in addition to the horizontal shift 9′ either to the left or to the right, all elements were simultaneously shifted 9′ downwards in the second frame. In the result of this vertical shift the angle between two populations of moving elements became 90°. The total number of elements was fixed at 12, 200 or 800 elements in each of three different experimental series.

3.1.4. Procedure

Since all moving elements had a common downward moving component, all displays appeared moving down. The observers were instructed to indicate in which direction from the horizontal axis, to the left or to the right, the whole pattern appeared to move. Like in Study 1 the total number of moving elements *N* and the

Table 2
Parameters of the best approximation and the estimated number of elements on which decisions about global motion direction are based in Study 2.

Observer		Number of motion elements (N)		
		12	200	800
KA	μ[a]	0.50	0.49	0.52
	σ[b]	0.24	0.21	0.28
	σ (95%CI)	0.20–0.28	0.18–0.23	0.24–0.31
	N'[c]	3.49	5.20	2.49
	N' (95%CI)	2.38–5.33	3.98–6.96	1.80–3.48
	JND	1.44	21.00	112.00
	%EV[d]	98.6	98.9	98.4
KK	μ	0.43	0.49	0.51
	σ	0.27	0.17	0.18
	σ (95%CI)	0.24–0.30	0.15–0.19	0.16–0.20
	N'	2.68	8.25	6.86
	N' (95%CI)	1.97–3.70	6.43–10.87	5.50–8.72
	JND	1.62	17.00	72.00
	%EV	99.1	99.2	99.4
AR	μ	0.52	0.49	0.51
	σ	0.35	0.18	0.15
	σ (95%CI)	0.30–0.41	0.15–0.20	0.13–0.18
	N'	1.24	7.45	9.88
	N' (95%CI)	0.76–1.98	5.63–10.16	7.25–14.05
	JND	2.10	18.00	60.00
	%EV	98.1	99.0	99.0

[a] μ = mean of the approximated psychometric function.
[b] σ = standard deviation (slope) of the psychometric function.
[c] N' = the estimated number of elements on which the decision about global motion direction is based on.
[d] %EV = percentage of explained variance.

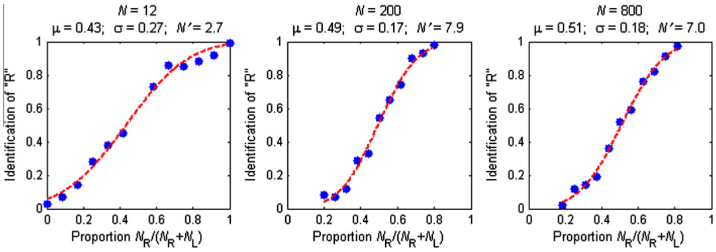

Fig. 4. Psychometric functions from Study 2 for orthogonally moving elements (N = 12, 200, and 800) for the observer KK.

proportion of the rightward moving elements $N_R/(N_R + N_L)$ was replicated 20 times in each series to gain 100 responses per stimulus condition.

3.2. Results and discussion

Psychometric functions for discrimination between two populations of dots whose motion directions were separated by 90° are shown in Fig. 4. It is clear that the slopes of the psychometric discrimination functions are not remarkably different from those obtained in the Study 1 with the opposite movement directions. Details of the psychometric functions and the inferred number of counted elements N' are shown in Table 2. Again, the average number of moving elements ($N' = 5.3$) that the observers were able to take into account when they made their decision about motion direction was modest. However, the discrimination between orthogonally moving 12 elements was less efficient than between 200 and 800 moving elements.

Considering that discrimination between two populations of dots whose directions differed by 90° was not superior to that when separation between directions was 180°, it is possible to conclude that a relatively poor motion pooling performance is not caused by the cancelling of opposite motion vectors at some early stages of motion processing.

4. General discussion

Our main goal, a simple experimental design in which the observer's performance was almost directly comparable with that of the Bernoulli sampling scheme, was obviously achieved. Unlike in many ideal observer models, there was no need to postulate visual noise against which the signal was compared. The only fundamental assumption required for the construction of an ideal observer is that the sample of elements chosen from all available elements in the motion display is randomly selected. The second principal postulate, whether each element can be counted only once or several times, is of less practical importance, since differences between binomial and hypergeometric distributions, corresponding to these two situations, are too small to be discriminated on the basis of available empirical data.

It may come as a surprise that the decision about global motion direction may be based on counting very few elements. Typically, it was as if only about 2–6 elements that observers made their choices between the two opposite motion directions upon. This low efficiency is not a trivial consequence of making motion direction discrimination artificially difficult. On the contrary, the stimulus conditions were deliberately chosen to make each elementary motion signal separable from others and identification of its motion direction absolutely certain when they were presented alone or together with other elements moving in the same direction. These results are clearly smaller than the statistical efficiencies for motion pooling set out in several previous studies (Barlow & Tripathy, 1997; Dakin et al., 2005; Watamaniuk, 1993). We are not aware of the reason for this discrepancy. Although there were obvious individual differences, the general pattern suggests that we cannot talk about a constant or even a relatively stable statistical efficiency. As the number or density of elements increases, the effective number of counted motion elements remains basically unchanged. It seems reasonable to say that observer is able to notice only a limited number of elements, irrespective of their total number or density. Provided that the Bernoulli trial model is correct, the motion pooling system seems to be characterized by a magic number of four, plus or minus two. It may not be a coincidence that the accuracy of numerosity judgments of regularly and densely spaced visual targets is also limited to just four elements (Atkinson, Campbell, & Francis, 1976).

Translated into Thurstone's random "images" it means that the width of the internal representation increases proportionally with the number of motion elements. The internal discriminal deviation was about three elements when a display contained 12 moving elements but increased to about 180 elements when the total number of elements was 800. Perhaps realistic for continuous attributes such as weight or luminance, the rapidly increasing discriminal deviation may sound weird for an attribute expressed in terms of positive natural numbers. Although such large noise is perhaps not entirely unrealistic, it is also conceivable that the Bernoulli trial model gives a simple and elegant alternative explanation.

The surprisingly low statistical efficiency of pooling elementary motion signals is certainly not simply the consequence of the experimental design used. For example, Tokita and Ishiguchi (2009) used an essentially identical proportion discrimination task, precisely to study whether human observers can identify the relative number of red and green dots as well as the relative number of parallel and converging lines. Analyzing the psychometric functions published in their study, it is possible to conclude that, for the discrimination of the relative number of red and green dots, eleven undergraduate students were, on average, able to take into account 69 elements from a total of 100. However, the ability to discriminate between the relative number of parallel and converging lines was much poorer and decisions were made on the basis of no more than two elements. Thus, with principally the same experimental design, the statistical efficiency of the human observer can, on the one hand, be close to 70% of that of the ideal counting device or, on the other hand, close to 1% or even less, depending on the perceptual task.

This low percentage is perhaps not surprising for visual attributes that cannot spontaneously jump into one's perception and require scrutinized attention to be noticed. Nevertheless, motion perception is often regarded as vital for survival and therefore is most likely served by reliable automatic processes that cannot easily be altered by voluntary intervention. However, some previous results indicate that pooling of elementary motion signals into global motion perception is under the control of attention (Burr, Baldassi, Morrone, & Verghese, 2009). As it also turns out, we are not very sophisticated in our ability to segregate items based on the nature of their motion (Horowitz, Wolfe, DiMase, & Klieger, 2007). Continuing along these lines of observations, the current study may indicate—counter to commonly held belief—that a motion pooling mechanism with such a limited capacity may not be entirely compatible with processes regarded parallel, effortless, or automatic. We are aware that this conclusion may seem counterintuitive and many readers are inclined towards more conventional discrimination models based on random internal "images" some of which can be regarded as sensory noise. However, it is also possible to see some of the inferences drawn from application of the Thurstonian models as contradicting our intuition. For example, when the number of moving elements is small ($N = 12$) the size of internal random "images" inferred from the slope of psychometric functions becomes unrealistically large (both having a standard deviation equal to approximately 2.7 elements, given that $\sigma = 0.32$ as in case of observer KA, see Fig. 3). It does not fit well with other observations that, for example three moving elements can create a subjective impression which is often equal to the impression created by twice as many elements.

Inevitably, these capacity limitations must have manifestations in other perceptual tasks which also require a combination of elementary motion signals for global perception. One obvious candidate for this type of task is motion transparency – seeing multiple motion components within the same region in the visual field. When two coherently moving sparse random dot kinematograms are superimposed, the observer is able to see global motion in two different directions. Not only is the maximum number of directions that can be perceived simultaneously severely constrained (Greenwood & Edwards, 2009), it is also a relatively inefficient process (Braddick, Wishart, & Curran, 2002; Edwards & Greenwood, 2005; Suzuki & Watanabe, 2009). In order to see two global motion directions simultaneously, observers require that about 42% of all dots move coherently in each of these two directions, instead of only about 5% required for seeing one of these components alone (Edwards & Greenwood, 2005). Although it could only be proven by carrying out additional studies, it seems logical that the constraints of motion transparency are consequences of capacity limitations in the motion pooling system itself. One possible framework for additional studies could also be provided by the Bernoulli trial model which can also be extended for the polytomous case (i.e. the case where the global motion pattern contains many directions of motion).

It is important to keep in mind, however, that comparison with an ideal counting device does not prove that the human observer behaves like a mathematically constructed mechanism. If the conclusion that the human observer is able to pay attention to only 4 ± 2 display elements seems psychologically unrealistic, then it is possible to elaborate other mechanisms that are still formally equivalent to a counting device with a strongly limited capacity. For example, it is possible to entertain the idea that all display elements are registered but, due to a crowding of motion elements or some other reason, one motion direction is often confused with the opposite motion direction. Although we almost certainly excluded cancelling opposite motion directions in an early stage of motion processing as a possible cause of this confusion, there may still be some other mechanisms that are responsible for capacity limitations.

Presented analysis also provides an interesting methodological lesson. It may be unexpected that the Thurstonian discrimination model can be replaced with an equally accurate deterministic model containing no diffuse "images" created by internal noise. Assuming that the motion direction discrimination is based on the limited number of selected motion elements, we were compelled to postulate that their internal images are precise and their relative number can be determined accurately. Thus, random may be not only "images" on an internal representation but the way how a subsample of elements is selected from the total number of elements and how many elements are selected out on every single trial. Since at least formally the Thurstonian and Bernoulli trial models describe empirical psychometric functions equally well, it is important to notice that we do not necessarily need to suppose the Thurstonian discriminative process which is usually regarded as the "essence of simplicity" (Luce, 1977). One advantage of the Bernoulli trial model over the Thurstone-type of models pertains to the estimation of real observer's efficiency. An ideal observer formulated in terms of the Thurstone's discriminative process is supposed to have a noiseless internal representation with zero variance. Without some arbitrary assumptions it would be impossible to compute the ratio between dispersions of real and ideal observer since the latter has zero variance. Compared to the Thurstone's models, in the framework of Bernoulli trial model, it is almost inevitable to define the ratio between the sample size N' and the total number of elements N as a measure of efficiency relative to an ideal performance.

We also have not enough information to decide which of these two formal representations – the Thurstonian and Bernoulli ones – is physiologically more plausible. Existing neurophysiologic evidence is unfortunately not precise enough to make an educated choice between these two alternatives as data is limited to approximations by the standard model only. Perhaps neurophysiologists feel more comfortable working with noisy internal "images" since neurons in the visual system typically have a spontaneous activity added to the externally evoked one. Whereas signal detection theory based models, bearing its roots in the Thurstonian paradigm (Lee, 1969) have been fitted to predict macaque's choice behavior related to the directional signals of a single cell in a wide range of stimulus configurations (Britten, Newsome, Shadlen, Celebrini, & Movshon, 1996; Celebrini & Newsome, 1994), it is also important to remember that a Thurstonian-type modeling – stochastic images representing stimuli – cannot explain, in principle, properties of some well-behaved discrimination functions that are typically observed and expected in behavioral experiments (Dzhafarov, 2003a, 2003b). Fortunately, the proposed design for the discrimination of proportions is so simple that it can be used to study not only human observers but other species as well perhaps starting from beetles and ending with monkeys. This is a particularly exciting prospect since beside behavioral experiments it would be possible to penetrate visual system at different stages of processing and record responses of single neurons.

One obvious benefit of the ideal observer analysis is that it specifies an agenda for further studies. Although the search for specific mechanisms explaining sources of statistical inefficiency would not be able to make perception function more effective, it can nevertheless suggest new testable hypotheses about how elementary motion signals are pooled together into global motion perception.

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Appendix A. Derivation of Eq. (1)

Whereas a fully analytic derivation of Eq. (1) is rather complex, one can find an arbitrarily exact approximation for the relationship between the length of the Bernoulli series and the standard deviation of the respective normal distribution.

To fix some preliminary estimates for the approximation, we verified that the ideal observer model would yield identical psychometric curves for $N' = 2j - 1$ and $N' = 2j$, where N' is the length of the binomial series reflecting the number of elements taken into account in the decision process, and j is any positive natural number. The probabilities of a correct choice for odd (P_o) and even (P_e) numbers of N' are expressed via the cumulative binomial series as follows:

$$P_o = \sum_{k=1+\left[\frac{N'}{2}\right]}^{N'} \binom{N'}{k} p^k (1-p)^{N'-k}, \quad N' = 2j-1 \tag{A.1.1}$$

$$P_e = \sum_{k=1+\left[\frac{N'}{2}\right]}^{N'} \binom{N'}{k} p^k (1-p)^{N'-k} + 0.5 \binom{N'}{\frac{N'}{2}} p^{N'/2} (1-p)^{N'/2}, \quad N' = 2j \tag{A.1.2}$$

where p is the proportion of elements moving to the right *vs* to the left, $N_R/(N_R + N_L)$.

As for any given N' the psychometric function is determined by the slope at the point where $p = 0.5$, it suffices to control whether the derivatives of P_o and P_e with respect to p are equal at the point where $p = 0.5$. It is not difficult to show, by using, for example, Wolfram Mathematica, that this is the case.

Further, using the set of possible odd values for N', it can be shown that the squared derivative of P_o or P_e is in perfect linear relationship with N'. As the slope of the psychometric function is the inverse of the standard deviation of the Gaussian fit of the respective function, it is clear that the sought for relationship is of the form $N' \sim 1/\sigma^2$. The exact form of the relationship was produced by generating theoretical psychometric functions from 2000 values of N' and approximating them by cumulative normal distribution. From the standard deviations of the Gaussian approximations, Eq. (1) was confirmed with as a model of perfect linear fit.

Appendix B. Supplementary material

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.visres.2011.07.004.

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II

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Reaction time to motion onset and magnitude estimation of velocity in the presence of background motion

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ABSTRACT

Reaction times (RT) to motion onset of a target grating moving at 0.4, 0.6, 0.8, 1.0 or 1.6°/s and magnitude estimation of the same velocities were studied in the presence of the surrounding background motion which was either in the same or opposite direction. Surprisingly, we found no relative motion effect: if the background motion, irrespective of its direction, affected the target, then it delayed the RTs and decreased velocity ratings. The background motion was effective on RTs to motion onset only when the target was relatively small and immediately surrounded by a moving background. Increases in RTs were mostly explained by an apparent slowdown of the target stimulus velocity which was caused by the interference from the moving background. The background motion also affected velocity ratings by decreasing them without systematic effect of the background motion direction.

1. Introduction

All textbooks like to stress the relational character of visual perception. Perceived attributes of a patch in visual field often depend on the physical attributes surrounding this area. As an analogy to brightness contrast – a gray target patch looks darker against a white surround than it does against a black surround – it was discovered that motion perception of an object also depends on the motion of the surrounding elements (Holmgren, 1973). Since motion can only be defined in a certain frame of reference, there are also different ways of describing visual motion. The first frame of reference is the observer, or some parts of her or him (e.g. retina) which is often called absolute visual motion (Wallach, O'Leary, & McMahon, 1982). There are, however, many instances where motion is clearly seen relative to other external objects (Gogel & McNulty, 1983; Wallach et al., 1982), suggesting that perceived motion is defined not in an egocentric but in an external frame of reference. Since the discovery of induced motion by Karl Duncker in 1929 (cf. Becklen & Wallach, 1985; Holmgren, 1973; Nakayama & Tyler, 1978; Tynan & Sekuler, 1975), many other examples of relative motion, such as motion contrast (e.g. Murakami & Shimojo, 1996) or heterokinesis (Nawrot & Sekuler, 1990), have been described. The external frame of reference can make a stationary object be perceived moving in the direction opposite to the direction of nearby objects or, dependent on stimulus configuration, moving in the same direction with the surround, a phenomenon know as motion capture or assimilation (Chang & Julesz, 1984; Ido, Ohtani, & Ejima, 2000; Murakami, 1998) or homokinesis (Nawrot & Sekuler, 1990).

It is generally believed that the center–surround opposition in the receptive fields of the movement sensitive neurons was created to facilitate perception of motion in the external frame of coordinates (Bradley & Andersen, 1998; Paffen, te Pas, Kanai, van der Smagt, & Verstraten, 2004; Treue, Hol, & Rauber, 2000). Many psychophysical results are interpretable in terms of the center–surround opposition. For example, Tynan and Sekuler (1975) observed that with the increasing speeds of the surround, the perceived speed of the center first decreases and then returns to baseline. The apparent center speed reached a minimum at about the point where the surrounding area and the center were moving at the same speed. Many other perceptual tasks have also revealed the center–surround antagonism (Baker & Graf, 2008; Holmgren, 1973; Murakami & Shimojo, 1996; Paffen et al., 2004; Tynan & Sekuler, 1975). Center–surround receptive field organization is believed to be responsible for the fact that increasing the size of a high-contrast moving pattern renders its direction of motion more difficult to perceive and reduces its effectiveness as an adaptation stimulus (Tadin, Lappin, Gilroy, & Blake, 2003). Murakami and Shimojo (1996) have called this directionally antagonistic unit that is inhibited by surrounding moving stimuli a "motion contrast detector". They have found that when the overall size of the stimulus is decreased, induced motion could change to motion capture and it is suggested that a population of detectors is distributed around a certain stimulus size at each eccentricity (Murakami &

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Shimojo, 1993). A stimulus of an optimal size results in one percept due to relative motion processing (induced motion). A smaller stimulus, where both the inducer and the target (induced stimulus) are within the center field, results in another percept due to non-selective pooling of motion information (motion capture).

Although any other object can be used as a reference for inferring motion, visual system clearly prefers those which are in close vicinity. The adjacency principle states that the contribution of relative cues of motion to the perception of motion increases as the separation of the objects decreases, either in the frontoparallel plane or in depth (Becklen & Wallach, 1985; Gogel & Tietz, 1976). The second parameter that effectively influences the magnitude of the contrast effect, is either the velocity of the inducing stimulus (in case of the stationary target) or the velocity of both areas (in case of target and surround); or to be more specific, the relative motion between the center stimulus (the target) and the surrounding stimulus (the background) in the latter case (Becklen & Wallach, 1985). When background velocity (or in case of an oscillating inducer – the oscillating frequency) increases, the contrast effect decreases. The third variable to consider is the direction of motion if the two areas (center and surround; object and background) are both moving. Tynan and Sekuler found that when the center and surround are moving in the same direction and the surround velocity increases, the perceived velocity of the center first decreases and then increases; when the center and surround are moving in opposite directions, the increase in surround velocity results in the increase of perceived velocity of the center (Tynan & Sekuler, 1975). This assimilation-type phenomenon has also been found by Chang and Julesz (1984) who reported that at a limited range in space, a target pattern was biased towards the direction of inducing stripes. Fourthly, the effect of stimulus size is important. Quite a few studies have reported that assimilation is confined to a relatively restricted region – less than 15′ in the work of Chang and Julesz (1984) and distances about three times larger (depending on stimulus velocity) in the work of Nawrot and Sekuler (1990). It has also been shown that increasing the stimulus size results in decreased perceived motion (e.g. Ryan & Zanker, 2001).

There is, however, another phenomenon that needs to be distinguished from the frame of reference. Like many other visual attributes, motion parameters of an object that are reliably identifiable in isolation can no longer be identified when the object is surrounded by other moving objects (e.g. Bex & Dakin, 2005). In the present study, the detection of target motion onset dependent on background motion is examined in the light of previous reports on motion contrast and motion capture phenomena. Surprisingly, there are no studies in which the observer's ability to detect motion onset was examined dependent on motion in surrounding areas. Due to excellent replicability, reaction time (RT) to motion onset is an ideal model for studying the influence of background motion on the perception of target motion. Numerous studies have shown that reaction times to the onset of motion can be described as a power function of velocity $RT = cV^n + RT_0$, where RT_0 is the asymptotic ("residual") value of RT at very high velocities, c is a constant of proportionality and the exponent n is typically less than one (Allik & Dzhafarov, 1984; Ball & Sekuler, 1980; Mashour, 1964; Tynan & Sekuler, 1982). Assuming that the variance of spatial positions (kinematic energy) passed by the moving object determines the moment when the observer notices motion, the exponent is very close to $-2/3$ (Allik & Dzhafarov, 1984; Dzhafarov, Sekuler, & Allik, 1993; Kreegipuu & Allik, 2007).

It is known, however, that RT data may deviate from other methods intended to measure the same perceptual phenomenon. For example, it is known that the visual latency decreases monotonically as the stimulus intensity increases. The estimate of the increase of the visual latency accompanied the decrease in low intensities is more pronounced in RT data than in any other estimation methods including the Hess and Pulfrich effects (Hazelhoff & Wiersma, 1925; Roufs, 1963; Williams & Lit, 1983). This and similar findings seem to suggest that different perceptual tasks may be based on different aspects of the internal representation (Allik & Kreegipuu, 1998; Murd, Kreegipuu, & Allik, 2009). Thus, we need to demonstrate that findings are not specific to one particular method alone and can be generalized to other estimation procedures as well. One suitable method for studying motion perception in the presence of motion in surrounding areas is magnitude estimation. Several studies have shown that magnitude estimation can be used for the construction of the subjective velocity scale (Algom & Cohen-Raz, 1984, 1987; Ekman & Dahlbäck, 1965; Mashour, 1964) suggesting that subjective velocity ratings could in principle reveal the effects of surrounding motion on the perceived target motion.

The main goal of this study is to establish how motion onset is detected and target velocity estimated in the presence of background motion.

2. Study 1: methods

2.1. Participants

Six voluntary observers (one male and five females, mean age 20.6 ± 1.9 years), one of them well-trained and five naïve concerning the purposes of this study, took part in all series of the experiment. They all reported to have normal vision.

2.2. Apparatus

Stimuli were generated with Cambridge *ViSaGe* visual stimulus generator (*Cambridge Research Systems Ltd.*) and presented on the monitor screen Mitsubishi Diamond Pro 2070SB 22 in. (active display area 20 in., 769 × 1024 pxl, frame rate 140 Hz) which from the viewing distance of 90 cm subtended 27.6° in width and 20.5° in height.

2.3. Stimuli

There were four principal stimulus configurations (schematically depicted in Fig. 1). The main display elements were target and background vertical sine gratings with minimal and maximal luminances of 0.13 cd/m^2 and 128.2 cd/m^2 respectively. The spatial frequency of the vertical grating was 0.65 c/° and the grating was presented at Michelson contrast of 99.8%. Around the central fixation point, a round area was separated by a gap either 0.03° (i.e., "no gap") or 1.2° (i.e., "wide gap"), forming a target area. The target area had a diameter of 8.26° (i.e., "large") or 1.2° (i.e., "small"). The whole screen area outside the gap served as a background. Each trial started with a background and target appearing on the screen and after a random interval of 800–1200 ms, the background started to move (if the background velocity was not 0°/s) horizontally either left or right. After a delay of 0 (simultaneous onset), 500 or 1000 ms, the target area started moving horizontally rightwards. Background velocities were V_B = 0, 0.4, 0.8, 1.6 or 3.0°/s. Target velocities were V_T = 0.4, 0.6, 0.8, 1.0 or 1.6°/s. Between trials, a neutral (gray) uniform display (with the luminance 65.4 cd/m^2) was shown for 1000 ms.

For measuring the RT to target motion onset without any background (i.e. the baseline RT), we used the same stimulus parameters, with only one change – instead of a vertical grating, the surround was a gray uniform display (with the luminance 65.4 cd/m^2).

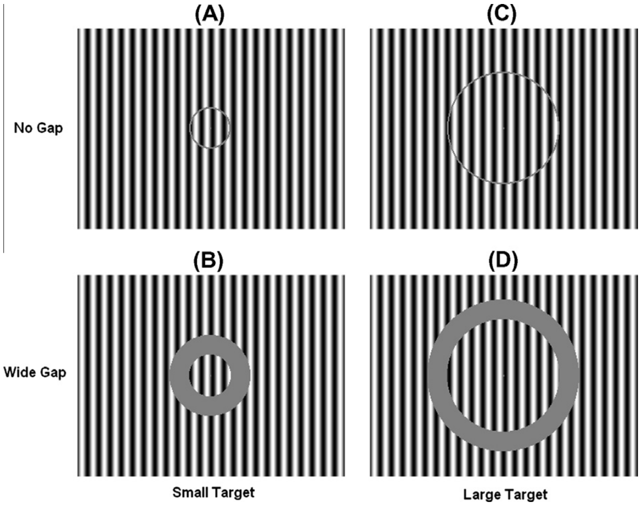

Fig. 1. Schematical view of the four principal stimulus configurations: (A) small target area and no gap, (B) small target and wide gap, (C) large target and no gap, and (D) large target and wide gap.

2.4. Procedure

The subjects sat 90 cm from the monitor screen in a semi-darkened room. The instruction was to keep the eyes on the fixation point and react to the motion onset of the target area by pressing a corresponding button on the response box. The observer's response ended a trial. One experimental session consisted of 4 × 150 trials. There were four different experimental sessions for all participants: (A) small target area and no gap, (B) small target and wide gap, (C) large target and no gap, and (D) large target and wide gap.

In addition there were two baseline RT sessions (for large target area and small target area), both consisted of 2 × 150 trials.

3. Study 1: results and discussion

In the RT analyses, very fast (RT < 100 ms) and slow (RT > 1000 ms) reactions were excluded and the data amount diminished by 6.9%.

We started the analysis from the time interval (SOA) between background and target motion. As expected, when the background and the target grating started to move simultaneously (SOA = 0), it took on average the longest time to notice the motion onset. Fig. 2 shows the RT to motion onset as a function of the target velocity separately for three SOA values across all other conditions. Contrary to the principle of relative motion, the beginning of the background movement in the opposite direction disrupted motion detection even more than movement of the background in the same direction. It is interesting that on average, the RTs were systematically shorter with SOA = 1000 ms than with SOA = 500 ms. It is easier to notice motion onset with the moving background that has lasted for a longer period of time. It may indicate that the visual integration time for motion may be in accordance with the previous studies (Allik & Dzhafarov, 1984; Sekuler, Sekuler, & Sekuler, 1990) in the range from 500 to 1000 ms.

We left out the simultaneous onset trials (SOA = 0) from further analyses to be certain that the background motion was seen long enough. When the two areas start to move at the same time, there is no background to begin with, and it seems to be a masking effect rather than a question of relative motion, especially when the target and the background are moving in the same direction. The difference between the effects of SOA = 500 and SOA = 1000 was small ($\eta' = 0.005$ i.e. a half percent of the total variance; $F(1, 1340) = 11.09$, $p = .133$), which allows us to average across the SOA > 0 factor in further analyses.

Baseline mean RTs for small target area were 321.1 (SD = 94.83), 290.22 (SD = 75.45), 285.54 (SD = 99.56), 267.71 (SD = 78.66) and 257.93 (SD = 81.28) for the respective target velocities $V_T = 0.4$, 0.6, 0.8, 1.0 and 1.6°/s. Baseline mean RTs for the large target were 309.66 (SD = 88.09), 277.92 (SD = 74.86), 261.84 (SD = 53.04), 263.07 (SD = 78.94) and 249.56 (SD = 65.21) for the respective target velocities $V_T = 0.4$, 0.6, 0.8, 1.0 or 1.6°/s.

Secondly, we looked at each stimulus configuration (Fig. 1A–D) separately. The results of a two-way ANOVA showed that the background and target velocity interaction emerged only in case of a small target and no gap [$F(32, 2066) = 1.80$, $p = .004$] (Fig. 3A). While target velocity had a main effect in every condition and needs no further explanation, since the dependence of velocity on the detection of motion onset is a well-documented finding (e.g. Allik & Dzhafarov, 1984; Mashour, 1964; Tynan & Sekuler, 1982), background velocity had a significant effect only when there was no visible gap between the target and the background and the target was small [$F(8, 2066) = 23.03$, $p = .00001$]. There was a small significant background effect in case of a large target with no background [$F(8, 2129) = 2.11$, $p = .03$], but Bonferroni post hoc test indicated none of the interconditional differences as being significant. Taking this under consideration, we separated the small target-no gap condition with a mean RT 376.46 ms (SD = 149.1) (Fig. 1A) and averaged across all other three (Fig. 1B–D), that showed similar tendencies as well as a lot shorter mean RTs (313.16 (SD = 107.95), 328.02 (SD = 102.83) and 328.04

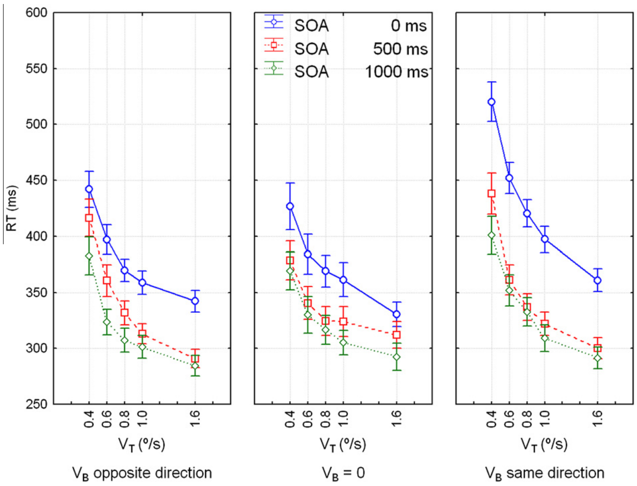

Fig. 2. The mean RT as a function of the target velocity (V_T) for three different SOA values shown separately for different background (V_B) conditions.

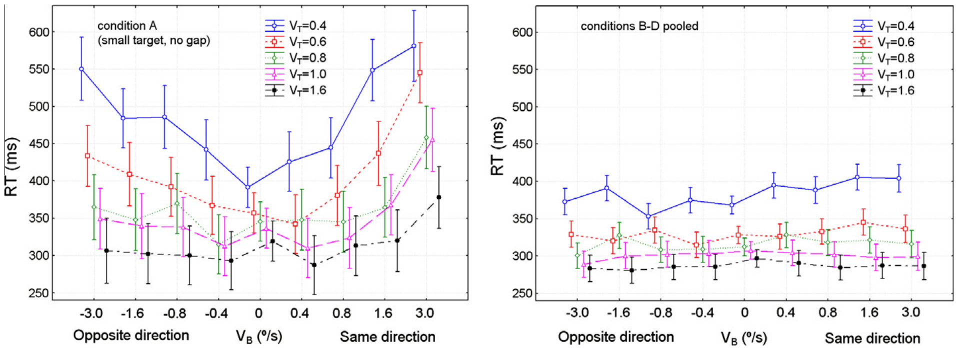

Fig. 3. The mean RT as a function of the background velocity (V_B) for five different target velocities (V_T). Left panel: small target and no gap condition (Fig. 1A). Right panel: all other conditions (Fig. 1B–D) pooled together.

(SD = 106.9) ms respectively), in further analyses. Nevertheless, there was a small tendency that the RTs to a larger target stimulus were faster than to a small one and the gap between the target and the background slightly shortened the time needed to detect motion onset.

The mean RTs to the target stimulus onset are plotted in Fig. 3 as a function of background direction and velocity V_B. The left panel shows the mean RTs for small target area and no gap, the right panel shows the mean RTs for all other conditions pooled together.

If background motion had no effect on the detection of motion onset, it would be expected that all five response curves corresponding to one specific target velocity V_T will remain approximately parallel to the horizontal axis. Only one condition – small target and no gap (Figs. 1A and Fig. 3: left panel) – appears to violate this property. In this condition and especially on the slowest target velocity $V_T = 0.4°/s$, the RTs form a V-shape, where the mean RT increases with the increase of the absolute velocity of the background V_B.

To summarize, the adjacency principle seems to be relevant only for small stimulus size, when the stimulus is in close vicinity with the surrounding area. At the same time, although the interference from the background was the strongest with the relatively small target area (1.2°), the size by itself is not the only condition leading to the interference of target and background movements. As can be seen in Fig. 3, it took slightly more time to detect motion onset when both the target and the background moved in the same direction ($V_B > 0$).

The most surprising result in Fig. 3 is the absence of any significant facilitation effects on the RTs. When the relative velocity between the target and the background increases (they are moving in the opposite directions), the RTs generally do not decrease, but time required for the detection of motion onset generally becomes longer. One obvious way to comprehend this increase in the RTs, is to look at the change in the apparent velocity of the target area under the influence of the background motion. It is possible that the target stimulus apparently slows down, especially when the target area is small and surrounded by an immediate background which moves either in the same or opposite direction. In order to test this possibility, we first found the best fitting values for RT_0 and c in the equation $RT = cV_T^{-2/3} + RT_0$ applied for a small target and no gap configuration with the stationary background ($V_B = 0$). After obtaining these values, we searched for the optimal change in the apparent velocity which explains the RTs for seven different background velocities, excluding $V_B = 3.0°/s$. The trials with $V_B = 3.0°/s$ behaved differently and the apparent slowdown would have been a lot bigger compared to other conditions. This is, of course, rather logical, because background moving very fast in the same direction creates a more crowded condition in the visual field. We aimed at applying one general rule to explain the RTs, which meant leaving out the overcrowded condition. The equation was $RT = 63.87(V_T + \Delta V)^{-2/3} + 271.6$ where ΔV is the apparent velocity increment or decrement. The best fitting values were $\Delta V = -0.292$, -0.235, -0.235, -0.127, -0.069, -0.163 and $-0.292°/s$ for the respective background velocities $V_B = -3.0$, -1.6, -0.8, -0.4, 0.4, 0.8 and 1.6°/s indicating only decrease in the apparent velocity.

Fig. 4 demonstrates the relationship between the RTs and the calculated apparent velocity. The correlation between observed and predicted values was $r = .98$, suggesting that besides the proposed main factor there are not very many other or are minor systematic or unsystematic effects.

4. Study 2: method

4.1. Participants

The same six observers as in Study 1 took part in all series of Study 2. One of the observers vision was corrected to normal, others had normal vision.

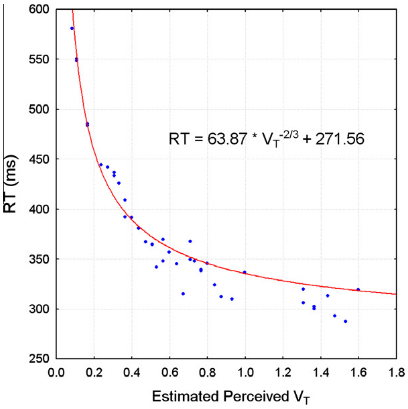

Fig. 4. The mean RT as a function of the perceived target velocity V_T for small area and no gap, assuming that the target velocity apparently slows down.

4.2. Apparatus

The same apparatus was used as in Study 1.

4.3. Stimuli

The same stimulus display elements and target and background velocities were used as in Study 1, with the following specifications: the target diameter was always 1.2° (i.e., "small"); SOA was 1000 ms; in addition we used the "no background" condition. There were three principal stimulus configurations: (A) target and background in close vicinity (Fig. 1A); (B) target and background separated by a gap (Fig. 1B); configuration E) target and a neutral (gray) background (with the luminance 65.4 cd/m^2), i.e., "no background". For configurations A and B each trial started with background and target appearing on the screen and after a random interval of 800–1200 ms the background started to move (if the background velocity was not 0°/s) horizontally either left or right. After a delay of 1000 ms target area started moving horizontally rightwards (duration explained in the following paragraph). For configuration E ("no background" condition), each trial started with the target appearing on the screen. Target motion onset was set to mimic configurations A and B, so that it was (800–1200) + 1000 ms after appearing on the screen.

Perceived velocity is not only a function of physical velocity, but also a function of movement duration and distance passed by (Algom & Cohen-Raz, 1984). Presenting the target stimulus for a fixed duration implies that targets traveling with different velocity can cover different distances. As we saw in the first experiment, the RTs can be described as a power function of velocity. This means that the targets with high velocity were perceived for a shorter period of time before they were noticed, compared to low velocity targets. In order to disentangle movement distance and duration from velocity, we used two different experimental sessions with different target motion duration times. In one of them the target motion duration was held constant ("fixed duration" condition): $t_T = 300$ ms. The duration of the fixed time interval was set approximately after the mean RT in Study 1. In the second session, the target motion duration was varied ("variable duration" condition), so that the duration was dependent on target velocity: $t_T = V_T^{-2/3}$. Each target velocity had its own duration: 1842.0, 1405.7, 1160.4, 1000 and 731 ms (for 0.2, 0.4, 0.6, 0.8, 1.0, and 1.6°/s respectively).

After target motion offset the display (with the moving background, if $V_B \neq 0°/s$) remained on the screen for 1500 ms. Between trials a neutral (gray) uniform display (with the luminance 65.4 cd/m^2) was shown for 300 ms.

4.4. Procedure

The subjects sat 90 cm from the monitor screen in a semi-darkened room. The instruction was to keep the eyes on the fixation point and estimate as quickly as possible how fast the target is moving in each trial by choosing a number between 1 and 10 on the keyboard (1 being the slowest, 10 the fastest subjective rating). One experimental session consisted of 8 × 150 trials, where stimulus configurations A, B and E were presented randomly. All participants completed both experimental sessions: with fixed target duration and with variable target duration.

5. Study 2: results and discussion

Fig. 5 demonstrates the mean velocity ratings for five target stimulus velocities ($V_T = 0.2$, 0.4, 0.6, 0.8, 1.0, and 1.6°/s) and the presence (filled symbols) or absence (empty symbols) of the gap

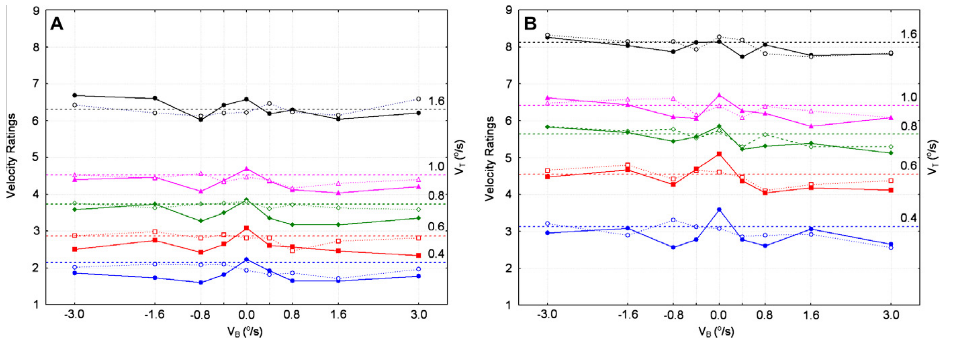

Fig. 5. The mean velocity ratings as a function of the background velocity (V_B) for five different target velocities (V_T = 0.4, 0.6, 0.8, 1.0, and 1.6°/s). Horizontal parallel broken lines represent the mean ratings in the absence of the background. Filled symbols and continous lines correspond to no gap; empty symbols and dotted lines correspond to the wide gap condition. Left panel (A): fixed target duration t_T = 300 ms. Right panel (B): variable target duration (see text for values).

between the target and background area dependent on the background velocity V_B. The horizontal parallel lines near each target velocity data represent the mean velocity ratings in the absence of the background (configuration E). Fig. 5A corresponds to a fixed target duration and Fig. 5B to variable target duration, which approximately imitates time the observer sees motion before he or she responds to its presence.

Since all target velocities are clearly horizontally separated, it means that on average target velocities are distinctive from each other. The target velocity explains more than half of the rating variance in fixed (partial eta-squared $\eta' = 0.55$ or about 55% of the total variance [$F(4, 4710) = 1414.0$, $p < .0001$]) and varied target duration ($\eta' = 0.57$ [$F(4, 4760) = 1562.3$, $p < .0001$]). It is surprising that the presence or absence of the background had a relatively small impact. Only at the lowest velocities the presence of the moving background slightly decreased the perceived velocity. In general, the background motion velocity affected estimated velocity but, contrary to the relative motion principle, irrespective of motion direction. Across all conditions the dependence from the background velocity had a W-shape. The results of the three-way ANOVA with test velocity, background velocity and gap as factors showed that the background velocity significantly affected ratings in both fixed [$F(8, 4710) = 5.18$, $p < .0001$] and variable [$F(8, 4760) = 10.51$, $p < .0001$] target duration. At variance from the proximity principle, the gap between the target and the background area had no effect on the perceived velocity when the target duration was variable [$F(1, 4760) = 1.050$, $p = .306$], but had a small effect – the gap between the target and background increased apparent velocity – when the target duration was fixed [$F(1, 4710) = 10.12$, $p = .002$].

As it is documented in previous studies (Algom & Cohen-Raz, 1984), the increase of the stimulus duration also increases the perceived velocity. It is clearly observed that all rating curves of variable stimulus duration (Fig. 5B) are shifted upward compared to the rating curves of the fixed stimulus duration (Fig. 5A).

6. General discussion

There is no doubt that the perceived trajectory of a moving dot is often determined on the basis of its relative position to other moving elements and common motion shared by all elements (Johannson, 1978). Even simpler tasks like the estimation of the perceived velocity are often reported to exhibit elements of the relative motion principle (Baker & Graf, 2010; Nakayama & Loomis, 1974; Nguyen-Tri & Faubert, 2007; Tynan & Sekuler, 1975). For example, Tynan and Sekuler (1975) suggested an inhibitory interaction where the apparent speed reduction depends upon the center–surround speed differential. Our study supports the claim that this dependence is not strong enough to support the relative motion principle. The stimulus speeds were different (while the target velocities in the present study ranged from 0.4 to 1.6°/s, the target velocity Tynan and Sekuler used was 2.8°/s with the background velocities of 1.4–5.6°/s) which may be one reason of discrepancy. Since no data support the simplest test-minus-surround velocity formula, it is necessary to introduce more sophisticated dependencies from the center–surround speed differential (cf. Baker & Graf, 2010). Another research tradition, however, stresses the antagonistic nature of the center–surround interaction in motion perception, which typically occurs in the elevation of the contrast thresholds for a moving target surrounded by a moving background (Tadin et al., 2003) or in the decrease of perceived speed in similar conditions (van der Smagt, Verstraten, & Paffen, 2010). It seems that nobody has yet figured out on what conditions movement of the surrounding increases the perceived speed of the target moving in the opposite direction, and when the perceived speed of the target apparently slows down.

One obvious candidate is the task that the observer is asked to solve in the experiment. It is well documented that certain perceptual effects from identical stimulus configurations can be present with one task and absent with another (Allik & Kreegipuu, 1998; Murd et al., 2009). So far, the center–surround interaction in motion perception has been studied either with measuring minimal contrast required for the direction discrimination (Tadin et al., 2003) or by matching the speed of a target stimulus to a reference one (Baker & Graf, 2010; van der Smagt et al., 2010). In this study, however, two another basic tasks – the detection of motion onset and magnitude estimation – were studied and with both of them, we failed to find the relative motion effect. In most cases and compared to the baseline RT results, the ability to detect the target motion onset deteriorated with the background motion. Even background movement opposite to the test movement direction, that is supposed to stress the motion contrast, more likely caused delays rather than facilitation in the detection of motion onset. Principally the same situation was present with the magnitude ratings of velocity: if the background motion affected apparent velocity then it likely decreased it. Thus, although the relative motion effect can explain many perceptual phenomena, including induced motion and motion contrast, this principle seems to be inapplicable in the simple motion onset detection and magnitude estimation tasks.

The observed deterioration of the motion onset detection and magnitude estimation certainly indicates that the background is distracting or even has a certain resemblance with visual crowding. Although it was first noticed that recognition of letters or symbols gets worse in the presence of other letters or symbols in close vicinity, the observed phenomenon was later extended to other stimulus modalities as well, including motion (Bex & Dakin, 2005). These authors reported that sensitivity to the direction of motion of a central target – highly visible in isolation – was strongly impaired by four drifting flanking elements. Their results seem to suggest that spatial interference is a consequence of the integration of meaningful image structure within large receptive fields (Bex & Dakin, 2005). What indicates the resemblance of the present findings to other crowding phenomena is the specific spatial configuration under which the interference between the target and the background motion occurred. The deterioration of the motion onset detection time was by far the most significant with a small target area (with a diameter of 1.2°) and no spatial gap between the target and the background area. Several previous studies (e.g. Chang & Julesz, 1984; Murakami & Shimojo, 1993; Nawrot & Sekuler, 1990) have also shown that the size of the target plays an important role in the amount of the effect the background has on the moving target. Whatever the nature of interference between the target and the background motion is, it is unlikely that it is the ''compulsory averaging'' of signals coming from different areas (e.g. Parkes, Lund, Angelucci, Solomon, & Morgan, 2001). This idea is further supported by the present finding that the background effect was almost reminiscent in the condition of wide gap separating a small test area from an area-wise far larger background, indicating the summative kinematic energy not to be a determining factor in the production of the interference.

As the interference between neighboring visual field areas is typically characterized as a disruptive process through which object representations are suppressed or lost altogether, it is possible to assume that interference like crowding also changes the appearance of objects (Greenwood, Bex, & Dakin, 2010). In this study, however, we proposed that the background motion alters the perceived velocity of the target by slightly slowing it down, as was recently also shown by van der Smagt et al. (2010). There is nothing unusual about it, since perceived speed may depend on many stimulus attributes, including contrast (Thompson, 1982) and stimulus size (Brown, 1931). It is also one of the best established and replicable regularities that the time needed to detect motion onset is a monotonically decreasing function of the test stimulus velocity (Allik & Dzhafarov, 1984; Ball & Sekuler, 1980; Mashour, 1964; Tynan & Sekuler, 1982). Thus, an expected consequence of the apparent slowdown is the corresponding increase in time that is needed to detect the beginning of motion. This simple model containing only one free parameter – the apparent decrease in velocity ΔV – provided a reasonably good fit to the RT data, implicating that even a simple motion detection time depends on apparent rather than physical velocity of the target. This explanation is in a harmony with Burr, Fiorentini, and Morrone (1998) who also showed that the effects of contrast on the RTs depend on the perceived, rather than on the physical speed of the stimuli.

One unresolved question is how exactly the results of our RT experiment are related to the velocity magnitude estimations. Generally, the results of these two studies are in a good agreement, showing no signs of the relative motion principle. If the background motion affected the detection or estimation of the target motion, then it was in the direction of deterioration by increasing the detection time or lowering magnitude ratings. It is most logical and parsimonious to explain the increase of the RTs by apparent decrease of the perceived velocity. However, it is difficult to compare the apparent decreases of velocity in these two different tasks directly. As it has been demonstrated in several previous studies (Murd et al., 2009; Sternberg & Knoll, 1973), even very similar perceptual tasks may be based on two different perceptual representations or on two different decision criteria applied to the same representation. Obviously more sophisticated experimental design is needed to establish the exact correspondence between the RT and magnitude estimation tasks.

Acknowledgments

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III

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Discrimination of numerical proportions defined by colour or orientation.
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Discrimination of numerical proportions defined by colour or orientation

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ABSTRACT

The observers' task was to discriminate numerical proportion of two spatially overlapping sets of elements distinguished either by colour or by orientation. All choice probabilities were described by a simple and noiseless Bernoulli response model (based on hypergeometric distribution) with a single free parameter K denoting the supposed number of inspected elements on which the answers were supposedly based. According to the Bernoulli model, these K elements are chosen randomly from the display, the size of K being limited by perceptual capacity, and their properties registered accurately. The number of accounted elements increased disproportionately with the growth of the total number of displayed elements N = 9, 13, 33, or 65, with colour being a stronger

feature for discrimination than orientation. It is concluded that the Bernoulli model leading to noiseless internal representation of elements' number, with stochastic and capacity-limited sampling of elements, is a viable alternative to the habitual Thurstonian-type modeling which relies on stochastic internal representations.

Discrimination of numerical proportions defined by colour or orientation

It does not require elaborate mental capacities to discriminate between two quantities of objects. Numerous carefully performed experiments have shown that many species such as bees (Gross et al., 2009), fishes (Krusche, Uller, & Dicke, 2010), salamanders (Krusche, Uller, & Dicke, 2011), pigeons (Emmerton & Renner, 2006), dogs (Ward & Smuts, 2007), chimpanzees (Beran, Evans, & Harris, 2008), to say nothing about human infants (Brannon & Van de Walle, 2001) or people whose language lacks words for numbers beyond five (Pica, Lemer, Izard, & Dehaene, 2004) are capable of discriminating relatively large quantities with a certain precision even when other cues are not available and there is no opportunity for one-by-one counting. However, it was proposed that an innate, unlearned approximate number sense may serve as an antecedent of higher numerical abilities (Halberda, Mazzocco, & Feigenson, 2008).

If the observer's task is to discriminate the relative proportion of two distinct sets of randomly distributed elements, two principal ways by which these two sets can be separated exist. First, the sets occupying two separate areas can be distinguished by their spatial position, (Allik & Tuulmets, 1991), or, second, they can be spatially intermixed but distinguished by a certain visual attribute, such as colour, orientation (Honig & Matheson, 1995; Honig & Stewart, 1993; Tokita & Ishiguchi, 2009) or motion in two different directions (Raidvee, Averin, Kreegipuu, & Allik, 2011). As it turned out, the ability to discriminate numerical proportion depends heavily on the visual attributes by which the two sets can be discriminated. Rather surprisingly, human observers are extremely inaccurate in discriminating proportion between two spatially overlapping sets of randomly distributed elements moving in two opposite directions (Raidvee, Averin et al., 2011). In a wide range of set sizes the decisions about motion direction are made as if only a very limited number of elements (in some cases less than 0.5%) are taken into account even if the motion direction of each element in isolation can be determined with near absolute certainty. In a similar discrimination task, the observers were able to discriminate the relative number of red and green dots as if they had taken into account 69 elements from a total of 100 (Tokita & Ishiguchi, 2009). However, the same observers ability to discriminate between the relative number of parallel and converging lines was much poorer, with precisions equal to discrimination decisions made on the basis of no more than two elements out of one hundred available (Tokita & Ishigichi, 2009; see also Raidvee, Averin et al., 2011 for interpretation).

Most explanations of the numerical discrimination assume that compared quantities have an imprecise internal representation: the ability to discriminate between two quantities improves as the overlap between these two internal representations diminishes. It is believed that like many other visual attributes the discrimination of two sets of objects worsens as their numerical size increases (Emmerton & Renner, 2006; Ross, 2003; Tan & Grace, 2010). Although this worsening is sometimes compatible with the Weber's law, studies have shown that the just noticeable difference in numerosity varies approximately as the 0.75th power of the total number of elements to be discriminated (Burgess & Barlow, 1983). It was shown that the occupancy index – the area the elements appear to occupy in the stimulus plane and which likely serves as a basis for numerosity discriminations – is also increasing as about the 0.75th power of the total number of elements (Allik & Tuulmets, 1991).

However, the analysis of numerical discrimination in terms of internal fuzzy representations is not the only and perhaps not even the best way of describing the discrimination of numerical proportions. Many numerosity discrimination tasks can be modelled by an urn problem which was devised by Jacob Bernoulli in his posthumous *Ars conjectandi* (1968/1713). 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 registered. Balls or pebbles once extracted can or cannot be returned to the urn, which leads to two distinct probability distributions for estimation of the correct number of balls of a given colour in the urn: the binomial and hypergeometric distributions, respectively. In all tasks where the observer is instructed to discriminate between two types of discrete objects belonging to the category A or B (the numbers of the respective object types denoted as N_A and N_B), one can apply the Bernoulli trial model in order to identify the number of elements (K) selected randomly from the total number of elements presented ($N = N_A + N_B$), that would reproduce the empirically obtained psychometric function of discrimination between numerical proportions (Raidvee, Põlder, & Allik, 2012).

The observer's decisions, as already said, are supposed to be based on these K elements selected randomly from all available elements N. A rational decision rule can be formulated very simply: if the number of the first category elements $K_A \subset N_A$ in the selection exceeds the size of the second subset $K_B \subset N_B$ ($K_A > K_B$, provided that $K_A + K_B = K$) then the answer "A" is chosen; otherwise the answer "B" is chosen. If the number of the accounted elements happens to be equal ($K_A = K_B$), the choice between two response categories is random with equal probabilities (assuming there is no response bias). Thus, the ratio of the accounted elements K to the actually presented number of elements N determines not only the slope of the psychometric discrimination function but also the efficiency relative to the ideal observer that, unlike the factual observer, is supposed to take into account all available information.

In this study we intend to establish a relationship between the number of elements K which are supposedly taken into account in numerical decisions, and the total number of elements N available on the display. As an ideal observer is able to base its decisions upon absolutely every piece of information present in the stimulus, we can use it as a benchmark for the performance of a real observer in a similar situation. By analyzing the difference between real and ideal observers, we hope to learn about the way information is coded in relation to an increase in the total number of elements N. The standard theory claims that the precision of numerical discrimination decreases as the numerical size increases. It is unknown, however, whether the same law of discrimination decline is equally applicable to all visual attributes. Previous experiments have shown that the discrimination of numerical proportions is relatively poor when two sets of objects are defined either by orientation (Tokita & Ishiguchi, 2009) or motion (Raidvee, Averin et al., 2011) and considerably more efficient when the difference between these two sets is marked by colour (Tokita & Ishiguchi, 2009). For this reason we choose one easy (colour) and one difficult (orientation) attribute to discriminate between two sets of objects.

METHOD

Four 20-year-old female observers with normal or corrected to normal vision were asked to decide which of the two distinctive sets of objects were more numerous. In two separate series these two sets of objects were distinguished either by colour or by orientation. A schematic view of the two types of stimulus configurations is depicted in Figure 1. In the first series a randomly distributed collection of red and green circles was presented. The red and green circles had equal luminances of about 23.5 cd/m². To diminish the impact of total red *vs* green area on the responses, size of the circles was randomly varied in the range of 11 to 22 minutes of arc. In the second series of the experiments a collection of short black line segments of luminance 0.3 cd/m² and tilt of 20° either to the left or to the right from the vertical direction was presented. The width and length of a line subtended 2' and 19' respectively (and height of its vertical projection 16'). Both types of stimuli were presented within an elliptical gray background with luminance of 54 cd/m² and with lengths of horizontal and vertical axes 8.86° and 8.70° respectively. This elliptical background was in the center of a rectangular area of luminance 64 cd/m² filling the rest of the screen. In order to avoid overlaps between elements, each element was positioned within an invisible inhibitory area which prevented other elements to be closer than 22'. Each stimulus element had a high contrast to guarantee its 100% identification would it have been presented in isolation. The total number of objects N presented on the display was kept constant through each experimental session and was equal either to N = 9, 13, 33, or 65 elements. During experimental sessions, the relative proportion of the type A and type B elements was varied in random order. The total number of elements was constant throughout a session. For the total number of elements $N = 9$ and $N = 13$, the relative proportions of A (red or tilted to the left) and B (green or tilted to the right) element categories were varied with a change of one element to the numerosity of both sets: from 1:8 to 8:1 and from 1:12 to 12:1, respectively. For the total number of elements $N = 33$, proportions 13:20, 14:19, 15:18, 16:17, and the reverse, were used; and for $N = 65$, proportions 23:42, 26:39, 32:33, and the reverse, were used. The stimuli were presented at a viewing distance of 170cm for 200 milliseconds, with 3 seconds for responding. In case of non-response, the trial was repeated at a later, randomly selected position of the experimental session.

All stimuli were generated on the screen of a Mitsubishi Diamond Pro 2070SB 22" colour monitor (frame rate was 140 Hz with the resolution 1024×769 pixels) with the help of a *ViSaGe* (Cambridge Research Systems Ltd.) stimulus generator. Every stimulus condition was replicated 100 times. Choice probability of the red circles was plotted as a function of the proportion of red elements N_A in the total number of elements on the display $N = N_A + N_B$ where N_B refers to the number of green elements. Similarly, in the orientation experiment, probability of the choice of the leftward tilted elements was measured as a function of the proportion of leftward tilted elements N_A in the total number of elements on the display N.

RESULTS

The choice probabilities as a function of the proportion between two types of elements $N_A/(N_A+N_B)$ are shown in Figure 2. All empirically obtained psychometric functions were approximated by a cumulative normal distribution and the best fitting values of the mean (μ) and standard deviation (σ) were determined (see Table 1). The goodness of fit was exemplary with the percentage of explained variance ranging from 92.54% to 99.98%. The median explained variance was 99.71% and 99.05% for colour and orientation based discrimination, respectively. Thus, on average, the approximation error was less than 1%. As expected, all means of the best fitting functions were close to 0.5. Only in a few cases was the bias towards a response category larger than 4%. The slope of the approximating function depended on the visual attribute that distinguished the two subsets. As expected, it was easier to discriminate proportions when elements differed by colour rather than orientation.

In our previous study we applied the aforementioned Bernoullian urn model approach to indicate that in a considerable number of trials of a proportion discrimination task, observers tagged the same element repeatedly which can only be done serially at two separate time moments (Raidvee, Põlder et al., 2012). More specifically, we used a mixed model approach to show that while the hypergeometric sampling scheme was the dominant one, inclusion of the binomial component improved the overall fit, leading to the conclusion that most likely the human observer does not stick to just one sampling scheme.

Why then even consider interpreting empirical data in light of pure binomial or pure hypergeometric response schemes?

Given that the Bernoulli's urn model describes sufficiently accurately the process of perception of numerical differences, the mixed model approach supposedly reflects the actual amount of sampling carried out in discrimination process, whereas some of the sampling could be redundant. Redundancy, of course, happens when an element is sampled repeatedly. The pure hypergeometric response model, on the other hand, involves only effective sampling, without taking into account any amount of redundancy that might have taken place, and allows, thus, to estimate the true efficiency of a human observer in different tasks.

Application of the pure binomial model to the current experimental task would gravely overestimate the redundant sampling and thus the number of elements sampled altogether. In our previous study we established a functional relationship between the normal approximation and the binomial response model (Raidvee, Averin et al., 2011) which supposes that all inspected elements are returned to the urn and, consequently, can potentially be picked up for another inspection. This functional relationship implies, for instance, that the psychometric function with a very steep slope $\sigma = 0.06$ (the observer S2, $N = 9$, colour) corresponds to a sequence of Bernoulli trials with length $K = 68$. It is extremely unrealistic that a set as small as nine elements are inspected one by one nearly seventy times without any knowledge of which elements have already been inspected. This is a very strong indication that predominantly, the observer is able to keep the already counted elements separate from the to be counted ones. Therefore, in this case, given that we choose to rely on one out of the two "pure" response schemes – either binomial or hypergeometric – we need to apply the hypergeometric response model which implies that the already counted elements are tagged and can not be inspected repeatedly.

Unfortunately the derivation of the analytic relationship between the slope of the normal approximation σ and the parameter K of the hypergeometric response model is not a trivial algebraic exercise, as the relationship also depends on the total number of elements on the display (N). To overcome this obstacle we searched for the best normal approximation of all combinations of N and K [only odd values are relevant (Raidvee, Põlder et al., 2012)] of the hypergeometric response model. The relationship between the slope of the cumulative normal distribution and K of the hypergeometric response model for given value of N can be described almost perfectly by the Cauchy distribution. In the lower panel of Table 1, values of K derived from the slopes of the cumulative normal function (upper panel) are given. The value of K demonstrates the number of elements needed to be randomly selected out of N elements and inspected to produce the psychometric function with a given slope σ.

Although the parameter K of the hypergeometric response model can take on only discrete values, fractions in Table 1 have a simple interepretation. For example, the value of $K = 5.75$ could mean that in 62.5% of all trials the observer effectively inspected 5 elements and in 37.5% of trials she answered on the basis of 7 elements (please note that, for any positive natural value of n, the inspection of an even number of elements $2n$ is, in terms of the response probabilities, equivalent to the inspection of $2n$-1 elements).

On average, in the discrimination task where distinction between two sets was indicated by colour, the observes relied on approximately two times more elements than in the task where elements were distinguished by their orientation. Thus, as a feature separating the elements, colour was about two times more effective than orientation.

The number of effectively sampled elements K was obviously not constant. When 9 elements were displayed the observers gave their answers based on average on 7 elements when they were distinguished by colour, and 4 elements when the discrimination attribute was orientation. In the displays containing 65 elements, about 11 elements were inspected in the orientation discrimination task and about 25 elements in the colour discrimination task. However, the growth of the number of inspected elements K was slower than the increase of elements N which resulted with the drop of efficiency. The observers were able to take into account about 78% and 44% of coloured and oriented elements respectively when there were 9 elements on the display. These percentages dropped to about 39% and 17% respectively when 65 elements were presented for discrimination of numerical proportions. As far as it can be judged by only 4 data points, the relationship between K and N was close to linear (r = .99 and .98 for colour and orientation respectively). An increase of N by ten elements resulted with the increase of the number of inspected elements K by 3.2 or 1.2 for elements distinguished by colour or orientation, respectively.

DISCUSSION

It was very rewarding that such a simple and noiseless model with a single free parameter, the number of inspected elements K on which basis the answers are supposed to be given, was able to predict the discrimination of numerical proportions with a great accuracy. This means that when two quantities are presented to an observer for discrimination their number, the most common way of conceptualizing this situation as transformation of these two quantities into two random variables ("images") taking on their values in some hypothetical internal ("perceptual") continuum is not the only way how to describe the situation (Dzhafarov, 2003a, 2003b). The Bernoulli trial model provides an alternative to the habitual Thurstonian-type modeling without invoking the concept of random images. In this alternative approach the observer has an exact internal representation of stimulus elements but is limited in capacity to represent all of them. Uncertain (stochastic) are not internal representations ("images") but selection of stimulus elements which would form an internal representation. The Bernoulli-type of modeling presumes that the selection of elements is completely random in the first approximation at least.

Although, at the level of psychometric function, the Thurstone-type and Bernoulli-type of modeling cannot be distinguished formally (Raidvee, Averin et al., 2011), the latter has obvious advantages when it concerns discrete quantities. What is particularly appealing in the Bernoulli-type of analysis is a very transparent relation to the Ideal Observer Analysis (IOA). An ideal observer is a theoretical device able to base its decisions upon absolutely every piece of information present in the stimulus being limited only by physical constraints placed upon the availability of information. The efficiency of a real observer is defined as the ratio of the amounts of information that is used by the real, compared to the ideal observer, to perform in similar situations (Rose, 1948). In the task to discriminate numerical proportions between two sets of elements, the ideal observer will take into account all elements available on the display. A real observer, however, is able to register and determine properties of a fraction of all elements which defines efficiency as a measuring device.

It is usually believed that the precision of discriminating numerical proportions decreases as the total number of elements increases. Indeed, the just noticeable difference in numerosity often increases with the total quantity (Allik & Tuulmets, 1991; Burgess & Barlow, 1983; Emmerton & Renner, 2006; Halberda & Feigenson, 2008). The above presented analysis showed that in terms of the amount of effectively used information, conclusions based on the Weber's fraction may be misleading. Irrespective of the distinctive attribute, colour or orientation, the number of counted elements increased disproportionately with the increase of the total amount of elements. Perhaps the most intriguing was our finding that the observers were able to pay attention to a larger number of elements while their number in the display increases. Interestingly, we were not able to see such an increase in the number of accounted elements in the task to discriminate proportion between two spatially overlapping sets of randomly distributed elements moving in two opposite directions (Raidvee, Averin et al., 2011). In a range of 12–800 elements the observers discriminated between two sets moving in the opposite directions as if they were able to register motion direction of about 4 ± 2 elements (Raidvee, Averin et al., 2011). Unlike motion, the capacity to take into account coloured and oriented elements enlarged with the growth of the total number and/or density of stimulus elements. 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 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 this 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 possibility of chunking.

Previous studies have also shown that colour is a stronger feature than orientation for segmenting the search elements (Anderson, Heinke, & Humphreys, 2010, 2011; Nothdurft, 1993; Zhuang & Papathomas, 2011). Thus, it was not big news that the observer can rely on a larger number of elements when the decisions about numeric proportion were based on colour rather than orientation. Under given stimulus conditions colour elements were accounted in numbers approximately two-fold of those of elements distinctive by their orientation. Nevertheless, all these differences were in quantity, not in the qualitatively different way of processing colour and orientation attributes. Perhaps the most profound difference in the processing colour and orientation cues was found in the tagging of the processed elements (Raidvee, Põlder et al., 2012). Perceptually 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 of tagging is simultaneously an indication that at least some of the mental operations are executed in a serial order, one after another. Using partly the same stimulus material it was shown that stimulus elements distinguished by orientation sometimes are counted two or more times while stimulus elements characterized by colour alteration are unlikely counted two or more times (Raidvee, Põlder et al., 2012). Although differences were rather subtle, they demonstrate a principally different mental architecture in the exploiting colour and orientation information.

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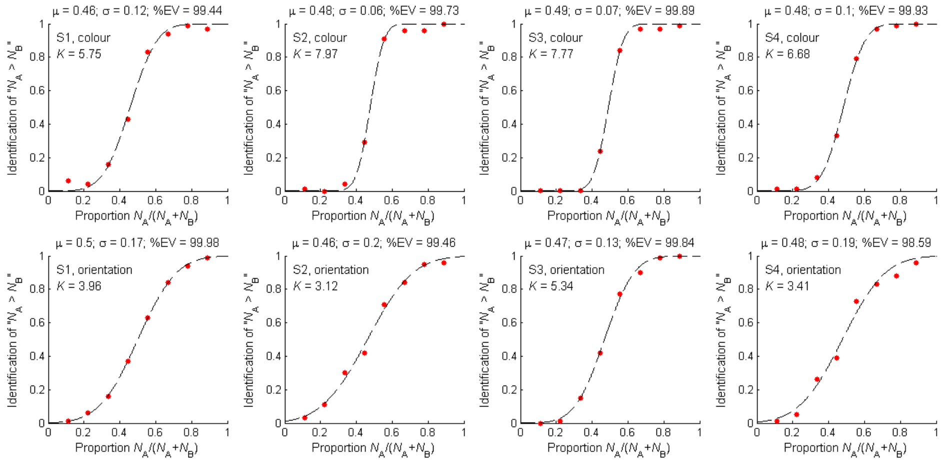
Table 1. Slopes of the psychometric functions (σ) and predicted number of elements (*K*) inspected by the observers.

	Observers					
N	**S1**	**S2**	**S3**	**S4**	**All**	***K/N* (%)**
σ (slope of psychometric function)						
Colour						
9	0.119	0.060	0.066	0.095	0.085	
13	0.092	0.081	0.086	0.098	0.089	
33	0.075	0.073	0.070	0.097	0.079	
65	0.067	0.088	0.066	0.087	0.077	
Orientation						
9	0.171	0.201	0.130	0.190	0.173	
13	0.148	0.169	0.107	0.219	0.161	
33	0.140	0.148	0.107	0.200	0.149	
65	0.119	0.150	0.110	0.164	0.136	
K (predicted number of sampled elements in hypergeometric response model)						
Colour						
9	5.75	7.97	7.77	6.68	7.04	78.3%
13	8.84	9.56	9.24	8.46	9.03	69.4%
33	18.61	19.06	19.75	14.23	17.91	54.3%
65	29.53	20.92	30.03	21.26	25.44	39.1%
Orientation						
9	3.96	3.12	5.34	3.41	3.96	44.0%
13	5.61	4.67	7.89	2.98	5.29	40.7%
33	8.46	7.70	12.58	4.30	8.26	25.0%
65	13.04	8.52	14.88	7.12	10.89	16.7%

Figure 1. Stimulus configurations in the two experiments.

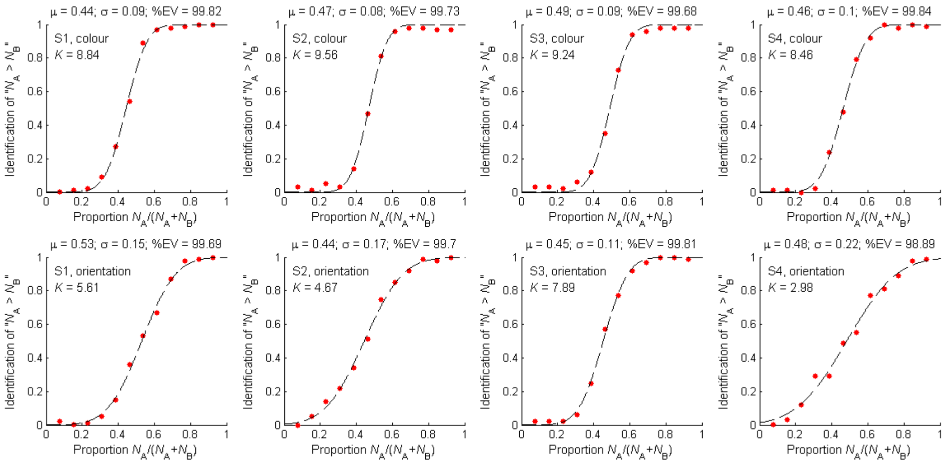
Schematic view of stimulus configurations used in the numerosity discrimination experiment using colour (left panel) or orientation (right panel) as a distinctive attribute.

N = 9



μ = 0.46; σ = 0.12; %EV = 99.44
S1, colour
K = 5.75
μ = 0.48; σ = 0.06; %EV = 99.73
S2, colour
K = 7.97
μ = 0.49; σ = 0.07; %EV = 99.89
S3, colour
K = 7.77
μ = 0.48; σ = 0.1; %EV = 99.93
S4, colour
K = 6.68
μ = 0.5; σ = 0.17; %EV = 99.98
S1, orientation
K = 3.96
μ = 0.46; σ = 0.2; %EV = 99.46
S2, orientation
K = 3.12
μ = 0.47; σ = 0.13; %EV = 99.84
S3, orientation
K = 5.34
μ = 0.48; σ = 0.19; %EV = 98.59
S4, orientation
K = 3.41
Identification of "N_A > N_B"
Proportion N_A/(N_A+N_B)

N = 13



μ = 0.44; σ = 0.09; %EV = 99.82
S1, colour
K = 8.84
μ = 0.47; σ = 0.08; %EV = 99.73
S2, colour
K = 9.56
μ = 0.49; σ = 0.09; %EV = 99.68
S3, colour
K = 9.24
μ = 0.46; σ = 0.1; %EV = 99.84
S4, colour
K = 8.46
μ = 0.53; σ = 0.15; %EV = 99.69
S1, orientation
K = 5.61
μ = 0.44; σ = 0.17; %EV = 99.7
S2, orientation
K = 4.67
μ = 0.45; σ = 0.11; %EV = 99.81
S3, orientation
K = 7.89
μ = 0.48; σ = 0.22; %EV = 98.89
S4, orientation
K = 2.98
Identification of "N_A > N_B"
Proportion N_A/(N_A+N_B)

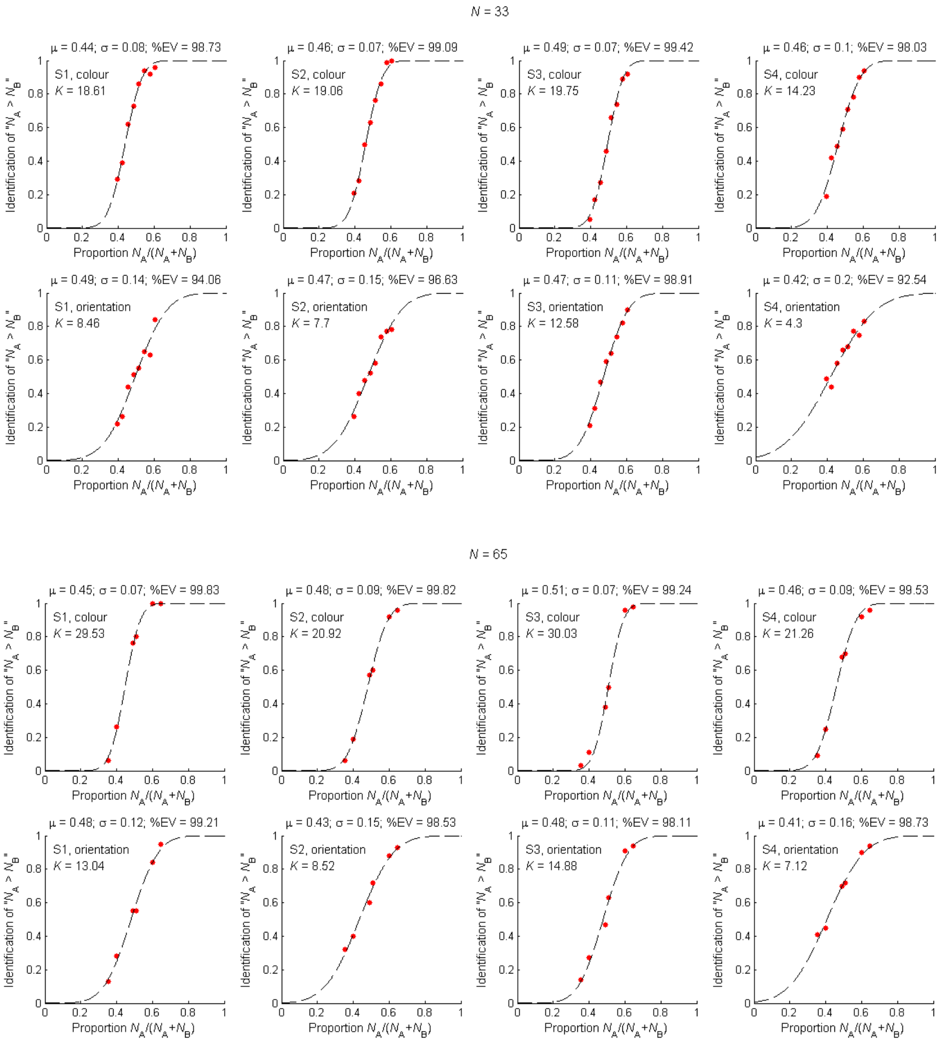


Figure 2. The best fitting theoretical cumulative gaussian models (dashed line) *vs* empirical results (red points).

The choice probability as a function of the proportion of the chosen response category for four observers, two numerosity discrimination tasks (colour and orientation), and four numbers of elements (N = 9, 13, 33 and 65). Each point is a probability estimate computed from 100 trials. The dashed line represents the best fitting theoretical cumulative gaussian model with its parameters μ and σ indicated above individual response curves.

Notes: μ = mean of the approximated cumulative gaussian function; σ = standard deviation of the approximated cumulative gaussian function reflecting the slope of the psychometric function; *%EV* = the percentage of the explained variance, R^2; N_A = total number of type *A* (red or tilted to the left) elements in the display; N_B = total number of type *B* (green or tilted to the right) elements in the display.

IV

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Visibility versus accountability in pooling local motion signals into global motion direction.
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Visibility versus accountability in pooling local motion signals into global motion direction

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ABSTRACT

The human observer is surprisingly inaccurate in discriminating proportions between two spatially overlapping sets of randomly distributed elements moving in opposite directions. It was shown that observers took into account 74% of all moving elements when the task was to estimate their relative number and only 21% of the same elements when the task was to discriminate between opposite directions. It was concluded that, in the motion direction discrimination task, observers are motion blind to a large number of elements, the majority of which are visible in a numerosity task. This type of motion blindness belongs to the attentional blindness category, where a strong sensory signal cannot be noticed when processing is diverted by parallel events. In addition, we found no evidence for the common fate principle, as the ability to discriminate numerical proportions remained the same, irrespective of whether all estimated elements were moving coherently in one direction or unpredictably in opposite directions.

The human observer is surprisingly inaccurate in discriminating proportions between two spatially overlapping sets of randomly distributed elements moving in opposite directions (Raidvee, Averin, Kreegipuu, & Allik, 2011). For a wide range of stimulus sizes, decisions about motion direction are made as if only a very limited number of elements (in some cases less than 0.5%) were taken into account, even if the motion direction of each element in isolation can be determined with almost absolute certainty. This is very intriguing, since observers seem to be under no illusion about the actual number of moving elements. They are well aware of the large number of moving elements on the screen but they seem to lack introspective knowledge about how many of these motion elements contribute to answers about the dominant motion direction. Thus, from a large number of visible moving elements, only a fraction is used in determining global motion.

One surprising corollary of this limited capacity for motion discrimination is the almost complete irrelevance of the total number of motion elements. If an observer's decisions are based on a limited subset of elements, then the duplication of a motion pattern that contains elements moving in opposite directions in an adjacent area of the visual field would not be expected to improve motion direction discrimination performance. In many other areas of visual perception, however, it is known that the duplication of the test stimulus leads to enhanced detection or recognition performance (e.g., Meese & Williams, 2000). Our intuition is also that doubling the stimulus would increase the probability of noticing its critical attributes. However, this may not be the case with discriminating between opposite motion directions, which is based on an account of a relatively small and fixed number of motion elements. Nevertheless, it would be most intriguing to test this prediction, which may, to many, seem counterintuitive.

Another challenge we face in this paper is the distinction between visible and accountable information. Memory researchers, for instance, realized long ago that not all potentially available memory content is necessarily accessible at every instance of recall from the memory (Tulving & Pearlstone, 1966). Except perhaps in the case of ideal observer analysis (cf. Rose, 1948), it is relatively rare that perceptual analysis makes the distinction between potentially available and actually used information (Allik & Pulver, 1994; Burgess & Barlow, 1983). However, there are several well-described experimental protocols (attentional blink, crowding, dual task, etc.) where a strong sensory signal cannot be noticed when attention is distracted by other stimuli (Dehaene & Changeux, 2011; Kanai, Walsh, & Tseng, 2010; Sergent, Baillet, & Dehaene, 2005). These situations are typically called attentional blindness, as opposed to perceptual blindness, which is caused by the degradation of a weak sensory signal itself (Kanai et al., 2010).

In this paper, we propose a different approach to quantifying the distinction between the visibility and accountability of motion elements. As in our previous study (Raidvee et al., 2011), we varied the proportion of leftward *vs* rightward moving elements to construct the psychometric function for the discrimination between opposite motion directions. On the basis of this psychometric function, it is possible to determine the number of moving elements that are taken into account in making decisions about global motion direction. The observer's decisions can be described by the Bernoulli trial scheme, in which the observer is randomly selecting out K elements from the actual number of motion elements, N, that are present in the stimulus and of which N_R are moving rightwards and N_L leftwards. The rational decision rule is very simple: if the number of the rightward moving elements, K_R, in the selection exceeds the number of the leftward moving elements, K_L, ($K_R > K_L$), then the rightward direction is chosen; otherwise, the leftward direction is chosen. If the number of accounted elements moving in opposite directions happens to be equal ($K_R = K_L$), then the choice between the two response categories is random, with equal probability of either (assuming there is no response bias). Thus, the ratio of the accounted motion elements, K, to the actually presented number of motion elements, N, (together with the actual value of N) determines the slope of the psychometric function. Given a certain N, it is possible to determine from the slope of the psychometric discrimination function the number of motion elements K that was taken into account in making decisions about the dominant motion direction. The formal expression of the response model described is given in the Appendix.

As already noted, unlike the ideal observer in determining motion direction, a human observer is limited to only a small fraction of moving elements, K, which is used for inferring the global impression of movement. Thus, there are many motion elements that are visible yet ignored by the observer when the decision about global motion direction is made. How can the total number of moving elements which is visible but not necessarily used for the determination of the motion direction be ascertained? One potential method is numerosity discrimination. Exactly the same motion element stimuli can be presented and the observer asked about their relative number. When the observer is instructed to discriminate the relative number in the two sets of moving elements, the decision obviously needs to be made on the basis of the quantification of as many elements as possible from these two sets. On the basis of the slope of the discriminating function, it is possible (given a certain value of N), again, to estimate how many elements from both sets are actually taken into account. This number is presumably larger than the number on the basis of which decisions about the motion direction are made. We believe that the differences in the outcomes for these two tasks – motion and numerosity discrimination – could be used as the first approximation to what could be called the visibility and accountability of motion elements: from a large number of motion elements that are visible when numerosity decisions are made, a supposedly smaller fraction is taken into account for the determination of the global motion impression.

It is well known that a common motion vector is a strong grouping factor of visual elements. Kurt Koffka (1935/1963) probably coined the term *common fate*, which played an important role in the formulation and spread of the Gestalt principles. However, like many other Gestalt "laws," the common fate principle is difficult to formalize, and has usually been communicated through visual examples alone (for some exceptions see Edwards, 2009; Sturzel & Spillmann, 2004; Uttal, Spillmann, Sturzel, & Sekuler, 2000). In this study, for the quantification of the difference between visibility and accountability, we present two spatially separated sets of moving elements by asking the observer to determine, as a first task, which of these two sets contains more elements; as a second task, we ask the observer in which direction (right *vs* left) either quantitatively identical replica of the stimulus appears to move; and as third task, we ask in which direction the two quantitatively identical replicas of the stimulus appear to move.

For the first task, it is irrelevant which direction the elements of these two sets are moving in, or whether they are moving at all. However, it is possible that the coherence among motion elements, as Gestalt psychologists claim, increases their conspicuity. If this holds true, then the numerosity discrimination between two sets of elements moving coherently in one direction is expected to be more accurate than the discrimination between two sets of elements that move incoherently in opposite directions. This difference, provided that it exists, would be a novel way to operationalize the common fate principle. It would thus be possible to say precisely how many more elements have been taken into account in a coherently moving pattern compared to an incoherently moving set of elements of the same size.

METHODS

Participants. There were four female participants, referred to as S1, S2, S3, and S4, with normal or corrected-to-normal visual acuity and no reported history of visual disorders. Their ages ranged from 20 to 32; three of them had prior experience with psychophysical experiments but two were naïve to the concept of the current experiments.

Apparatus. Stimuli were generated using a Cambridge Research Systems *ViSaGe* image generator driven by a Pentium computer. Stimuli were displayed, at a viewing distance of 170 cm, on a Mitsubishi Diamond Pro 2070SB 2200 monitor (active display area 20″), operating at a refresh rate 140 Hz with a spatial resolution of 1024 × 769 pixels. A schematic view of the stimulus configurations is shown in Figure 1. The physical properties of the stimulus displays were similar for all three types of experiments. The stimuli consisted of a set of identical circles, each with a circumference of 3′ and a luminance of 67 cd/m^2, which were simultaneously presented onto either one or two background areas: i.e., two adjacent elliptical dark areas with luminance close to zero and lengths of horizontal and vertical axes of 5.05° and 4.7°, respectively. The elliptical backgrounds were surrounded by a rectangular area of luminance 7.5 cd/m², filling the rest of the screen, thus subtending 13° horizontally and 9.8° vertically. The distance between the elliptical areas was equal to their distance from the display boundaries, 0.97°. Each element was surrounded by an inhibitory area which prohibited the elements from being closer than 7.6′ to each other. The minimal distance of an element from the edge of the test area (i.e., the elliptical background) was 15.2′. The observers were instructed to fixate on the center of the screen.

Motion discrimination. In each trial, two frame stimuli of *N*-elements was presented on the screen. Each frame was separated by an inter-stimulus interval of 30 ms and lasted for 100 ms. Each element in the second frame was displaced 11.4′ to the left or the right of its original position in the first frame. The proportion of leftward (N_L) and rightward (N_R) displacing elements was varied, with the observers' task to indicate in which direction, to the left or to the right, they saw a larger number of elements moving. If all elements were moving in the same direction then observers had no problems identifying motion direction, since coherently shifting elements produced a very compelling impression of motion.

In the first series of experiments ("single test area"), motion elements appeared in only one of the two test areas (see Figure 1A). There was no previous information on which of the two areas contained motion elements or which test area would remain empty. Motion elements were assigned to either the left or right area randomly, with equal probability. The total number of elements in a test area was constant at 33, with the relative proportion of rightward moving elements, N_R, *vs* leftward moving elements, N_L, randomized throughout the experimental session and varied at 6 levels: 10:23, 13:20, 16:17, 17:16, 20:13, and 23:10. Each condition (corresponding to one proportion) was administered 200 times (40 times in 5 separate sets): 100 times with the elements appearing in the left test area and 100 times with the elements appearing in the right area.

In the second series of experiments ("double test area"), both of the test areas were filled with moving elements (Figure 1B). Each test area contained N_L elements displacing to the left and N_R elements displacing to the right. The spatial configurations of the elements in the two test areas were not identical and were determined randomly for each test area. As in the "single test area" experiment, the observers' task was to indicate in which direction they saw the larger number of elements moving. Thus, relative to the "single test area" task, in this series of experiments, the total number of motion elements (N) as well as the number of rightward (N_R) and leftward displacing elements (N_L) was doubled. The total number of elements equaled 33 for each test area (thus totalling 66), with the relative proportion of rightward moving elements, N_R, *vs* leftward moving elements, N_L, randomized over the experimental session and varied at 6 levels, being equal for both areas and thus totaling either 14:52, 20:46, 26:40, 32:34, 34:32, 40:26, 46:20, or 52:14 across the two areas. Each condition (corresponding to one proportion) was administered 100 times (20 times in 5 sets).

Numerosity discrimination. In the numerosity discrimination task, both test areas contained identical motion elements, some of which were moving to the left and others to the right. Unlike the motion discrimination task with double test areas, the number of motion elements in the left and the right test areas was not equal and varied from trial to trial.

The observer's task was to ignore motion information and to indicate which of the two test areas, the left or the right, contained more elements. There were two types of trials, corresponding to coherent and incoherent motion conditions. In the coherent motion ("common fate") trials, all N elements in both test areas were moving in only one direction, to the left or to the right. In the incoherent motion trials, half of all elements were moving to the left and the remaining half to the right. The total number of moving elements remained constant at $N = 66$, but the exact proportion assigned either to the left or to the right test area was randomized across individual trials and varied at 6 levels: 26:40, 29:37, 32:34, 34:32, 37:29, and 40:26. Each proportion was repeated 300 times (30 times in 10 sets): 100 times for the "common fate" condition, with all elements moving rightwards; 100 times with all elements moving leftwards; and 100 times with half of the elements moving leftwards and the other half moving rightwards. All conditions were randomized within one experimental session.

The time provided for responding was always three seconds. If there was no answer the trial was cancelled and repeated later in a random position among the remaining trials. All stimulus conditions within one experimental session were randomized.

Data analysis. In order to find out the number of elements, K, the subjects based their decisions on in each type of experiment, the hypergeometric response model (formalized in the Appendix) was fitted to the data. In order to account for the bias inherent in the responses, the empirical psychometric curves were shifted along the abscissa so that the mean response would be equal to 0.5. As this kind of transformation would further prohibit the direct application of discrete computational methods in the assessment of model fit, we chose to compare the empirical and theoretical curves via the cumulative normal distribution. Specifically, for each empirical function, the best-fitting theoretical model (out of all possible theoretical models) was the one with the smallest calculated area integral between the functions (i.e., the two normal approximations of both the empirical and theoretical response curves). Finally, as an estimate of model fit, we found the ratio of the calculated area integral to 0.5 (the theoretical maximal area that can be observed between empirical and theoretical functions).

RESULTS

The results are given in Table 1 and Figures 2 and 3. We can estimate the discrepancy between the elements' visibility and accountability by comparing the experimental series in which exactly $N = 66$ elements were presented in both test areas as a two-alternative forced choice task. Decisions about the proportion of the leftward *vs* the rightward elements were made as if 17, 9, 19, and 11 elements had been taken into account by observers S1, S2, S3, and S4, respectively. In the relative numerosity discrimination task, however, decisions were made on the basis of a considerably larger number of elements. The numerical proportion was decided as if 47, 51, 51, and 47 elements had been counted by observers S1, S2, S3, and S4 respectively. In terms of percentages, on average, 21% (in the motion discrimination task) *vs* 74% (in the numerosity discrimination task) of all elements was available for inspection. Roughly speaking, in the numerosity discrimination task, decisions were based on the taking into account over three times more elements than in the motion direction discrimination task. Thus, we can conclude that, in the motion discrimination task, observers can see a considerable number of motion elements, many of which they are not able to determine the actual motion direction for. This may also be called motion blindness.

One could argue that this inability to perceive or determine the actual motion direction was due to the mutual cancellation of opposite motion vectors between adjacent elements. Previous work has indicated that the low efficacy of motion direction discrimination in this type of display is not improved in the case of orthogonally directed motion vectors (Raidvee et al., 2011). As numerosity discrimination is not perfect either, it is conceivable that the mutual cancellation of elements would somehow interfere with this process as well. In order to test for this possibility, direction discrimination was compared among the two "common fate" conditions and one bidirectional condition. These results are depicted in Figure 3 and clearly indicate absolutely no effect for the common fate principle on the observers' capacity for numerosity discrimination. The slope of the psychometric function remained virtually unaltered, whether all elements moved coherently in one direction or they moved unpredictably in opposite directions.

As expected, motion discrimination performance was not improved substantially by replicating the stimulus in an adjacent area. Thus, when the motion elements were presented in only one test area with $N = 33$, the decisions about the proportion of the leftward *vs* rightward elements in the "single test area" condition were based as if 13, 13, 11, and 15 elements had been taken into account by observers S1, S2, S3, and S4, respectively (see Figure 2, second *vs* third row). In terms of variance in responses (σ), the discrimination of motion direction in the "single test area" condition was roughly on par with the "double test area" condition. Nevertheless, in terms of the number of elements sampled, in two subjects the discrimination was facilitated, whereas in the other two it was hindered, by the stimulus replica. Nevertheless, the difference between the mean numbers of elements taken into account in the two tasks was only 1: 13 in the "one test area" and 14 in the "double test area" experiment. As the differences in the estimated number of elements sampled by the subjects are neither large nor systematic (+4 and +8 for subjects S1 and S3 compared to –4 and –4 for subjects S2 and S4, respectively) it is hard to arrive at any conclusion about the effect of stimulus duplication on motion discrimination decisions, other than to say that the effect is probably not extensive. Together with our previous findings, we can conclude that the slope of the psychometric function is, on the whole, insensitive to the total number of moving elements, provided that it is expressed as a function of the proportion of leftward and rightward moving elements.

DISCUSSION

The results present three major points of interest. First, confirming our previous findings (Raidvee et al., 2011), we found our observers to be very poor at discriminating direction between two spatially overlapping sets of randomly distributed elements moving in opposite directions. Even in displays containing a relatively small number of elements ($N = 66$), observers' decisions were based on only about one-fifth of these elements. In our previous study, data indicated that, typically, motion direction information of only 4±2 elements was taken into account when global motion direction was inferred from local motion signals pointing in opposite directions. However, in this study we saw that, by increasing the contrast of the motion elements by three times, it is possible to somewhat increase the size of the sample on the basis of which global motion direction is inferred. Nevertheless, even in these improved conditions, the motion direction was ignored for the vast majority of elements. It is likely that we have reached the natural limit: exceeding this would be very difficult if not impossible.

It seems that observers were blind to motion information carried by the majority of motion elements. The comparison with the numerosity discrimination task shows that many of these neglected elements are seen and have been taken into account when the observer is asked to estimate which side, left or right, contains more elements, irrespective of their motion direction. Thus, about two-thirds of all elements are visible when it concerns the numerosity task, but the qualities required for pooling local motion information are not present ("motion blindness"). In our previous study (Raidvee et al., 2011), we demonstrated that the dispossession of motion information is not due to the cancellation or nulling of opposite motion vectors between closely located neighbors. The same extent of motion blindness was observed between orthogonally oriented motion vectors, which are known to be processed by separate visual mechanisms (Levinson & Sekuler, 1975).

What is the mechanism by which this motion blindness operates? Since the direction of each motion element can be determined with nearly 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 et al., 2010). Unfortunately, we have very little information about spatial, temporal, or other limits of this form of motion blindness.

Second, the replication of the stimulus in another inspection area was not beneficial for the decision about which direction more visual elements were moving in. If perception is indifferent to the total number of elements, then psychometric curves represented as a function of the proportion of moving elements, $N_L/(N_L+N_R)$, should have an equal slope. As in our previous study (Raidvee et al., 2011), we were not able to observe any systematic change in the slope of psychometric functions while the number of moving elements was duplicated in another inspection area. Consequently, even though with a larger array of motion elements, observers were able to determine motion parameters of a large number of elements, this number was fairly small, relative to the total number of moving elements. Thus, the human observer seems to be temporarily motion blind towards the majority of elements moving unpredictably in opposite directions. Although we are not the first to report about such wastefulness in coding motion (Braddick, Wishart, & Curran, 2002; Edwards & Greenwood, 2005; Suzuki & Watanabe, 2009), some questions about the ubiquitous textbook statement that our very survival critically depends on being able to perceive movement accurately (e.g. Palmer, 1999) remain to be answered.

Finally, we found that the common fate of moving elements has negligible, if any, effect on the numerosity discrimination between two sets of moving elements. Irrespective of whether all elements were moving coherently in one direction or incoherently in opposite directions, the ability to discriminate numerical proportion remained the same. Although in some cases the common fate principle can be demonstrated (Sekuler & Bennett, 2001; Sturzel & Spillmann, 2004; Uttal et al., 2000), our results clearly contribute to the line of evidence showing that this principle cannot be considered universal. The common fate of moving elements may be beneficial in some other tasks but it seems to have no advantage when it comes to the estimation of their relative numerosity.

Appendix: Formal expression of the psychometric model

The probabilities of a certain response for odd and even K according to the hypergeometric response model are given by Equations (A.1) and (A.2):

$$P_{\mathrm{hyp}\{K\ \mathrm{is\ odd}\}} = \sum_{i=1+\left\lfloor \frac{K}{2} \right\rfloor}^{K} \frac{\binom{N_L}{i}\binom{N_R}{K-i}}{\binom{N}{K}}, \qquad K = 2k-1 \qquad \text{(A.1)}$$

$$P_{hyp\{K\ \mathrm{is\ even}\}} = \sum_{i=1+\frac{K}{2}}^{K} \frac{\binom{N_L}{i}\binom{N_R}{K-i}}{\binom{N}{K}} + 0.5\frac{\binom{N_L}{\frac{K}{2}}\binom{N_R}{\frac{K}{2}}}{\binom{N}{K}}, \qquad K = 2k \qquad \text{(A.2)}$$

where

- k is any positive natural number;
- N_L is the number of elements in the stimulus that are moving leftwards or are presented in the left-hand test area (depending on the task);
- N_R is the number of elements in the stimulus that are moving rightwards or are presented in the right-hand test area (depending on the task);
- N is the total number of elements in the stimulus ($N = N_L + N_R$);
- 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 equality (A.1) = (A.2) holds, given equal values for k (Raidvee et al., 2011).

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Table 1. Number of elements sampled by the best-fitting theoretical model in the different types of experiments.

Numerosity discrimination (*N* = 66)

Subject	**S1**	**S2**	**S3**	**S4**
K	47	51	51	47
K / N (%)	71.21	77.27	77.27	71.21
S	0.0010	0.0004	0.0010	0.0004
%Error	0.207	0.084	0.206	0.088
%EV	99.79	99.92	99.79	99.91

Motion discrimination: "double test area" (*N* = 66)

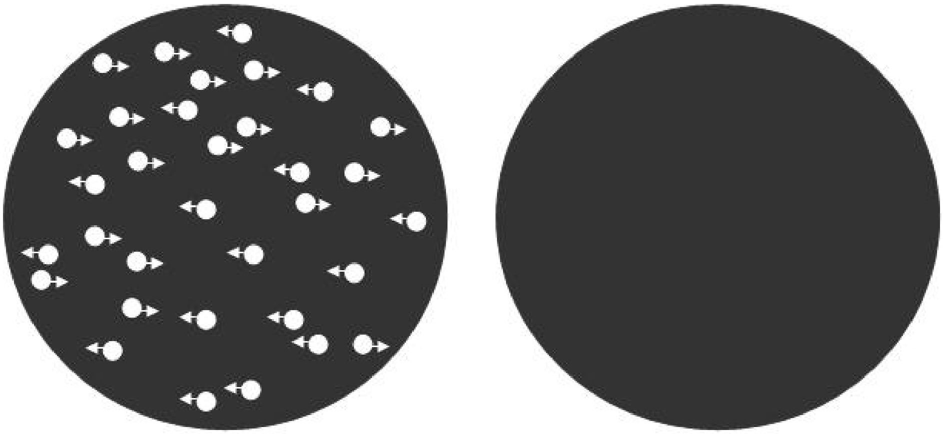
Subject	**S1**	**S2**	**S3**	**S4**
K	17	9	19	11
K / N (%)	25.76	13.64	28.79	16.67
S	0.0014	0.0036	0.0015	0.0017
%Error	0.276	0.728	0.293	0.335
%EV	99.72	99.27	99.71	99.67

Motion discrimination: "single test area" (*N* = 33)

Subject	**S1**	**S2**	**S3**	**S4**
K	13	13	11	15
K / N (%)	39.39	39.39	33.33	45.45
S	0.0046	0.0004	0.0036	0.0037
%Error	0.930	0.087	0.716	0.748
%EV	99.07	99.91	99.28	99.25

Note: *N* = number of elements on the display; *K* = number of elements sampled by the best-fitting hypergeometric model; *S* = Area integral between empirical *vs* best-fitting theoretical curves; %Error = S / 0.5 · 100, the percentage of variance unexplained by the theoretical model; %EV = the percentage of variance explained $(1 - S/0.5) \cdot 100\%$.

A



B

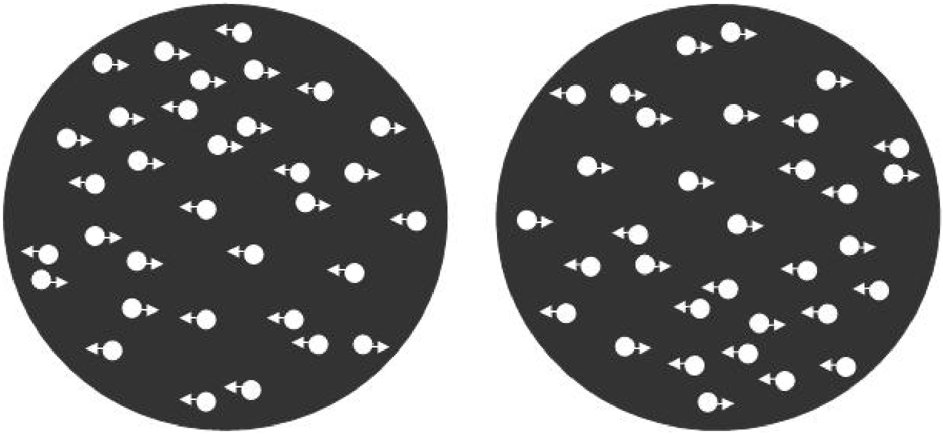


Figure 1. The two stimulus configurations in the three types of experiments.

Schematic view of the stimulus configurations used in the motion discrimination task with the "single test area" (A); and the motion discrimination task with the "double test area" and the numerosity discrimination experiment (B).

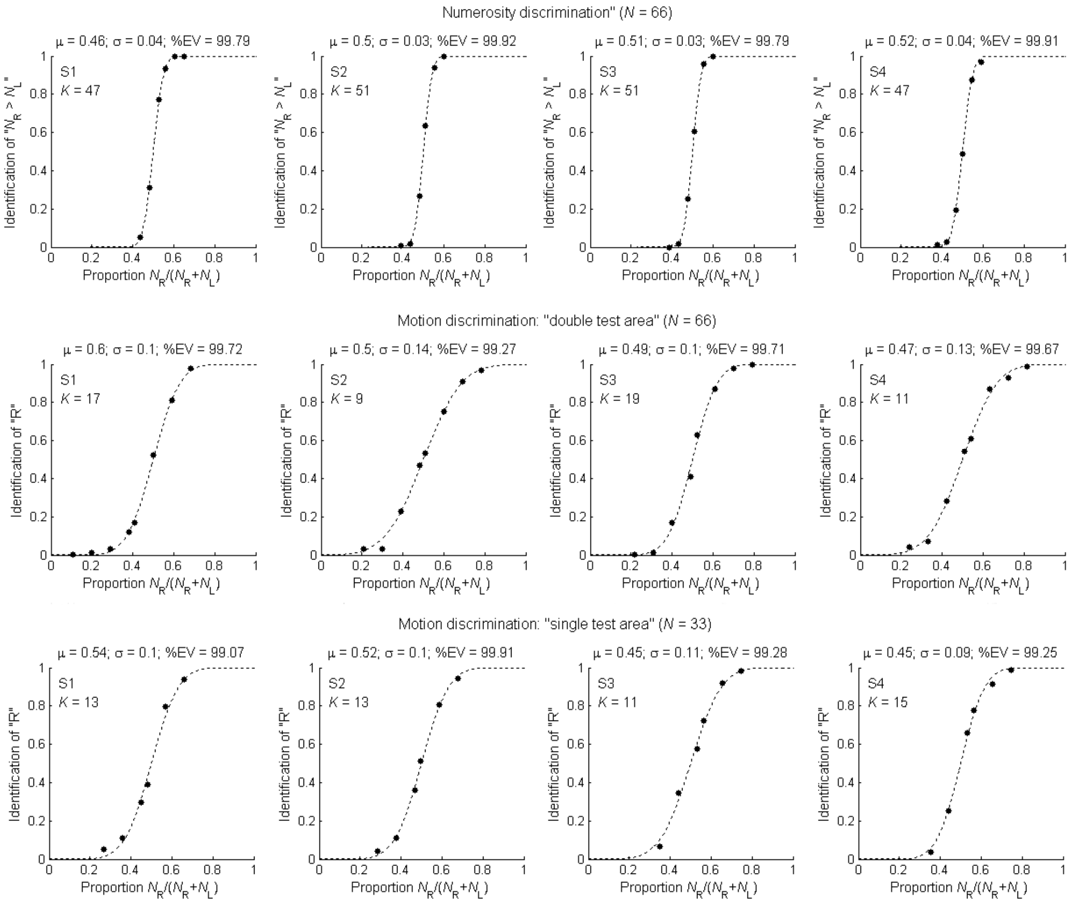


Figure 2. The best fitting normal approximations to theoretical hypergeometric models (dotted line) *vs* empirical data points. The choice probability as a function of the proportion of the chosen response category for the four observers and the three tasks: numerosity discrimination task (first row); motion discrimination task with "double test area" (second row) and motion discrimination task with "single test area" (third row). *Note:* μ = mean of the approximated psychometric function; σ = standard deviation (slope) of the psychometric function; %EV = the percentage of variance explained $(1 - S/0.5) \cdot 100\%$, where S = area integral between empirical *vs* best-fitting theoretical curves; N = total number of elements in the display; N_L = total number of leftward moving elements in the display; N_R = total number of rightward moving elements in the display; K = estimated number of the motion elements taken into account in the decision process.

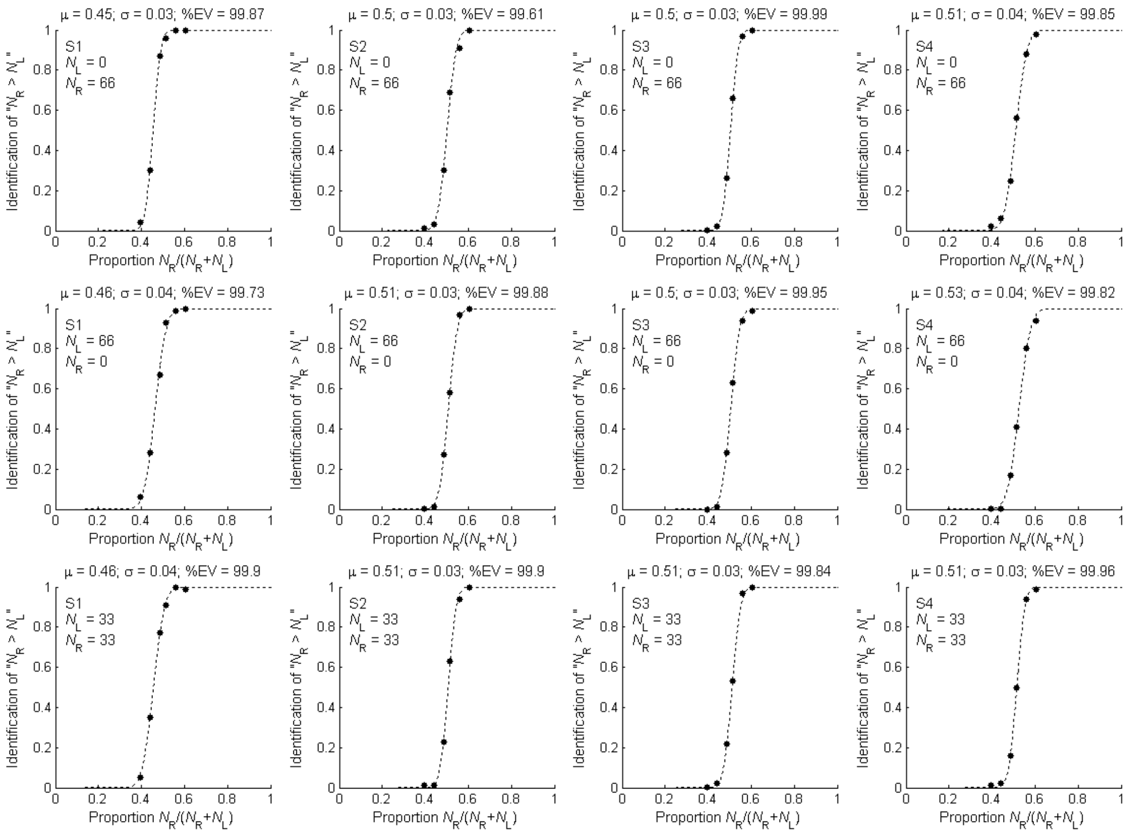


Figure 3. ***Common fate*** **principle: the best fitting normal approximations (dotted line)** ***vs*** **empirical data points.** The choice probability as a function of the proportion of the chosen response category for the four observers in the numerosity discrimination task: all elements moving rightwards (first row); all elements moving leftwards (second row); 33 elements moving leftwards and 33 moving rightwards. *Notes*: μ = mean of the approximated psychometric function; σ = standard deviation (slope) of the psychometric function; *%EV* = the percentage of the explained variance, R^2; N_L = total number of leftward moving elements in the display; N_R = total number of rightward moving elements in the display.

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A New Approach for Assessment of Mental Architecture: Repeated Tagging

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Abstract

A new approach to the study of a relatively neglected property of mental architecture—whether and when the already-processed elements are separated from the to-be-processed elements—is proposed. The process of numerical proportion discrimination between two sets of elements defined either by color or by orientation can be described as sampling with or without replacement (characterized by binomial or hypergeometric probability distributions respectively) depending on the possibility to tag an element once or repeatedly. All empirical psychometric functions were approximated by a theoretical model showing that the ability to keep track of the already tagged elements is not an inflexible part of the mental architecture but rather an individually variable strategy which also depends on conspicuity of perceptual attributes. Strong evidence is provided that in a considerable number of trials, observers tagged the same element repeatedly which can only be done serially at two separate time moments.

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Introduction

The way mental processes are organized—their architecture—has been one of the main concerns for both psychologists and neuroscientists [cf. 1]. The question of whether people perform perceptual and mental operations in parallel or in series, has been pivotal in many of these pursuits [2,3]. Overwhelmingly, the debate about serial *vs* parallel processing has been concentrated on reaction time data. In a seminal experiment, Sternberg [4] demonstrated that when observers judge whether a test symbol is contained in a short memorized sequence of symbols, their mean reaction-time increases linearly with the length of the sequence. The linearity and slope of the function were interpreted as strong evidence in favor of an internal serial-comparison process whose average rate is between 25 and 30 symbols per second. However, as it was soon shown by a thorough theoretical analysis, the distinction between serial and parallel processing is constrained by model mimicking: parallel models can lead to exactly the same predictions as serial ones despite the completely different psychological assumptions they are based on [3,5].

One lesson that can be derived from the serial *vs* parallel controversy is that it cannot be resolved in isolation from other relevant attributes of the cognitive architecture. For example, it became evident that the questions about stopping rule – the conditions under which the system ceases processing and generates a response – or the questions about capacity limitations, are inevitably linked to the question about serial *vs* parallel architecture [3]. Considering this lesson, it is surprising that even though a number of studies exist on serial *vs* parallel processing in the context of enumeration accuracy of independent sets, e.g. [6,7], the serial *vs* parallel debate has almost entirely escaped the numerosity discrimination accuracy problem. At least one study has shown similar counting and subitizing processes to those measured in standard enumeration tasks to be involved in the number discrimination task with a single stimulus set [8]. Yet, not much information is available about the nature of processes involved in numerosity discrimination in case the stimulus display contains multiple distinct sets.

In the following, we use the term *counting* as referring to any process aimed at finding the total number of elements in a set. The term is neutral with respect to the temporal properties of the processes involved: counting can be parallel, serial, or mixed.

It has long been known that it takes at least 5–6 years before children are able to learn all principles that are needed for counting, including assignment of numerals for objects [9]. But even after learning to count it is not guaranteed that perceptual mechanisms follow the principles used in verbal and propositional thinking. 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. 9]. Perceptually 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.

To the best of our knowledge, there is no generally accepted method for establishing whether or not the tagging process follows exactly the one-to-one principle. Unlike many previous studies which have used analysis of reaction times to differentiate between serial *vs* parallel processing styles, we attempt to reveal this property of mental architecture on the basis of probability distribution of responses. Our approach stems from an ideal observer analysis which purpose is to establish an absolute scale of performance for an ideal perceptual device that is limited only by stochastic characteristics of the stimulus itself [10]. Let's suppose that the observer's task is to discriminate the numbers of two distinct sets of randomly distributed elements. These two sets can be distinguished by their spatial position, occupy two separate areas, for example [11], or they can be intermixed but distinguished by a certain visual attribute, such as color or orientation [12]. This is a relatively simple task, as even pigeons, with a brain weighing less than 3 g, can be trained to discriminate numerical proportion in the mixtures of two types of elements with considerable accuracy [13,14]. As expected, an ideal perceptual device can notice even one element difference irrespective of the total number of elements. Real observers, human or nonhuman, usually perform less accurately, presumably because their decisions seem to be based on only a fraction of available items. It is conceivable that instead of all presented elements the real observers are able to take into account only a fraction of the elements, especially when these elements have a random spatial distribution and are presented for a very short time. Formally, this situation resembles the inverse probability problem in which a sample of randomly selected elements serves as a basis for inference about the true proportion of elements hidden from the observer. Jacob Bernoulli in his posthumous *Ars conjectandi* (1713/1899) devised an ingenious urn problem 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 colored balls or pebbles which are drawn, one after another, randomly from the urn and their color is noted. 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 color: 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 distribution) 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 than hypergeometric distribution, it would provide evidence that some of these elements are inspected twice or more times which, understandably, can only be done serially at two or more different time moments. On the other hand, the scheme of sampling without replacement (leading to the hypergeometric distribution) implies that there is accurate one-to-one tagging of which elements are already counted and which are not, leading to an element being inspected only once, maximally. The attribution of one-to-one counting tags (corresponding to the sampling scheme without replacement) is by itself neutral to the problem of parallel or serial counting.

If an observer strictly adhered to the hypergeometric model (see equations (3) and (4) in the Methods section) with the parameter K (the number of elements taken into account in the decision process) being equal to the total number of elements in the stimulus display, N, then he or she would always determine correctly which of the two types of the elements is more numerous. The fact that the real observers in our experiments make errors indicates, within the proposed approach, that either they only take into account proper subsets of the elements (adhering to the hypergeometric model with $K<N$) or they count some of the elements more than once, adhering, at least partially, to the binomial model. Our analysis below indicates that both these possibilities take place: to account for the data best we need to assume that the observers in some trials use the hypergeometric model and in other the binomial model, with K varying from trial to trial. In relation to the seriality vs parallelity of counting, the conformity of the data with the hypergeometric model (i.e., sampling without replacement, one-to-one tagging of selected elements) leaves the question of seriality vs parallelity open. But once the data are shown to require the binomial model for at least a fraction of all trials, one has to accept that some elements can sometimes be counted more than once, and this can only be done serially, at two or more separate time moments.

The overall aim of the experiments was to introduce a new approach for the assessment of mental architecture, namely the property of whether, in the process of proportion discrimination of multiple stimulus sets, certain elements were being counted repeatedly. In our view, the aim was achieved by showing that this is indeed the case at least in some of the trials.

Methods

Ethics Statement

The study has been approved by the local Research Ethics Committee.

Four 20-year-old female observers with normal or corrected to normal vision were asked to decide which of the two distinctive sets of objects were more numerous by pressing one of two buttons. In two separate series these two sets of objects were distinguished either by color or by orientation. A schematic view of the two types of stimulus configurations is shown in Figure 1. In the first series a randomly distributed collection of red and green circles was presented. The red and green circles had a luminance of about 23.5 cd/m^2. To diminish the impact of total red *vs* green area on the responses, size of the circles was randomly varied in the range of 11 to 22 minutes of arc. In the second series of the experiments a collection of short black line segments of luminance 0.3 cd/m^2 and tilt of 20° either to the left or to the right from the vertical direction was presented. The width and length of a line subtended 2′ and 19′ respectively (and height of its vertical projection 16′). Both types of stimuli were presented within an elliptical gray background with luminance of 54 cd/m^2 and with lengths of horizontal and vertical axes 8.86° and 8.70° respectively. This elliptical background was in the center of a rectangular area of luminance 64 cd/m^2 filling the rest of the screen. In order to avoid overlaps between elements, each element was positioned within an invisible inhibitory area which prevented other elements to be closer than 22′. Each stimulus element had a high contrast to guarantee its 100% identification would it have been presented in isolation. The total number of objects N presented on the display was kept constant through each experimental session and was equal either to $N=9$ or 13 elements. These two relatively small values were chosen because the difference between the response probabilities from the binomial *vs* hypergeometric models is greater in case the total number of elements is small. During experimental sessions, the relative proportion of the type A and type B elements was varied. For example, for the total number of $N=9$ the relative proportions of A (red or tilted to the left) and B (green or tilted to the right) element categories were the following: 1:8, 2:7, 3:6, 4:5, 5:4, 6:3, 7:2, and 8:1. The stimuli were presented at a viewing distance of 170 cm for 200 milliseconds, with 3 seconds for responding.

All stimuli were generated on the screen of a Mitsubishi Diamond Pro 2070SB 22″ color monitor (frame rate was 140 Hz

Figure 1. Stimulus configurations in the two experiments. Schematic view of stimulus configurations used in the numerosity discrimination experiment using color (left panel) or orientation (right panel) as a distinctive attribute.
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with the resolution 1024×769 pixels) with the help of a *ViSaGe* (Cambridge Research Systems Ltd.) stimulus generator. Every stimulus condition was replicated 100 times. Choice probability of the red circles was plotted as a function of the proportion of red elements N_R in the total number of elements on the display $N=N_R+N_G$. Similarly in the orientation experiment, probability of the choice of the leftward tilted elements was measured as a function of the proportion of leftward tilted elements $N_{(\backslash)}$ in the total number of elements on the display $N=N_{(\backslash)}+N_{(/)}$.

Mathematical expression of the psychometric models

The probabilities of a certain choice response for odd and even K from the binomial model are given by equations (1) and (2):

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

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

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 choice response for odd and even K from the hypergeometric model are given by equations (3) and (4):

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

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

$$K=2k$$

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.

As stated above, one only needs to consider either odd or even values of K because 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.

Results

The obtained psychometric functions are shown in Figure 2. The probability of the choice of "red" (color experiment) or "leftward tilt" (orientation experiment) are plotted as a function of the proportion of the respective type of elements in the total number of displayed elements. As expected, the choice probability monotonically increases with the increase in the proportion of the indicated elements.

It is assumed that the observer's decisions between response categories A and B are based on the inspection of K elements that are randomly selected from all available elements N. If the number of the A-type elements K_A in the selection exceeds the number of B-type elements ($K_A>K_B$), then the response category "A" is chosen; in the opposite case the response category "B" is chosen. If the numbers of A and B elements happen to be equal ($K_A=K_B$) for an even number of selected elements K, then the choice between "A" and "B" response categories is random with probability 0.5. Following this simple decision rule it is easy to compute all theoretical cumulative probability functions for

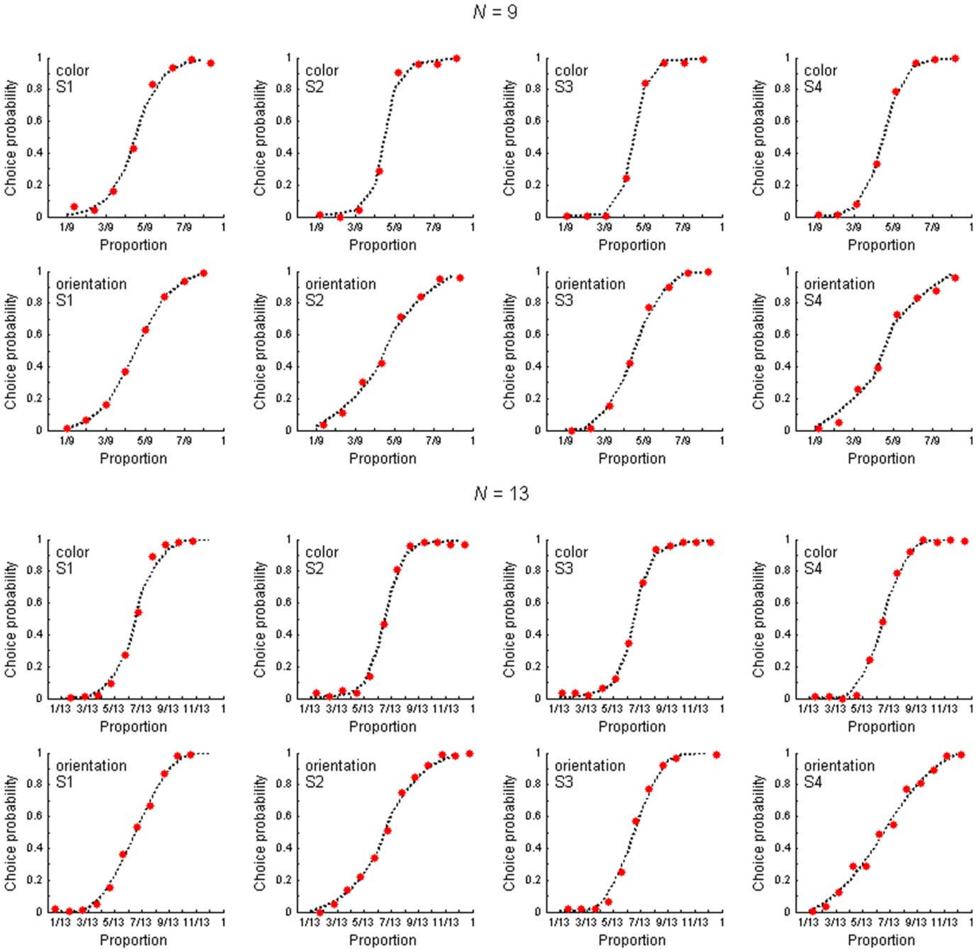

Figure 2. The best fitting theoretical models (dotted line) *vs* empirical results (red points). The choice probability as a function of the proportion of the chosen response category for four observers, two discrimination tasks (color and orientation), and two numbers of elements ($N = 9$ and 13). Each point is a probability estimate computed from 100 trials. The dotted line represents the best fitting theoretical mixture model shown in Tables 1.A and 2.A.
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binomial and hypergeometric distributions. Figure 3 demonstrates these theoretical binomial and hypergeometric models for odd numbers of selected elements K (the sample size). One only needs to consider odd numbers of elements since $K = 2k-1$ (odd) and $K = 2k$ (even) yield identical predictions. The equivalence of $K = 2k-1$ and $K = 2k$ is easy to demonstrate numerically for any arbitrary k value or demonstrate their formal equivalence by using, for example, Wolfram's *Mathematica*. However, an analytic proof seems to go beyond ordinary algebra. The mathematical formulations of response probabilities from both types of models – binomial and hypergeometric – are given in the Methods section.

Only in a few cases were the empirical psychometric functions close enough to one of these model predictions. This outcome is expected since it would be unrealistic to assume that the observer can use a fixed number of elements K in each trial through the whole sequence of trials. It is more realistic to assume that the number of selected elements K is a variable and changes from one trial to another. Also, there is no clear reason to hold any one specific combination of theoretical models strictly superior to the others as, within error limits, many mixture models are able to provide a comparable fit. Therefore, the emphasis of the current analysis is to estimate the relative performance of the hypergeo-

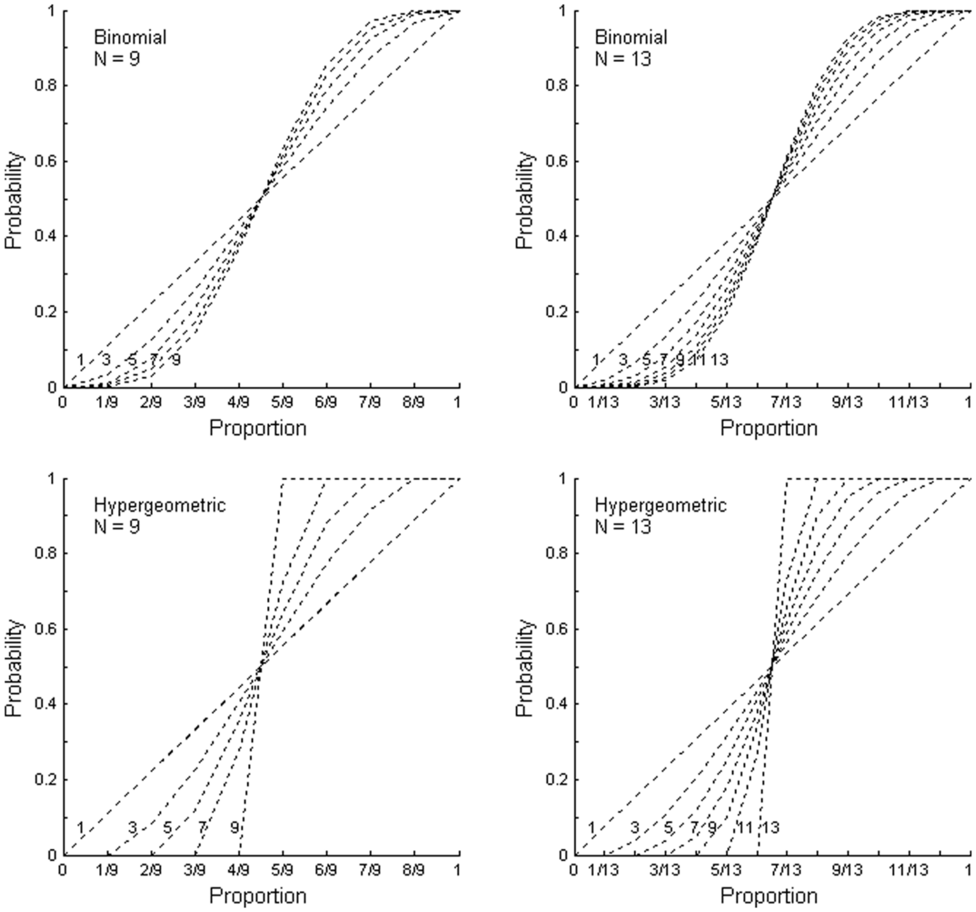

Figure 3. All possible theoretical models. All possible theoretical models corresponding to binomial (bin_K) or hypergeometric (hyp_K) distributions with the length of trials *K*.
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metric models to that of a combination of both hypergeometric and binomial models. We are greatly indebted to Ehtibar Dzhafarov for suggesting the described approach. At the heart of the underlying logic lies the assumption that in case any binomial component(s) is/are able to improve the overall fit of the mixture model (with the maximum number of possible mixture components held equal to the number of respectively possible hypergeometric models) then that would be an indication in support of serial processing in at least some of the trials.

An approximation algorithm based on least squares optimization was written which looked for the weighted combination of all theoretical models which minimizes the sum of squared errors between theoretical predictions and points of empirical functions. Prior to plotting the best mixture of theoretical models *vs* the empirical psychometric functions, the latter were shifted to the left or right to make their mean (μ) equal to 0.5. If the mean of all responses deviates from the expected 0.5 then it characterizes a response bias towards one of the two response alternatives. As expected, the empirical means were close to 0.5, ranging from 0.44 to 0.53.

The best predictions of the mixtures of theoretical models are shown in Figure 2 as continuous psychometric functions. The parameters of these best fitting mixture models are shown in Tables 1.A and 2.A. The number in the column corresponding to the theoretical model (bin_K or hyp_K) indicates the percentage of trials in which each of these models is expected to be used. For example, in the first row in Table 1.A the mixture model is described as **31**•hyp_5+**26**•hyp_7+**15**•hyp_9+2**8**•bin_3, which means that for the observer S1 the best fit was obtained when the hypergeometric model with the sample size of either $K=5$, $K=7$ or $K=9$ was supposed to be used in 31%, 26% and 15% of all the

Table 1.

A. The combinations of theoretical hypergeometric and binomial models providing the best fit to the empirical psychometric functions ($N=9$).								
Observer	**hyp_3**	**hyp_5**	**hyp_7**	**hyp_9**	**bin_3**	**bin_5**	**bin_7**	**bin_9**	**%Error**
COLOR ($N=9$)									
S1		31	26	15	28				1.5677
S2			45	39	15			1	1.0888
S3			61	32	7				0.2616
S4		29	48	15	8				0.3019
ORIENTATION ($N=9$)									
S1			23		9	60		8	0.0005
S2		10		12	77	1			0.8859
S3	16	73		11					0.9085
S4	18			19	63				1.2777

B. The combinations of theoretical hypergeometric models providing the best fit to the empirical psychometric functions ($N=9$).										
	COLOR					**ORIENTATION**				
Observer	**hyp_3**	**hyp_5**	**hyp_7**	**hyp_9**	**%Expl**	**hyp_3**	**hyp_5**	**hyp_7**	**hyp_9**	**%Error**
S1	30	36	18	16	1.5958	71		29		0.0095
S2	18		42	40	1.0914	91			9	0.9217
S3	8		60	32	0.2647	16	73		11	0.9085
S4	12	23	50	15	0.3034	85			15	1.3358

Note: N = number of elements on the display; %Error = the percentage of variance unexplained by the mixture of the theoretical models; bin_K = the binomial model sampling K elements; hyp_K = the hypergeometric model sampling K elements.
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individual trials, respectively, and the binomial model with the sample size of $K=3$ was used in the remaining 28% of the trials. Even a visual inspection can reveal that the fit to all 16 empirical psychometric functions shown in Figure 2 was excellent. This was confirmed by more formal tests showing that the predicted psychometric functions were able to explain on average 98.86% of the total response variance. Thus, only about 1.14% of total variance on average remained unexplained and could be attributed to measurement error.

The maximum number of components in the best fitting mixture models is four in case $N=9$ (Table 1.A) and six in case $N=13$ (Table 2.A) in order to keep the number of regressors equal to that of the competing mixture composed of hypergeometric models only. The best predictions obtained by hypergeometric models alone are given in Tables 1.B and 2.B. In most cases does the fit of the mixture containing binomial model(s) surpass that of the respective mixture containing only hypergeometric models. In Tables 1.A and 2.A, in cases where the binomial component improved the fit, the number presenting the proportion of unexplained variance is underlined. Since in 12 out of 16 cases addition of the binomial component improved the fit one can conclude that there were a significant number of trials in which the observers were not able to track exactly the elements that were already counted and those that were not.

In general, it is known that numerical discrimination based on color is more efficient than one based on geometric attributes, such as orientation [cf. 12]. This seems to be in agreement with our results: across all conditions and observers on average 5 elements were taken into account in orientation discrimination task and 7.5 elements when color was the distinguishing attribute.

In both types of tasks the hypergeometric distribution provided a better fit than the binomial one: in 65.3% of all trials when applied to discrimination on the basis of orientation, and in 88% of trials when applied to discrimination based on color. It was not entirely surprising to discover some small individual differences since it was previously shown that some participants adhered to a serial processing profile in most conditions while other participants could exhibit parallel-like strategy in some conditions at least [15].

Discussion

In order to enumerate objects accurately it is necessary to follow certain rules. One of these basic rules is the maintenance of the one-to-one relationship between objects and tags assigned to these objects: every object needs to be tagged only once. It is generally unknown whether and how well different perceptual processes are able to separate the to-be-counted items from the already-counted ones. In this study we have proposed a new approach to this problem. Although the question of whether and when people can perform perceptual and mental operations in parallel or in series has been dominating debates about mental architectures, it was also made clear that this central question can be answered only when other related questions such as stopping rules, selective influence [16,17], and capacity limitations have been answered as well [1,18]. The one-to-one principle of tagging obviously belongs to the same category of the related problems. In this study we presented strong evidence that it is reasonable to assume that in a considerable number of trials observers behave as if they are not able to keep track of the elements they have already counted. It is very likely that when forming their decision, they have taken the same element into account repeatedly. Since the same element can be visited twice or more times only on different time moments, this is a strong indication that at least some operations are executed serially.

The obtained evidence does not allow to assert that the adherence to the one-to-one tagging principle is an inflexible part

Table 2.

A. The combinations of theoretical hypergeometric and binomial models providing the best fit to the empirical psychometric functions (*N* = 13).

Observer	hyp_3	hyp_5	hyp_7	hyp_9	hyp_{11}	hyp_{13}	bin_3	bin_5	bin_7	bin_9	bin_{11}	bin_{13}	%Error
COLOR (*N* = 13)													
S1	13	2	54	7	11	13							3.3804
S2				41	43		16						1.5035
S3			5	12	58	4	21						0.1676
S4			65	29		6							1.5758
ORIENTATION (*N* = 13)													
S1		72	28										0.7928
S2	47		17		8	8	20						1.3801
S3			74	20			6						2.1331
S4	61				5		34						1.0062

B. The combinations of theoretical hypergeometric models providing the best fit to the empirical psychometric functions (*N* = 13).

	COLOR							ORIENTATION						
Observer	hyp_3	hyp_5	hyp_7	hyp_9	hyp_{11}	hyp_{13}	%Expl	hyp_3	hyp_5	hyp_7	hyp_9	hyp_{11}	hyp_{13}	%Error
S1	13	2	54	7	11	13	3.3804		72	28				0.7928
S2	17			40	43		1.5111	72		9	2	9	8	1.3822
S3	24		3	10	59	4	0.1789	6		76	18			2.1339
S4			65	29		6	1.5758	98				2		1.0200

Note: *N* = number of elements on the display; %Error = the percentage of variance unexplained by the mixture of the theoretical models; bin_K = the binomial model sampling *K* elements; hyp_K = the hypergeometric model sampling *K* elements.
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of the mental architecture. Previous studies have shown that depending on the observer and stimulus conditions the parallel processing strategy can be used in some and the serial processing strategy in other situations [15]. Our results seem to suggest that in perceptual tasks that can be solved more automatically and spontaneously, like discriminations based on color, 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. However, these are not inflexible rules. For instance, one of the four observers performed better in the orientation based discrimination task than in the color discrimination task. This seems to suggest that avoidance of repeated tagging 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 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. We can only guess the number of different strategies used during one session but at least three appear to be the norm in most cases.

The observed individual differences are particularly interesting in the light of a recent report showing that the ability to discriminate numbers of elements in two sets was correlated with a psychometrically measured intelligence [19]. It is an intriguing possibility that the ability to keep track of elements which have already been counted (together with the sample size one is able to base his/her decisions upon), forms a precondition for numerical intelligence which, in turn, among other faculties, gives rise to general intellectual abilities.

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Author Contributions

Conceived and designed the experiments: AR JA. Performed the experiments: AP. Analyzed the data: AR JA AP. Contributed reagents/materials/analysis tools: AR. Wrote the paper: JA AR AP.

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