



**Universiteit Utrecht**

## **Motion direction and perceived relative position: A review and psychophysical study into motion integration**

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### **Abstract**

Perceiving motion relies on neurally complex mechanisms. We review some of the processes preceding the perception of motion, most notable how motion signals can be integrated into a behaviourally useful motion percept by lateral modulatory mechanisms during early visual processing. We show that these motion integration processes can have perceptual manifestations (e.g. motion integration effects) in the localization of moving patterns and that the influence of motion on position is not restricted to the object containing the motion but also to, for instance, spatially distant stationary and moving objects. In an attempt to further investigate the motion integration process we created a psychophysics experiment to look at the perceptual effects of motion integration by measuring the differences in behavioural responses due to a dissociation between perceived position and actual physical position (e.g., due to mis-localization) of a steady-state moving grating away from the fixation area. Participants were asked to fixate on a fixation dot and identify the displacements of two consecutively displayed horizontal bars containing such a grating in a 2AFC response task. The direction of motion in the two displayed bars was either in equal or in opposite directions. We found significant effects when the two moving sine wave patterns were in opposite compared to equal directions, indicating the presence of an influential motion integration process. Because we do not want changes in eye position to be confused with changes in visual field position and hence complicate interpretation, we also assessed the question whether we could enforce ourselves to keep looking on the fixation dot while presented with the same set of stimuli. No significant differences in eye position distributions were found between any of the stimulus configurations.

**Keywords:** *Motion detection; Motion integration; Motion perception; Perceived relative position; Psychophysics; Population receptive field; Stable eye position; Two-alternative forced choice test*

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Visual perception connects us to the world around us by interpreting surrounding light to useful information. Our world is a dynamic one however, containing objects constantly changing over space and time. Whereas our eyes are only capable of detecting the array of light reflected by these objects, the neural process of motion detection (and ultimately motion perception) is responsible for the perceived speed and direction properties of a moving object and hence facilitates a very important function of visual processing: to respond optimally to motion (Gibson, 1979).

Extracting motion properties from retinal signals leaving our eyes is a computational process because it inherently relies on a number of different cues indicating a spatial relationship within or between an object over time. Our visual system however is built of receptive fields, each one covering just a piece of the visual world (Van Essen & Maunsell, 1982). How and what is it then, that enables us to detect, interpret and perceive motion occurring anywhere in the visual world?

*We will review the apparatus and computations that are thought to underlie these processes. Then, we will show how we can extend our understanding of these processes by investigating specific perceptual effects related to perceived relative positions of stimuli using behavioural responses in a psychophysical experiment.*

## The apparatus of motion and vision

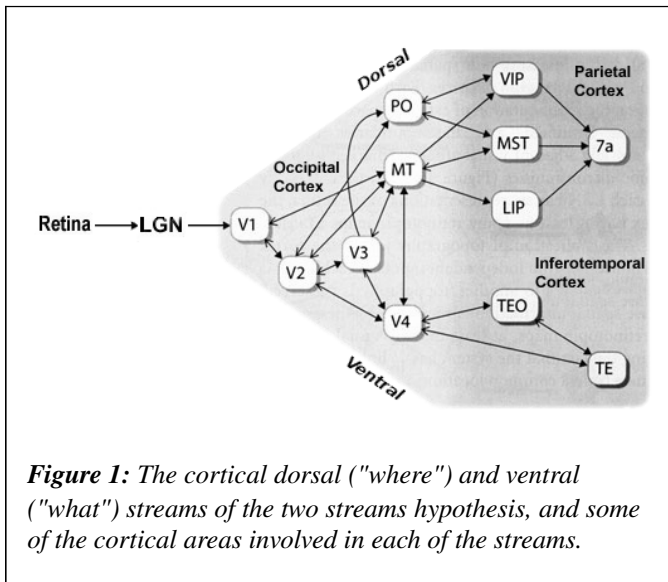
**Early vision** – As light enters our eyes, most of its induced retinal signals project against a structure in the brain called the lateral geniculate nucleus (LGN), a thalamic area. The LGN is seen as the primary relay center for visual information. Cortically, our visual system is organized hierarchically into different visual

areas within the occipital lobe of the brain (V1, V2, etcetera), with V1 being an area where information from the LGN is received and distributed across higher levels (Van Essen & Maunsell, 1982).

The second major region in the visual cortex is the V2 area, receiving information from V1 and relaying it to higher regions. It should be mentioned that information from V1 is not exclusively relayed to higher regions via V2; V1 itself also has many connections to higher regions like V5/MT (for example see review of Douglas & Martin, 2004; Born & Bradley, 2005), indicating that this system is not as hierarchically simple as one might initially think.

Each of these cortical visual areas contains a retinotopic map with neighbouring fields mapped side by side representatively for the visual world. Both V1 and V2 are responsible for detecting the basic localized features of vision like location and orientation (Hubel & Wiesel, 1968; DeValois et al., 1982). Visual processing beyond V2 continues among others in the V3 region, in humans subdivided into V3 dorsal, V3 ventral (VP), V3A (Tootell et al., 1997; Wandell et al., 2007), and an area called V3B (Smith et al., 1998) lateral to V3A. Human V3A appears to be relatively motion-selective (Tootell et al., 1997), and it also seems to be vital in less localized functions like analysing what is going where using form features like contour curvature (Caplovitz & Tse, 2007).

**The V5/MT area** – Visual area 5 (V5), also called visual area MT (middle temporal), is known to play a major role in motion perception but much less localized than previous areas (Zeki et al., 1991; Tootell et al., 1995). Although its hierarchical name as the fifth visual cortical area might suggest it mainly gets its input from areas like the aforementioned V3 region(s), it is actually the V1 area which provides the largest input of visual information to the V5/MT area (Born & Bradley, 2005).



**Figure 1:** The cortical dorsal ("where") and ventral ("what") streams of the two streams hypothesis, and some of the cortical areas involved in each of the streams.

Other studies even show that V5/MT might process some visual information before it reaches V1 (Beckers & Zeki, 1995).

Although the V5/MT area contributes to the global perception of motion, it is not the only region involved. In non-human primates like macaques, most of the output of V5/MT appear to go towards the cortical surrounding areas like the medial superior temporal (MST) areas which also extract motion information and contribute to the computational process of motion perception (Tanaka & Saito, 1989). DeYoe et al. (1996) noted that more research is required in the V5/MT and surrounding areas and gave the MT and adjacent regions the nomenclature MT+.

In an attempt to better identify a human homologue to the macaque MT+ region and to create a retinotopic map of the human MT+ region and its possible subdivisions, Amano and colleagues (2009) found two distinct visual field maps and dubbed them TO-1 and TO-2 (named after their temporal-occipital location in the cortex). The latter had a larger receptive field size as compared to the former, in line with the hierarchical increase in estimated receptive field sizes of the visual cortex.

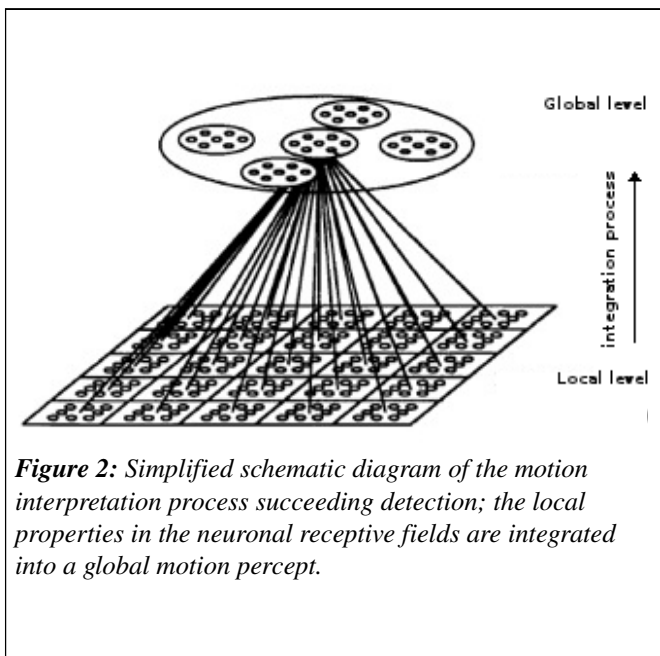
**The two streams hypothesis** – It is hypothesized that as visual information enters the occipital lobe it follows two distinct pathways or streams (Goodale & Milner, 1992), a controversial but widely accepted distinction.

The first of these streams, the ventral stream, appears to be mainly involved in object recognition (the what-pathway). The other stream, the dorsal stream, is thought to process spatial characteristics (and as such dubbed the where-pathway, see figure 1 for an impression of the cortical flow of the streams and some of the areas involved). Although it has long been thought that these are two very distinct streams, later evidence showed that these pathways do not remain strictly segregated throughout the visual cortex (Sawatari & Callaway, 1996).

Motion is intuitively a phenomenon based on spatial awareness (is it going somewhere, and where is it going?), and is therefore in the literature mostly related to the dorsal stream.

**Local versus global** – Although we have identified the cortical areas involved in vision and motion perception and to some extent found a processing stream that could facilitate some computational underpinnings of motion processing, we still need to bridge the gap as to how it is possible that this apparatus is capable of one of the most important goals of motion processing: recovering global motion (like motion trajectories) from local motion properties in order to facilitate behavioural responses to these movements (Gibson, 1979).

Because we have also shown that the size of the receptive field increases within the visual cortex hierarchy, we might also find some answers here concerning the mechanisms underlying this local-global interaction (see figure 2 for an illustration). To do so, we



first need to look at how we detect motion and then look into how we interpret signals from local motion detectors, a process that is widely thought of as including sequential computational stages.

## First processing stage: detect motion

**Processing retinal image features** – The light falling upon our eyes needs to be encoded somehow into a relatively sparse set of features able to encode for any of the characteristics found in the object in the visual world to allow our brain to efficiently process them (also called sparse coding, see Lennie, 2003 for a strong metabolic argument for such a mechanism). It is thus the task of local (early vision) motion detectors to detect and encode primitive image features (for instance luminance or chrominance), match primitive features into complex features (for instance edges), and detect any spatial and temporal displacement.

Encoding however could occur either before matching or after matching. Psychophysical findings using random-dot cinematography suggests that strong

coherent motion percepts can arise from stimuli lacking any spatial features (Williams & Sekuler, 1984), which favours the matching before encoding idea. On the other hand, motion is more likely to be seen between displaced edges of the same orientation than between edges of different orientation (Ullman, 1979), supporting the idea that the complex “edge” features are matched after they have been encoded.

According to these findings, there appear to be two different “ranged” motion detection systems; one that is capable of encoding primitive features and detect small spatiotemporal displacements, and one that is capable of matching more complex features and detecting larger spatiotemporal displacements.

Neurophysiological studies however have shown that the matching that occurs in the motion detectors in early vision (V1) is richer than simply detecting local luminant energy over small displacements, because V1 cells are capable of detecting (one-dimensional) contours in a particular orientation (Hubel & Wiesel, 1968; DeValois et al., 1982). These findings therefore seem to conflict with the idea of two separated systems. Cavanagh & Mather (1982) suggested that there still might be a dichotomy, but of a different kind: one that distinguishes first-order motion (using stimulus attributes like luminance) from second-order motion (using stimulus attributes like texture).

**Computational models** – Some computational models have been proposed that could help us understand this dichotomous problem and which supposedly underlie the motion detection process.

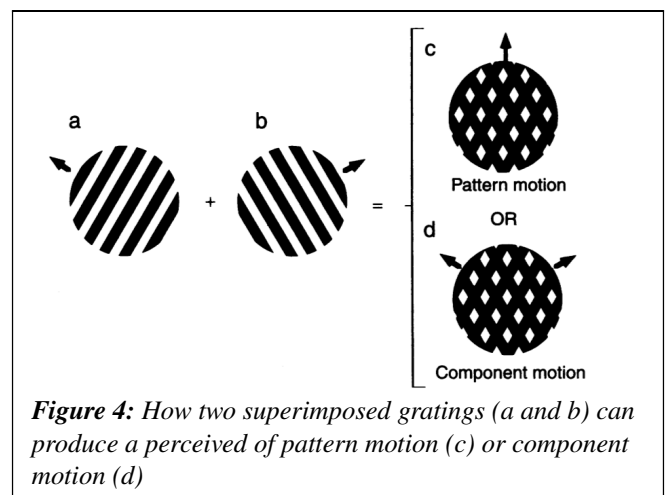
Reichardt (1961) was the first to propose a complete model to explain the computations underlying the motion detectors. He specified a type of cell that could compute a spatiotemporal displacement by comparing the outputs of two luminance-sensitive receptors using a temporal

## Second processing stage: Interpret motion signals

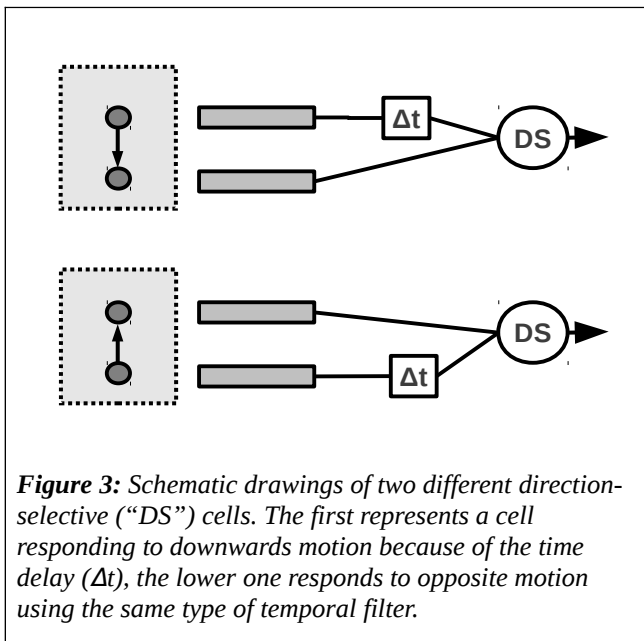
No matter the precise dichotomy in the motion detection process and no matter how similar the computational implementations of the aforementioned models are, the V1 neurons which are thought to facilitate this motion detection stage still only processes motion signals in an one-dimension manner like orientation selectivity (Hubel & Wiesel, 1968) whereas the retinal surface is two-dimensional. Detected motion caused by an object moving across the retinal surface hence requires a second stage in visual processing to be able to extract two-dimensional properties like the trajectory that an object follows.

How is it then, that we integrate information from primary (one-dimensional) motion detectors to interpret the two-dimensional retinal image?

**Component versus pattern motion** – An example of this motion integration process is the phenomenon that we can perceive a pattern to be moving in a different direction than each of its components. Simple stimuli eluding this phenomenon are “plaid patterns” and are widely studied (i.e. Adelson & Movshon, 1982). Plaid patterns are built by superimposing two drifting gratings,



**Figure 4:** How two superimposed gratings (a and b) can produce a perceived of pattern motion (c) or component motion (d)



**Figure 3:** Schematic drawings of two different direction-selective (“DS”) cells. The first represents a cell responding to downwards motion because of the time delay ( $\Delta t$ ), the lower one responds to opposite motion using the same type of temporal filter.

filter (e.g., a temporal delay) between these two outputs and called it a directionally-selective (DS) cell (see figure 3 for an illustration of this relatively simple mechanism). Different DS cells respond to different directions, allowing a population of these cells to respond to a specific direction of movement.

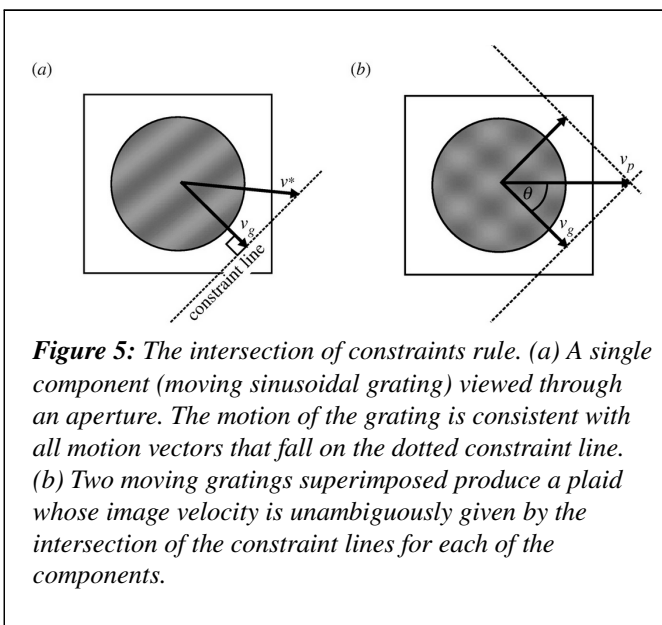
Whereas the Reichardt model uses a “correlational” approach (the amount of luminance in one receptor is correlating with the amount of luminance in another receptor after a time delay), Adelson & Berger (1985) introduced an “energy” approach where motion detection is a result of spatial frequency changes over time. This is accomplished by stacking space-time separable filters, which are filters in which the spatial profile remains the same shape over time but is scaled by the value of a temporal filter.

Van Santen & Sperling (1985) showed algebraically that the Adelson & Berger and Reichardt models are the equivalents of each other, indicating that the computations that underlie both models are formally the same. Because of the difference in usage of spatial and temporal filters, these two models do however suggest a different neural implementation.

resulting in either a percept of a coherently two-dimensional pattern movement or two moving one-dimensional components depending on a variety of stimulus parameters (see figure 4).

**The intersection of constraints rule** – Being two-dimensional, pattern motion can not be detected by the V1 neurons however, because we attributed a small receptive field to this type of neuron earlier on resulting in a V1 neuron only being able to extract the one-dimensional velocity component perpendicular to the local line feature inside its receptive field. This problem that the true motion direction is locally ambiguous is also called the aperture problem.

Adelson & Movshon (1982) introduced a simple rule for combining velocity information from components that solves this aperture problem. By intersecting all possible directions of the two components in an aperture, the direction of the pattern motion can be calculated (see figure 5). Their rule, the intersection of constraints (IOC) rule thus not only solves the aperture problem, but also computationally relates pattern direction to component direction.



**Segmentation processes** – Besides being a robust example of a motion integration process, the dichotomy of pattern versus component motion shows us that integration of primary motion detectors is also selective because it could result in two different percepts.

What is it then, that moves? In a natural scene, the trajectories of multiple objects in the three-dimensional world can overlap in the two-dimensional representation of that world on our retina. Yet we are clearly able to determine speed and direction properties for each of these global trajectories.

In this case, simple motion integrating processes are not sufficient for interpreting motion alone, but a segregation process with more global knowledge must also be present.

## Neural implementation of the motion integration process

We have asked the question how our visual processing system is capable of recovering global motion (like motion trajectories) from local motion properties (like orientation). We have seen that our visual processing system is capable of interpreting multiple low-level one-dimensional signals to extract information from the two-dimensional image on our retina. Also, proper motion interpretation appears to require global information of the visual scene to facilitate segmentation processes.

These manifestations of the motion interpretation mechanism shows that we are somehow capable of combining the information of smaller receptive fields (in the early vision apparatus) with information from larger receptive fields (from for instance the MT+ region). What could be the neural circuitry underlying this mechanism?

**Feedforwarding motion signals** – In line with the component versus pattern motion phenomena, early neurophysiological single-unit research has been conducted to assess where in the cortex motion integration processes takes place. The neurons in V1 as well as a vast majority of the neurons in V5/MT (around 60%) responded to the motion of the individual component gratings in a plaid pattern but not to the overall motion of the plaid pattern; in V5/MT however, roughly 25% of the neurons responded to the direction of the plaid pattern (Movshon et al., 1985; Rodman and Albright, 1989). This indicates that some specific neural events correlate with the integration of motion signals in a hierarchical feedforward fashion from V1 upwards to V5/MT.

**Extending the receptive field** – Another attempt to better understand the cortical implementation of motion integration was made by investigating how outputs of locally tuned detectors are combined to enable elementary spatial contour detection (Field et al., 1993; Kovacs, 1996; Hess & Field, 1999). Similar to the receptive field of a single neuron, an 'association field' of a cortical network was proposed, where an association between motion direction and spatial position supposedly takes place.

In V1, the neighbouring surround of the center of the receptive field of a neuron can have an interaction with that center by facilitating or suppressing the response of the center (Hartline, 1940), facilitating for instance the orientation selectivity which we discussed earlier (e.g., for a review see Angelucci & Bullier, 2003). The region where this center-surround interaction occurs is now also called the classical receptive field.

Stimulating the visual space outside a neuron's classical receptive field cannot evoke a response, but can however modulate that neuron's response when a

stimulus is presented in both its receptive field and its surroundings. This modulation is called the extra-classical receptive field effect and is the result of both neural feedforward as well as feedback mechanisms within the cortical hierarchy (Rao & Ballard, 1999).

**Population receptive field, pRF** – Since these results, motion integration is assumed to at least involve on some some neural feedback modulatory mechanisms between cortical areas, intuitively involving from higher regions like for instance MT+ because these regions have larger receptive fields than the receptive fields of the early motion detectors in V1. More recent published work by Dumoulin & Wandell (2008) describes a new method to estimate both the retinotopic representations and neuronal population receptive field (pRF) sizes in the MT+ region in a more accurate fashion by computing a model of the pRF using responses from a wide range of stimuli presented across visual space. Using this method, we can accurately tell which region of the visual field stimulates which neuronal (or cortical) area.

**Lateral modulatory** – Watamaniuk & McKee (1995) studied motion trajectories occluded only by motion in either the same or different direction as the motion trajectory itself. They found that the mechanism detecting motion trajectories does not reflect the same organization as (other) segmentation processes (which we have previously defined as being critical in the process of motion interpretation), and that the integration of information about motion trajectory must therefore occur in a network of low-level motion detectors independent of these segmentation processes.

These segmentation processes are thought to be working early in visual processing (Braddick, 1988) however, which gave rise to the question how motion integration effects could arise on this level. Watamaniuk

and colleagues (1995) found that trajectory motion is highly detectable among noise because local component motion signals are enhanced when motion detectors with similar directional tuning are stimulated in a sequence along their preferred direction. Verghese and colleagues (1999) studied the detectability of brief and extended trajectories and found that there was a non-linear interaction between local motion detectors, as twice the trajectory was more than two times more detectable.

Apparently, local motion detectors feedforward information to other local motion detectors tuned for the same direction of motion. So besides hierarchical feedback modulatory mechanisms, lateral modulatory also appears to be involved in the process of motion integration (see also Angelucci & Bullier, 2003). These results are ground for more research into the exact neural implementation of this process on all levels of visual processing.

## Researching motion integration effects

Since the results of Watamaniuk & McKee (1995) and Watamaniuk and colleagues (1995) more research has been conducted into the effects of motion integration processes on perception, specifically how lateral/feedback neural mechanisms are used to integrate the outputs of local motion detectors.

**Spatial integration using contours** – Whereas the aforementioned research highlights the importance of a form of temporal integration facilitating trajectory extraction, Ledgeway & Hess (2002) used a similar approach to search for a form of spatial integration by investigating the detectability of local steady-state motion signals. Specifically, they were interested if they could investigate the rules that underlie how local motion

signals were combined to define spatial contours. They found that contours composed of elements all of which contain motion in the same direction of the contour are less detectable than contours composed of elements which contain motion in line with the contour. Moreover, it was the direction of motion rather than just the axis of motion that was important; equal ( $0^\circ$ ) or exact opposite ( $180^\circ$ ) motion was more correct detected than motion in any other angle with equal motion performing better than opposite motion.

In subsequent research using the same spatial contours, Ledgeway & Hess (2006) investigated the extent of sensitivity to specific spatial properties (namely spatial frequency and orientation selectivity) of the spatial integration process. They found that the integration process underlying the extraction of contours is very little dependent on the spatial frequency of the stimulus. Interestingly, they found that in contrast to spatial frequency cues, both orientation- and direction-based cues contribute to contour detection.

**Motion and perceived position** – A very early paper by Thorson and colleagues (1969) indicated that there is something strange about the localization of moving patterns. If any of two locations in visual space along an imaginary scale were successively stimulated with a bright dot, the second dot appeared to be displaced almost twice as far on the scale and hence the apparent movement was perceptually considerably displaced. Ramachandran & Anstis (1990) found that a stationary window containing moving patterns can, under some circumstances, be seen to be displaced in position, again indicating that the visual system uses motion systems to determine relative positions. This phenomenon even occurred when that window contained a moving grating and was phased out in the background, so there was no clear information about the location of the borders of the windows that contained the moving patterns.



Whitney & Cavanagh (2000) provided direct evidence that the localization of a physically and perceptually stationary stimulus depends on motion-processing mechanisms that are active even at some distance from the stimulus. Apparently, the influence of motion on position is not restricted to the object containing the motion.

Next to that, the position and movements of the eyes are also influencing the perceived position of an object (Ross et al, 1997; Cai et al., 1997). More recent, it was also determined that the motion of another object can alter the perceived position of other moving objects (Whitney & Cavanagh, 2002) which could not be accounted to eye movements.

## Motion direction and perceived relative position

We have seen that there is lateral modulatory involved in the motion integration process because local motion detectors are able to feedforward information to other local motion detectors tuned for the same direction of motion (Watamaniuk & McKee, 1995; Watamaniuk et al., 1995; Angelucci & Bullier, 2003). We also know that in contrast to spatial frequency cues, both orientation- and direction-based spatial cues contribute to the perception of motion (Ledgeway & Hess, 2006) and that this is most apparent when the direction of motion is in either equal or exact reversed directions (Ledgeway & Hess, 2002). Also, Whitney & Cavanagh (2000) stated that the influence of motion direction can manifest itself in the perceptually displaced position of stationary stimuli.

**Main psychophysics experiment** – In an attempt to further investigate the motion integration process we use a psychophysics experiment to look at the perceptual

effects of motion integration by measuring the differences in behavioural responses due to a dissociation between perceived position and actual physical position (e.g., due to mis-localization) of a steady-state moving grating.

When presented with two consecutively displaced stimuli consisting of such a steady-state moving grating (cf., Ledgeway & Hess, 2002; Ledgeway & Hess, 2006), we can measure their perceived relative positions using a two-alternative forced choice test. It is important that this mis-localization is not the result of changes in the population receptive field size, so we need to construct stimuli such that we keep the aperture where the displacement occurs of constant size. Also, the location of a stimulus on the retina is intuitively of great importance for the perceived position of that stimulus, so we need to make sure that the observers always fixate on a constant location in visual space using a fixation dot in the center of the aperture.

We hypothesize that observers will be perform good in reporting the actual physical relative positions of the two presented bars when they are displaced over a larger part of the stimulus aperture, but that performance drops as soon as the displacement occurs within a smaller part of the stimulus aperture (e.g., when the displacement is small as compared to when the displacement is large). When the amount of displacement drops and ultimately reaches zero degrees, we expect a motion integration process to slowly start to interfere with the perceived displacement, and use the nearby information from the motion direction to make a judgement of the bar's relative displacement.

As a result, we hypothesize that observers will perceive the second bar as more displaced towards the direction of the motion in the second bar when the motion direction in the two bars is in opposite direction, as this appears to be a condition which a large influence

on motion perception (Ledgeway & Hess, 2002). For equal motion directions between the bar presentations, we expect the responses to be constant and fairly physical accurate, e.g. we do not expect response biases to be caused by the stimuli because here they are the same.

**Eye-tracking experiment** – Watamaniuk & Heinen (1999) found some connections originating from the V5/MT area towards the areas controlling eye movements, and we earlier indicated that V5/MT might even process some visual information before it reaches V1 (Beckers & Zeki, 1995). Because the motion will also stimulate the (large) receptive field of V5/MT, this could lead to eye movements.

For the main psychophysics experiment, it is of the utmost importance that we can enforce ourselves to fixate on a specific location in the psychophysics set-up and that these eye movements do not occur, as we do not want changes in eye position to be confused with changes in visual field position.

To test for this, an eye tracking experiment was created where we displayed each of the stimulus configurations from the main psychophysics experiment. Because we use a edged fixation dot (double disc fixation dot), we hypothesize that participants are able to fixate on this dot no matter the stimulus configuration.

## Design and methods

**Subjects** – For the main psychophysics experiment, measurements were obtained from seven subjects (2 female, ages 22-29 years). For the eye tracking experiment, measurements were obtained from two subjects (both male, ages 23 and 27 years, one also participating in the psychophysics study). All subjects had normal or corrected-to-normal visual acuity and have

all been participants in a psychophysics experiment before.

**Apparatus and stimulus presentation** – Visual stimuli were generated using the PsychToolbox version 3 (Brainard, 1997; Pelli, 1997) in the Matlab 7.11 64-bit programming environment running on a Mac G4 computer. The display configuration was a regular cathode ray-tube (CRT) monitor (Iiyama 22 inch) directly in front of the subject using a chin rest and in a fully darkened room. The display output was gamma corrected. The refresh rate of the monitor was set to 60 Hz, and the resolution was set to 1024 by 768 pixels.

For the eye tracking experiment, an EasyGaze binocular eye tracker using infrared illumination with an accuracy of less than one degree visual angle from Design Interactive was used. This accuracy was deemed to be sufficient as any involuntary eye movements would probably exceed this (the offset of the stimulus was at least 2.5 degrees above the fixation dot). The (calibrated) eye tracker operated at a frequency of 53 Hz.

The stimuli in both experiments consisted of moving sine wave patterns within a bar in two consecutive stimulus presentations, with a displacement between the two presentations. These stimuli were generated on the fly using the OpenGL hardware accelerated texture presentation functionality provided by the PsychToolbox and Matlab to allow for the precise timing required in the experiment. All software was custom written.

**Stimulus description** – The bar in which the sine wave pattern moved had a width of 2 degree visual angle, and the moving sine wave pattern had a frequency of 2 cycles per degree and a speed of 3.75 degree per second. The presentation of one bar took 0.75 seconds and the bar was always presented horizontally. The circular presentation window had a radius of 7.51 degree

visual angle. On the outer 1 degree, a sine wave fade was applied to prevent hard edges. The same fade was applied to the upper and lower 1/3th edges of the bar.

In the center of the screen was a fixation dot present with a radius of 0.2 degree visual angle. This fixation was a double disc dot with in the background a grey dot having a 0.5 degree radius, causing it to appear as a border around the inner fixation dot to prevent involuntary eye movements and help fixation. The inner dot was coloured either red (need response), green (response given) or blue (indicating to press a key to start the next trial).

The pattern movement in the bar was either in upwards or downwards direction, and the presentation of the second bar was either displaced 0, 0.0625, 0.125, 0.1875, 0.25 or 0.5 degrees above or below the first bar around a vertical offset from the fixation dot of either 3.382, 4.133, or 4.885 degrees (the top most three values possible to display in the stimulus window on a logarithmic scale).

The pattern in the second bar moved either in the

same or in the opposite direction. This way, four different motion direction configurations where created (up, up; up, down; down, up; down, down). See figure 6 for an example of the stimulus.

## Eye tracking experiment

**Procedure and task** – Each subject was presented with all 132 possible previously described stimulus configurations (4 different motion direction configurations x 11 displacements x 3 bar position offsets) in random order. The task was to keep looking at the fixation dot and to press a key when the second bar disappeared.

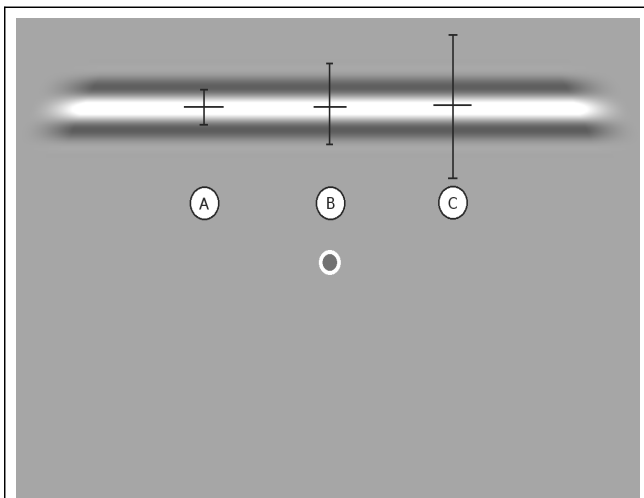
**Collected data and data analysis** – All (calibrated) eye position coordinates were logged in such a way that they could be linked to the stimulus configuration where they were recorded. The positions of the left and right eyes were average for each recording.

We will “bin” the eye positions with every bin containing the eye position measurements of one trial (e.g. 2 seconds of eye position data). For each bin, the mean X and Y fixation point and the distance of each X and Y eye position to these means will be calculated and translated to degrees of visual angle. This will result in an eye position distribution per bin which can be compared to other bins.

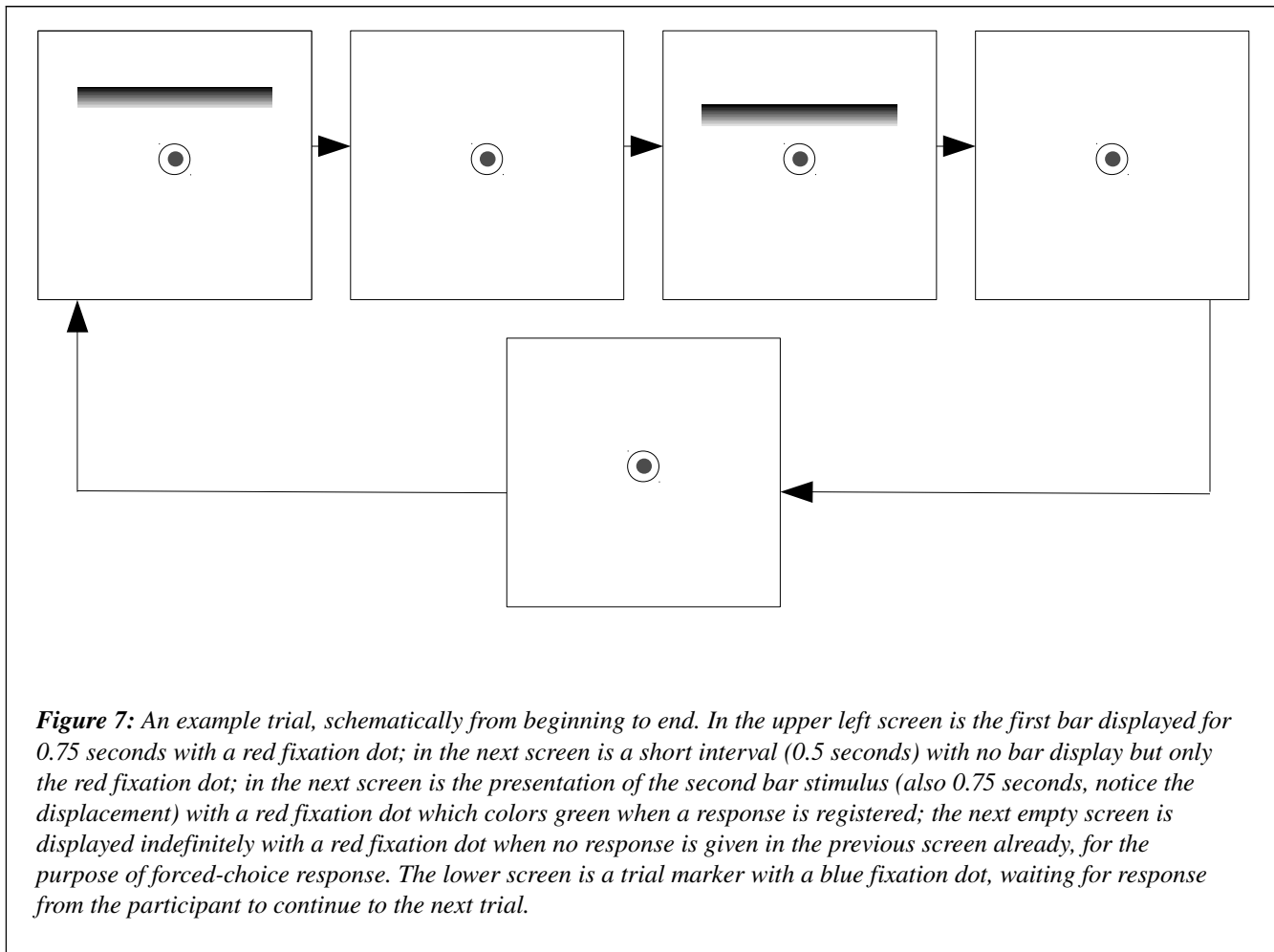
When we find bins which have significant different eye position distributions around their means, we can then determine which specific stimulus configuration elicited the eye movements and discuss that later on.

## Main psychophysics experiment

**Procedure and task** – Each subject was presented with 10 series of each 132 trials (4 different motion direction configurations x 11 displacements x 3 bar position offsets), interrupted by a break every 10% of the



**Figure 6:** Example bar stimulus with three different displacements. The center mark was the bar position measured from the fixation dot upwards; the top and bottom marks were the positions of the first and second bar presentation. The sine wave pattern had a frequency of 2 cycles per degree; in this example however it is visualized as 1 cycle per degree to enhance visibility.



trials to allow the subject to rest. This way, each subject was presented with all trials containing each of the different displacements around each of the different bar position offsets.

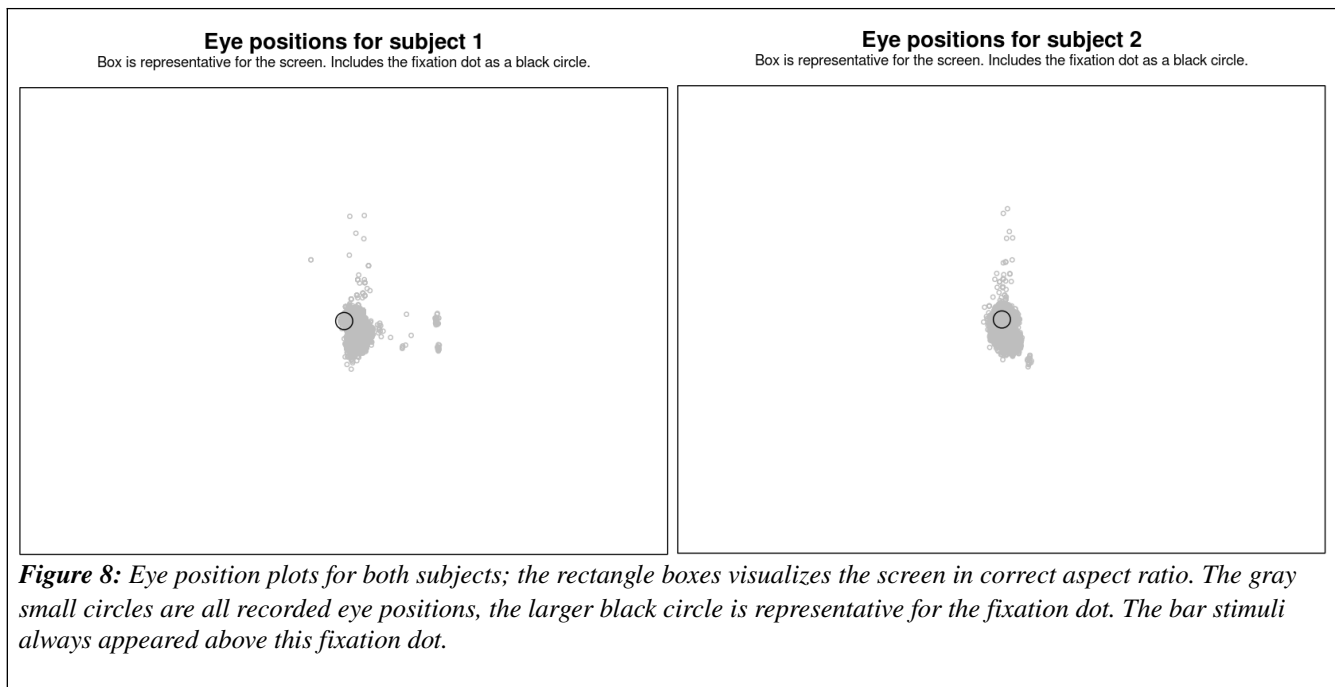
Subjects were asked to discriminate whether the second bar was presented above or below the first one, as quick as possible. Response was given in 2AFC (two alternatives, forced-choice, either 'up' or 'down' response using the arrow keys on the keyboard). A series of 16 practice trials were presented before the actual experiment. See figure 7 for the different screens in an example trial.

**Collected data and data analysis** – From the experiment, the response and response times were collected together with the different variables in one trial which were (i) the motion direction configuration of the

trial, (ii) the displacement between the two presented bars, and (iii) the vertical bar position offset as seen from the fixation dot. Data will be analysed using R and test results will be reported in APA style (see APA publication manual, 2009). Box plots will be reported in standard five-number plots with sample minimum, Q1, Q2 (median), Q3 and sample maximum. Welch's t-test df modification will be applied when required.

To test for response differences between the four different motion directions, we can use a logistic regression where we predict the probability of an 'up' response given a displacement in each of the four motion direction configurations.

Although it would be interesting to test for the effect of a motion integration process when the two consecutive bars are not displaced (because any mis-localization here could be attributed to motion integration), we use a GLM



logistic regression approach due to its increased statistical power in predicting the probability of binomial variables.

We will use this (i) to validate the assumption that the “up” responses are logistically distributed over the different displacements and can be predicted by the motion direction configuration (significance of the  $\chi^2$  test) and (ii) to test for a significant contribution of each of the four motion direction configurations to this distribution (significance of the  $e^b$  coefficient, e.g. the increase in odds ratio).

First we test this for each subject and then for each of the bar positions (which is the vertical offset from the fixation dot).

Then, we will create a full model in which we predict the “up” response using the displacement and the motion direction configuration across all subjects and all bar positions. We will test this model identically to the previous two, and use it to search for any effect sizes.

To test for effect sizes, the difference in means between the logit fitted values of a motion direction configuration and the values of a standard logistic

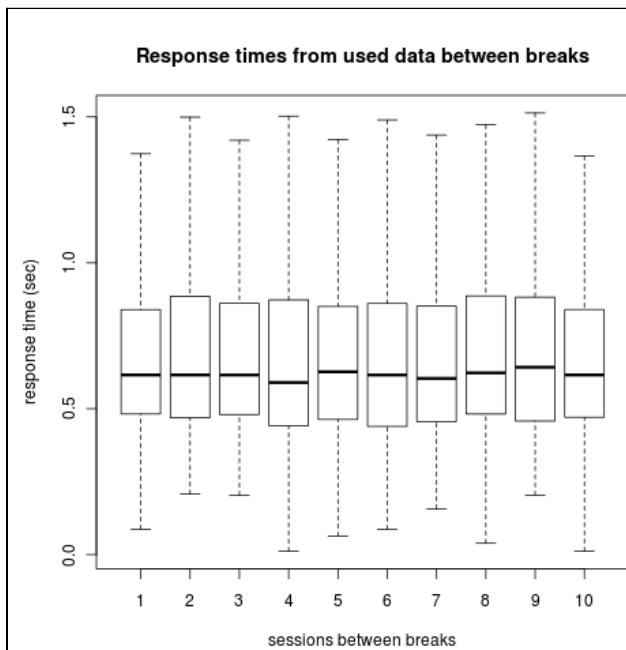
function with the same parameters can be compared using a simple t-test.

## Results

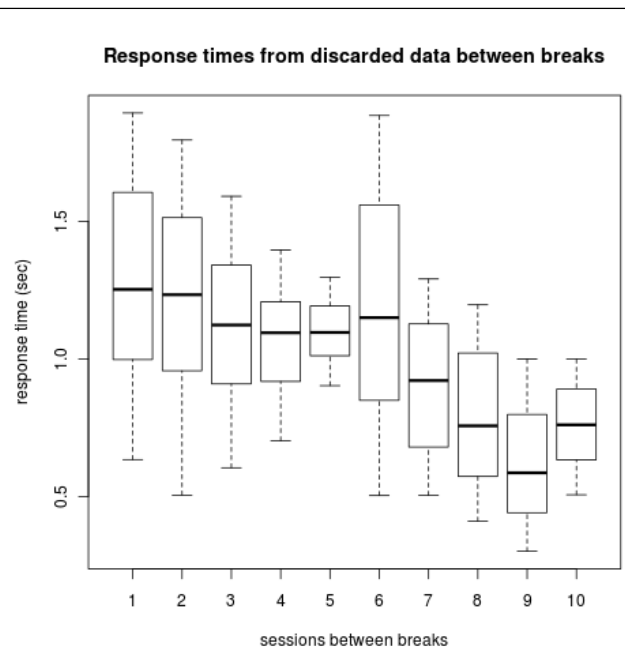
### Eye tracking experiment

Each of the two subjects was analysed separately. First, x/y position plots were generated including all eye positions recorded. See figure 8. In these plots we see most of the eye positions are in or around the fixation dot, with some positions further above (subjects 1 and 2) and some to the right (subject 1).

Using the bin calculation method, we found no differences between bins for both subject 1,  $F_{(131, 16143)} = 2.10$ ,  $p = n.s.$ , as for subject 2,  $F_{(131, 16143)} = 1.18$ ,  $p = n.s.$  This indicated that further research into the distribution of eye positions in each of the separate bins (for instance, for each of the displacements of the stimuli) was not required because the distribution across bins did not differ.



**Figure 9:** Box plot of response times of the subjects who experienced no problems. These five subjects were combined in this graph, but tested individually. The distribution of the responses seems constant across the sessions.

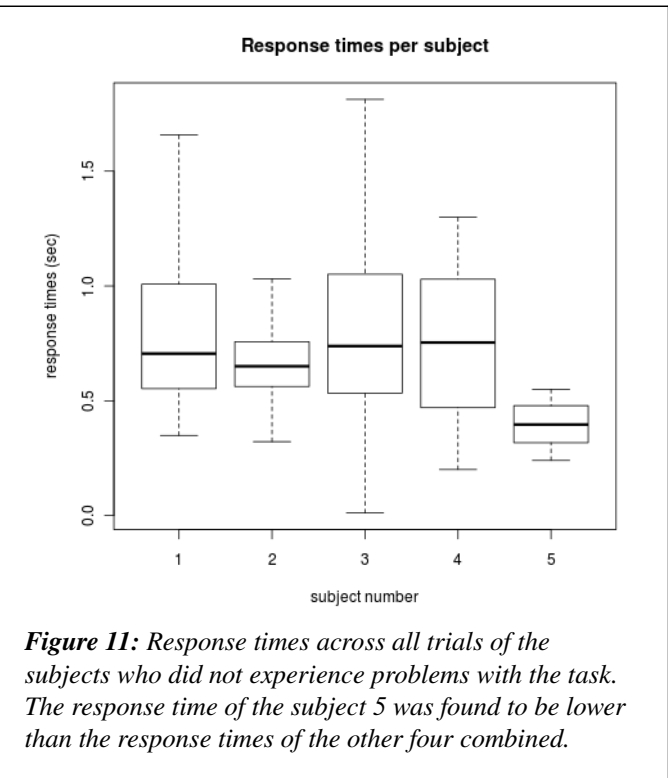


**Figure 10:** Box plot of response times of the subjects who experienced problems. These two subjects were combined in this graph, but tested individually. Compared to the graph left, you can clearly see the difference in response time distribution.

## Main psychophysics experiment

While doing the experiment, two of the seven subjects experienced dizziness and very dry eyes. One of these subjects even experienced some nausea and headache during the task. To see whether this had any influence on the results, response times from each individual subject were tested using an ANOVA to see if they significantly changed between breaks. For the two subjects who experienced problems a strong effect was found,  $F_{(9, 1310)} = 325.93$ ,  $p < .001$  and  $F_{(9, 1310)} = 401.48$ ,  $p < .001$ . The response times of these two subjects improved over time, which indicated a practice effect. As a result, the data of these two was excluded from further analysis. For the other five, no such effect was found (also see figures 9 and 10).

As described there are four motion direction configurations in our set-up. For convenience, we will name these motion direction configurations by



**Figure 11:** Response times across all trials of the subjects who did not experience problems with the task. The response time of the subject 5 was found to be lower than the response times of the other four combined.

concatenating the motion direction descriptions of the two consecutively presented bars; “DownDown”, “UpUp”, “DownUp”, and “UpDown”.

subject	DownUp		UpUp		DownDown		UpDown		Full model		
	$e^b$	$p$	$e^b$	$p$	$e^b$	$p$	$e^b$	$p$	$\chi^2$	$p$	-2LL
1	29.49	< .001	115.75	< .001	495.26	< .001	1328.17	< .001	78.4	< .001	1233.6
2	120.35	< .001	124.76	< .001	941.00	< .001	317.43	< .001	35.9	< .001	1267.3
3	1069.86	< .001	51.35	< .001	140.13	< .001	1714.17	< .001	129.9	< .001	1377.4
4	201.10	< .001	38.46	< .001	158.00	< .001	534.80	< .001	34.5	< .001	1310.5
5	1.19	n.s.	1.97	n.s.	5.65	< .001	2.34	.042	2.4	n.s.	-

**Table 1:** The results of the logistic regression for each of the subjects individually. Each of the motion direction configurations contributed significantly to the changes in “up” response per displacement in four out of five participants. The “up” responses from subject 5 could not be attributed to the displacements in the “DownUp” and “UpUp” configurations, but very slightly in the other other two configurations ( $e^b$  values near 1, indicating small changes in odds ratio for an “up” response).

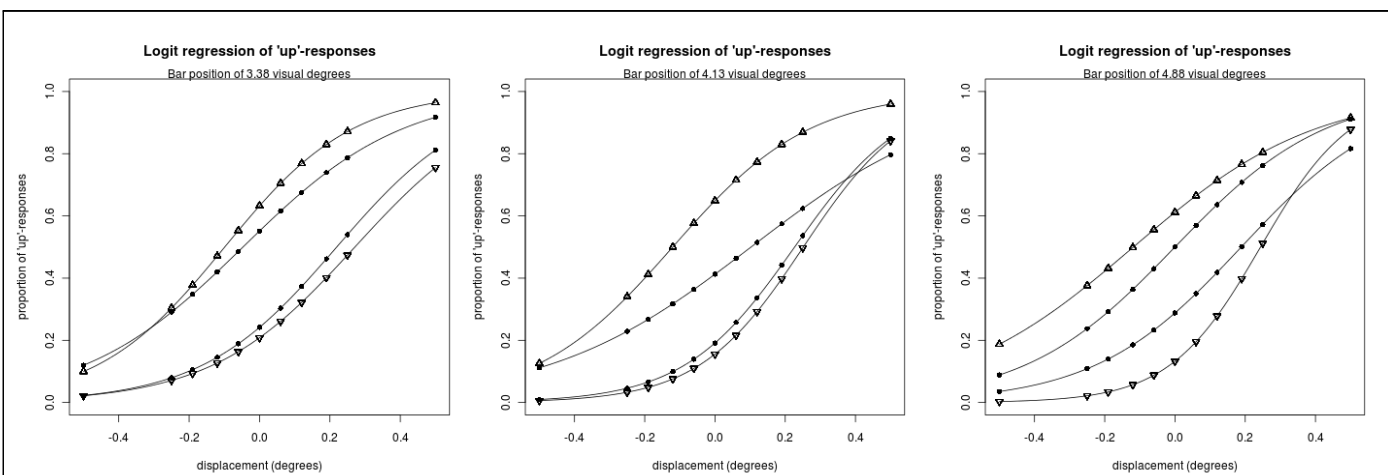
bar position	DownUp		UpUp		DownDown		UpDown		Full model		
	$e^b$	$p$	$e^b$	$p$	$e^b$	$p$	$e^b$	$p$	$\chi^2$	$p$	-2LL
3.382°	240.92	< .001	81.25	< .001	184.00	< .001	138.00	< .001	70.1	< .001	1708.8
4.133°	164.92	< .001	31.18	< .001	570.96	< .001	829.51	< .001	83.9	< .001	1747.5
4.885°	46.61	< .001	105.63	< .001	120.51	< .001	2216.62	< .001	103.8	< .001	1813.0

**Table 2:** The results of the logistic regression for each of the bar positions separately. The contribution to the responses in each of the displacements for all four motion direction configurations were significant. The fit of the model (log-likelihood, here denoted as -2LL) increases when the bar is placed further away from the fixation dot.

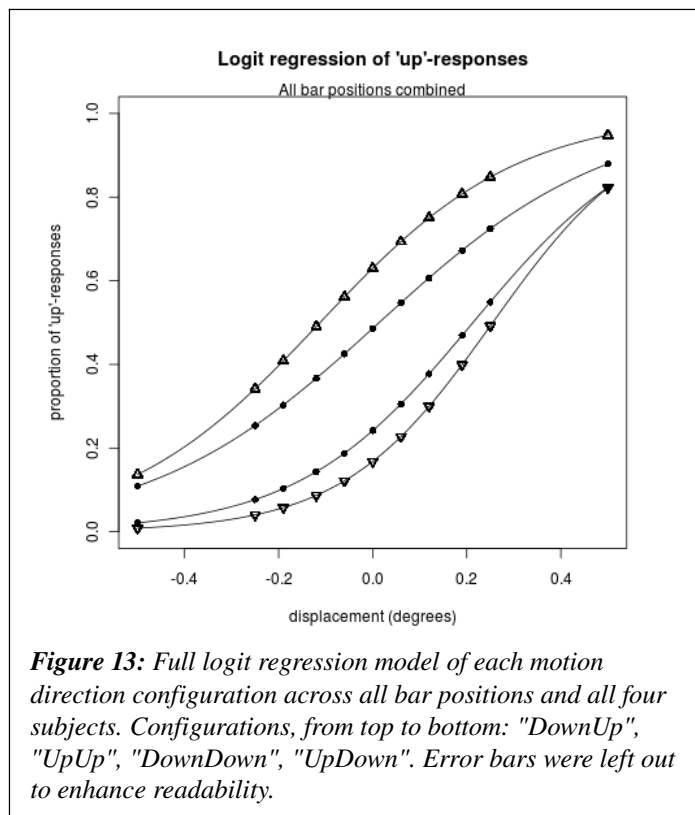
First, the logistic analysis was performed across all bar positions but separately for each subject. The logistic functions of each motion direction configuration contributed significantly to the “up” responses on the displacements for four out of five subjects, but not for the fifth subject (see table 1). For this fifth participant, only small effects in the “DownDown” configuration ( $e^b = 5.65$ ,  $p < .001$ ) and in the “UpDown” configuration ( $e^b = 2.34$ ,  $p = .042$ ) were found and not in the other two configurations. This resulted in an absence of overall effect across all motion direction configurations ( $\chi^2 = 2.4$ ,  $p = n.s.$ ). The response times from the fifth participant also appeared different from the other four (figure 11), and they were proven to be significantly lower compared to the response times of the other four combined,  $t(6368.48) = -74.58$ ,  $p < .001$ . The data from this participant was therefore left out from further analysis.

The same analysis was performed across all four remaining subjects but separately for each of the three bar positions (3.382, 4.133, and 4.885 degrees vertical offset from the fixation dot). For all of these positions, the four motion direction configurations performed significantly in explaining the probability of an “up” response across displacements (see table 2).

The overall fit of the model (e.g. across all motion direction configurations) increases with the bar position (see the -2LL values in table 2), and both the difference between “DownUp” and ”UpUp” configurations, and the difference between “DownDown” and ”UpDown” configurations appear to increase with the offset of the bar (see figure 12). This indicates that we might find a larger effect of motion integration in more peripheral areas. The differences in the motion direction effects between the different bar positions could not be



**Figure 12:** The logit regression of the responses on the displacements in each of the four motion direction configurations (from upper line to lower line: “DownUp”, “UpUp”, “DownDown”, “UpDown”), in each of the different bar positions. Error bars were left out to enhance readability. It appears that the “DownUp” and “UpUp” and also the “DownDown” and “UpDown” lines are farther apart from each other when presented further away from the fixation dot, supporting the idea of a larger effect in more peripheral areas.



**Figure 13:** Full logit regression model of each motion direction configuration across all bar positions and all four subjects. Configurations, from top to bottom: “DownUp”, “UpUp”, “DownDown”, “UpDown”. Error bars were left out to enhance readability.

statistically proven however, because all of these differences were either not significant or had a small effect size due to the small amount of samples per bar position.

We now know that motion direction contributes significantly to the responses in our task within the four

participants and on all bar positions. To test whether the four motion direction configurations were distinct from each other across any bar position and across all subjects, a GLM logistic model was created similar to the previous ones but this time including all samples.

The variance in response could be significantly explained by a full model of the displacements across all subject and all of the four motion direction configurations including each bar position ( $\chi^2 = 255.6$ ,  $p < .001$ ). Each of the motion direction configurations contributed significantly to this model;  $e^b_{DownDown} = 212.86$ ,  $p < .001$ ,  $e^b_{UpDown} = 527.16$ ,  $p < .001$ ,  $e^b_{UpUp} = 59.54$ ,  $p < .001$ , and  $e^b_{DownUp} = 115.13$ ,  $p < .001$ , see figure 13 for a plot of this model. The full model had the largest fit (as compared to each of the previous models based on either subject or bar position),  $-2LL = 5392.4$  (see also tables 1 and 2), and was therefore used to search for effect sizes.

The hypothesized constancy of the response bias was tested by comparing the “DownDown” and “UpUp” configurations (e.g. no change in motion direction between presentations). When comparing the differences in means between the logit fitted values of each of these



motion direction configurations and the values of a standard logistic function, we found an unexpected significant difference,  $t(2628.6) = -21.78$ ,  $p < .001$ , and with a medium effect size,  $r = .39$ .

A similar test was performed to test the motion integration effect by testing (i) the differences between the “DownUp” and “UpUp” configurations, and (ii) the difference between the “DownDown” and “UpDown” configurations. Here, the differences in the number of “up” responses can only be explained by the difference in motion direction and hence by the hypothesized presence of a motion integration process.

Significant effects were found with (i) “DownUp” contributing to the integration effect,  $t(2636.4) = 7.94$ ,  $p < .001$ ,  $r = .23$  as well as (ii) “UpDown”,  $t(2638.0) = -3.65$ ,  $p < .001$ ,  $r = .11$ . There also was a significant difference between these two,  $t(2632.1) = 3.02$ ,  $p < .001$ ,  $r = .24$ . It should be noted that the former two t-test statistics should be compared using their absolute (e.g. unsigned) values, as the “UpDown” effect decreases the probability for an “up” response, whereas the “DownUp” effect increases the probability for an “up” response. We can thus say that the “DownUp” effect is significantly larger than the “UpDown” effect due to the latter t-test.

## Discussion and future directions

Using a two-alternative forced-choice task where participants were asked to fixate on a stationary dot and identify the displacements of two consecutively displayed horizontal bars containing a moving sine wave grating, we tried to search for and investigate perceptual motion integration effects. We also conducted an eye-tracker experiment to see if we could fixate ourselves on the fixation dot in the stimulus configuration.

**Using the eye-tracker experiment**, we found that observers had no significantly different set of eye positions between any of the different stimulus configurations.

This tells us that in the stimulus aperture that we created, either no eye *movements* occurred because of the stimulus presentation or that there was no significant *difference in eye positions* across the stimulus configurations. Both situations however tells us that eye gazing in this particular psychophysics set-up was relatively stable, which was a important presumption to test (i) because Watamaniuk & Heinen (1999) found some connections originating from the V5/MT area (which was constantly stimulated with different stimulus configurations in our experiment) towards the areas controlling eye movements, and (ii) because we earlier indicated that this V5/MT might even process some visual information before it reaches V1 (Beckers & Zeki, 1995), thus having the possibility to induce eye movements because we constantly stimulated different V1 receptive fields.

Although not significant, an indication of this effect can still be seen in the eye position plots in figure 8, where we can see that the eye positions which were away from the fixation dot were generally always in the direction of the stimulus presentation (e.g., above the fixation dot). This is nicely visible for subject 2 in particular. For subject 1, we also see some positions located to the right of the fixation dot (again, although apparently not significant), which could be small random artefacts for example because this subject slightly rotated his head sometimes (for a review of these, see for instance Shaunak et al., 1995).

**In the main psychophysics experiment**, we hypothesized that observers will be perform good in reporting the actual physical relative positions of the two presented bars when they are displaced over a larger part

of the stimulus aperture, but that performance drops as soon as the displacement occurs within a smaller part of the stimulus aperture. In the largest displacements ( $-0.5^\circ$  and  $0.5^\circ$ ), observers had a proportion of 'up' responses which fairly resembled the true physical displacements (see figure 13). The fact that the logistic regressions for each of the motion direction configurations differed from each other was due to the variance around the  $0^\circ$  displacement condition, telling us that there is at least some effect of motion direction on the perceived relative displacement of two consecutively bars and hence validating that part of our hypothesis.

The presence of that effect was statistically proven by looking at the responses in the situation where the two consecutively displayed bar were in *equal* motion directions, and comparing it to the situation where the second of the two subsequent consecutively displayed bars was in *opposite* motion direction. This was done for (i) when the motion in the initial bars both were in the upper direction ("UpUp") and (ii) when the motion in the initial bars both were in the lower direction ("DownDown"). We found in situation (i) a significant effect with  $r = .23$  and in situation (ii) a significant effect with  $r = .11$ . This supports the idea that there is a different effect of equal and opposite motion direction on motion perception (cf. Ledgeway & Hess, 2006) and that the direction of motion, next to being critical for contour detection, is also critical in perceived relative displacement.

The two aforementioned (i) and (ii) situations were also compared and had a significant difference with (i) having a larger effect,  $r = .24$ , indicating that not only did a motion integration effect exists, but there was also difference between the two situations where we thought this effect would be visible.

One line of reasoning could be because of some sort of eccentricity effect. Higher levels of initial bar offset

appeared to give increased effects (see figure 12), although this could not be statistically proven because of the small amount of samples. The two streams hypothesis gives a supported argument for the potential cause of this effect: whereas both the ventral ("what") and dorsal ("where") pathways are processing the neural responses in the more foveal areas (cf., Sawatari & Callaway, 1996); for the more peripheral areas (higher levels of initial bar offset) this is mainly the dorsal pathway because here the influence of the ventral pathway is limited (Goodale & Milner, 1992). As the relative contribution of the dorsal pathway in these visual areas is therefore larger and because we find motion to be largely related to the dorsal pathway in literature, the increased effects of motion integration processes in the trials with a bar positioned further away from the fixation dot could be explained because here the bars are simply positioned in the more peripheral areas. This would also clutter the significant  $r = .24$  difference between "DownDown" versus "UpDown" and "UpUp" versus "DownUp" configurations, because we ignored this eccentricity data here. Future research could be conducted to statistically prove this presumption.

Another line of reasoning for this effect could be that the visual systems compensates for the neural delays of processing visual information by spatially extrapolating the bar forward in space along its expected trajectory (Nijhawan, 1994; Khurana & Nijhawan, 1995) which could have a difference of effect when it is along a trajectory leaving the foveal area as compared to a trajectory entering the foveal area again using the supporting arguments from the two streams hypothesis. However, Whitney and colleagues (2000) later showed that such a model is not tenable.

The results of Whitney & Cavanagh (2000) showing that the influence of motion direction can manifest itself in the perceptually displaced position of stationary

stimuli could also be the other way around; that the influence of the stationary object (here the fixation dot) could have some sort of effect on the moving stimuli. There might also be a temporal effect within the association field of the motion from the first and/or second consecutively presented bars in addition to the spatial effect of the motion in the first bar on the second bar (cf. Whitney & Cavanagh, 2002). The constant size of the population receptive field could also be involved here, as this potential temporal component could reside and influence anywhere and any process between for instance V1 and V5/MT. Future research could be conducted to address these kind of questions.

As to the encountered practice effect in the main psychophysics study, it is to be expected that subjects who are not used to psychophysical experiments could experience some difficulties, especially with tasks outside of the fixation area. However, the two participants who showed the practice effect and were consequently filtered out, were used to psychophysical experiments including some with tasks beyond area of fixation. Apparently, this task is very difficult to perform even after the initial practice trials. Figure 10 gives the impression that these two participants started to perform likewise to the other participants after the sixth break however, which is only after a lot of trials (~650). For subsequent studies, it might therefore be more suitable to use more experienced observers to prevent these kind of practice effects and therefore also prevent possible limitations on the data analysis.

The third participant whose data was discarded from the logistic regression analysis had no apparent problems with the task, but still performed significantly different from the other participants. It is possible that motion integration, as addressed earlier, has a temporal component and that the integration process did not yet start or that any other temporal influence was missing

when this participant gave his or her response. The significantly faster responses compared to the other participants support this idea. Also interesting to see is that this participant had an effect of motion integration only in the “DownDown” versus “UpDown” configuration, be it very small ( $e^b$  values near 1, relatively low especially compared to the other observers). Whether this has any relation with the previously stated possibility of a larger effect in the peripheral areas, or that the same hypothetical temporal component influences this, is yet unknown.

## Conclusion

Because we found a significant difference between the “DownDown” versus “UpDown” and “UpUp” versus “DownUp” configurations, we conclude that this is due to the presence of a motion integration process which results in perceived relative (mis-)localization in line with the motion direction of the second presented bar. The motion integration process appears to use the information from the motion direction to make a decision about relative displacements.

We also conclude that the stimulus set-up we used is suitable for research into the perceptual effects of motion integration because it allows us to measure these kind of processes without the confounding effect of eye movements which could potentially be confused with changes in visual field position and hence make any interpretation about perceived relative (mis-)localization difficult.

## References

- Adelson, E.H., & Bergen, J.R. (1985). Spatiotemporal energy models for the perception of motion. *Journal of the Optical Society of America A*, 2, pp. 284-299.
- Adelson, E.H., & Movshon, J.A. (1982). Phenomenal coherence of moving visual patterns. *Nature*, 300, pp. 523-525.
- Amano, K., Wandell, B.A., & Dumoulin, S.O. (2009). Visual Field Maps, Population Receptive Field Sizes, and Visual Field Coverage in the Human MT+ Complex. *Journal of Neurophysiology*, 102(5), pp. 2704-2718.
- Angelucci, A., & Bullier, J. (2003). Reaching beyond the classical receptive field of V1 neurons: horizontal or feedback axons? *Journal of Physiology*, 97(2-3), pp. 141-154.
- Beckers, G., & Zeki, S. (1995). The consequences of inactivating areas V1 and V5 on visual motion perception. *Brain*, 118(1), pp. 49-60.
- Born, R.T., & Bradley, D.C. (2005). Structure and function of visual area MT. *Annual Review of Neuroscience*, 28, pp. 157-189.
- Braddick, O.J. (1988). Contours revealed by concealment. *Nature*, 333, pp. 803-804.
- Brainard, D. H. (1997). The Psychophysics Toolbox. *Spatial Vision*, 10, pp. 433-6.
- Cai, R.H., Pouget, A., Schlag-Rey, M., & Schlag, J. (1997). Perceived geometrical relationships affected by eye-movement signals. *Nature*, 386, pp. 601-604.
- Caplovitz, G.P. , & Tse, P.U. (2007). V3A processes contour curvature as a trackable feature for the perception of rotational motion. *Cerebral Cortex*, 17(5), pp. 1179-1189.
- Cavanagh, P., & Mather, G. (1989). Motion: the long and short of it. *Spatial Vision*, 4, pp. 103-129.
- DeValois, R.L., Yund, E.W., & Helper, N. (1982). The orientation and direction selectivity of cells in macaque visual cortex. *Vision Research*, 25, pp. 1874-1884.
- DeYoe, E.A., Carman, G.J., Bandettini, P., Glickman, S., Wieser, J., Cox, R., Miller, D., & Neitz, J. (1996). Mapping striate and extrastriate visual areas in human cerebral cortex. *Proceedings of the National Academy of Sciences USA*, 93, pp. 2382-2386.
- Douglas, R.J., & Martin, K.A.C. (2004). Neuronal circuits of the neocortex. *Annual Review of Neuroscience*, 27, pp. 419-451.
- Dumoulin, S.O., & Wandell, B.A. (2008). Population receptive field estimates in human visual cortex. *NeuroImage*, 39, pp. 647-660.
- Field, D.J., Hayes, A., & Hess, R.F. (1993). Contour integration by the human visual system: evidence for a local 'association field'. *Vision Research*, 33, pp. 173-193.
- Gibson, J.J. (1979). *The Ecological Approach to Visual Perception*. Boston: Houghton Mifflin.
- Goodale, M.A., & Milner, D. (1992). Separate visual pathways for perception and action. *Trends in Neuroscience*, 15, pp. 20-25.
- Hartline, H.K. (1940). The receptive fields of optic nerve fibers. *American Journal of Physiology*, 130, pp. 690-699.
- Hess, R.F., & Field, D.J. (1999). Contour integration: new insights. *Trends in Cognitive Sciences*, 3, pp. 480-486.

- Hubel, D.H., & Wiesel, T.N. (1968). Receptive fields and functional architecture of monkey striate cortex. *Journal of Physiology*, 195(1), pp. 215-243.
- Khurana, B., & Nijhawan, R. (1995). Extrapolation or attention shift? *Nature*, 378, p. 566.
- Kovacs, I. (1996). Gestalten of today: early processing of visual contours and surfaces. *Behavioural Brain Research*, 82, pp. 1-11.
- Ledgeway, T., & Hess, R.F. (2002). Rules for combining the outputs of local motion detectors to define simple contours. *Vision Research*, 42, pp. 653-659.
- Ledgeway, T., & Hess, R.F. (2006). The spatial frequency and orientation selectivity of the mechanisms that extract motion-defined contours. *Vision Research*, 46, pp. 568-578.
- Lennie, P. (2003). The cost of cortical computation. *Current Biology*, 13, pp. 493-497.
- Movshon, J.A., Adelson, E.H., Gizzi, M.S., & Newsome, W.T. (1985). The analysis of moving visual patterns. In: C. Chagass, R. Gattass, & C. Gross (Eds.), *Pattern recognition mechanisms* (pp. 117-151). Rome: Vatican Press.
- Nijhawan, R. (1994). Motion extrapolation in catching. *Nature*, 370, pp. 256-257.
- Pelli, D. G. (1997). The VideoToolbox software for visual psychophysics: Transforming numbers into movies. *Spatial Vision*, 10, pp. 437-442.
- Rao, R.P., & Ballard, D.H. (1999). Predictive coding in the visual cortex: a functional interpretation of some extra-classical receptive-field effects. *Nature Neuroscience*, 2, pp. 79-87.
- Reichardt, W. (1961). Autocorrelation, a principle for the evaluation of sensory information by the central nervous system. In: W.A. Rosenblith (Ed.), *Sensory communication* (pp. 303-317). Cambridge: MIT Press
- Rodman, H.R., & Albright, T.D. (1989). Single-unit analysis of pattern-motion selective properties in the middle temporal visual area (MT). *Experimental Brain Research*, 75(1), pp. 53-64.
- Ross, J., Morrone, C., & Burr, D.C. (1997). Compression of visual space before saccades. *Nature*, 386, pp. 598-601.
- Ramachandran, V.S., & Anstis, S.M. (1990). Illusory displacement of equiluminous kinetic edges. *Perception*, 19, pp. 611-616.
- Sawatari, A., & Callaway, E.M. (1996). Convergence of magno- and parvocellular pathways in layer 4B of macaque primary visual cortex. *Nature*, 380, pp. 442-446.
- Shaunak, S., O'Sullivan, E., & Kennard, C. (1995). Eye movements. *Journal of Neurology, Neurosurgery & Psychiatry*, 59, pp. 115-125.
- Smith, A.T., Greenlee, M.W., Singh, K.D., Kraemer, F.M., & Henning, J. (1998). The processing of first- and second-order motion in human visual cortex assessed by functional magnetic resonance imaging (fMRI). *Journal of Neuroscience*, 18, pp. 3816-3830.
- Tanaka, K., & Saito, H. (1989). Analysis of motion of the visual field by direction, expansion/contraction, and rotation cells clustered in the dorsal part of the medial superior temporal area of the macaque monkey. *Journal of Neurophysiology*, 62, pp. 626-641.
- Thorson, J., Lange, G.D., & Biederman-Thorson, M. (1969). Objective measure of the dynamics of a visual movement illusion. *Science*, 164, pp. 1087-1088.

- Tootell, R.B.H., Mendola, J.D., Hadjikhani, N.K., Ledden, P.J., Liu, A.K., Reppas, J.B., Sereno, M.I., & Dale, A.M. (1997). Functional analysis of V3A and related areas in human visual cortex. *Journal of Neuroscience*, *17*, pp. 7060-7078.
- Tootell, R.B.H., Reppas, J.B., Kwong, K.K., Malach, R., Born, R.T., Brady, T.J., Rosen, B.R., & Belliveau, J.W. (1995). Functional analysis of human MT and related visual cortical areas using magnetic resonance imaging. *Journal of Neuroscience*, *15*, pp. 3215-3230.
- Ullman, S. (1979). *The interpretation of visual motion*. Cambridge, MA: MIT Press.
- Van Essen, D.C., & Maunsell, J.H.R. (1983). Hierarchical organization and functional streams in the visual cortex, *Trends Neuroscience*, *6*, pp. 370-375.
- Van Santen, J.P.H., & Sperling, G. (1985). Elaborated Reichardt detectors. *Journal of the Optical Society of America A*, *2*, pp. 300-320.
- Verghese, P., Watamaniuk, S.N.J., McKee, S.P., & Grzywacz, N.M. (1999). Local motion detectors cannot account for the detectability of an extended trajectory in noise. *Vision Research*, *39*, pp. 19-30.
- Wandell, B.A., Dumoulin, S.O., & Brewer, A.A. (2007). Visual field maps in human cortex. *Neuron*, *56*, pp. 366-383.
- Watamaniuk, S.N.J., & Heinen, S.J. (1999). Human smooth pursuit direction discrimination. *Vision Research*, *39*, pp. 59-70.
- Watamaniuk, S.N.J., & McKee, S.P. (1995). Seeing motion behind occluders. *Nature*, *377*, pp. 729-730.
- Watamaniuk, S.N.J., McKee, S.P., & Grzywacz, N.M. (1995). Detecting a trajectory embedded in random direction motion noise. *Vision Research*, *35*, pp. 65-77.
- Whitney, D., & Cavanagh, P. (2000). Motion distorts visual space: Shifting the perceived positions of remote stationary objects. *Nature Neuroscience*, *3*, pp. 954-959.
- Whitney, D., & Cavanagh, P. (2002). Surrounding motion affects the perceived location of moving stimuli. *Visual Cognition*, *9*, pp. 139-152.
- Whitney, D., Murakami, I., & Cavanagh, P. (2000). Illusory spatial offset of a flash relative to a moving stimulus is caused by differential latencies for moving and flash stimuli. *Vision Research*, *40*, pp. 137-149.
- Williams, D.G., & Sekuler, R. (1984). Coherent global motion percepts from stochastic local motions. *Vision Research*, *24*, pp. 55-62.
- Zeki, S.M., Watson, J.D.G., Lueck, C.J., Friston, K.J., Kennard, C., & Frackowiack, R.S.J. (1991). A direct demonstration of functional specialization in human visual cortex. *Journal of Neuroscience*, *11*, pp. 641-649.