

**Flickering illusion as a possible method for the investigation of the binding
problem**

Doctoral Thesis

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I. List of publications providing the basis and related to the topic of the thesis

I.

Kaposvári P, Bognár A, **Csibri P**, Utassy G, Sály G.
Fusion and fission in the visual pathways.

Physiol Res. 2014 Jun 5.

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II.

Kaposvári P, Csibri P, Csete G, Tompa T, Sály G

Auditory modulation of the inferior temporal cortex neurons in rhesus monkey

PHYSIOLOGICAL RESEARCH 60:(Suppl. 1) pp. S93-S99. (2011)

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III.

Csibri P, Kaposvari P, Sary G

Illusory flashes and perception.

JOURNAL OF VISION 14:(3) p. 6. (2014)

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1.Introduction

Our brain does much more than passively replicate or “reflect” the outside world based on information falling on the retina. Vision is an active process that is based on the acquired knowledge about the world we live in. There are regularities and constants, which come from daily physical laws of the world. But they are not precise applications of the physical properties, rather a range of possibilities and capabilities of organisms. For example, in the case of shading, the visual system assumes that the light always comes from above because, in the human’s ecological niche, the light usually comes from above, from the sun. Thus, the gradient change in brightness in two-dimensional, drawn circles, depending whether the top or the bottom is brighter, causes an impression of shadows in a three-dimensional spherical or concave shape (Figure. 1). These illusory experiences provide a great opportunity to examine visual perception and the neural activity underlying vision.

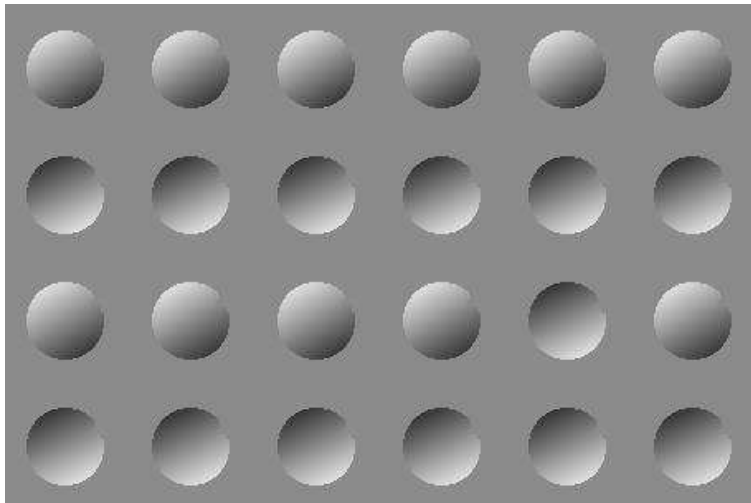


Figure 1. *Two dimensional circles on a grey background. Depending whether the perceived illumination comes from the top or from the bottom, the circles seem to be concave or convex.*

Every organism has a characteristic living environment, and every environment provides the most important stimuli for this organism. These stimuli arrive from different dimensions to be processed by the different sensory systems that have evolved to process them. A particular sensory system typically develops to sense a certain range

of stimuli and gives an unreliable or distorted “image” about stimuli outside that range. For this reason, it is easy to understand the simultaneous presence of sensory systems with different sensitivities within the same organism, since this will broaden the view of the surroundings and increases the chance of recognizing relevant events. In neuroscience, it is more and more evident that we cannot regard the brain as made up of independent, unimodal streams of information-processing pathways joining only at the association areas (Schiller, 1996). Since stimuli originate from the same “world,” they inform the organism about a given event. Linking the different modalities gives the possibility – in theory – of using the advantages of a given modality for a different one. This is called multisensory integration. Multisensory integration has several advantages in perception and action, many of which have been proven in experiments. Multisensory integration can shorten the reaction time in behavioral studies (Gielen *et al.*, 1983); it can decrease the time required for sensory encoding and motor response (Bell *et al.*, 2005); and it can also accelerate sensory processing by decreasing the sensory threshold (Rowland *et al.*, 2007). Besides enhancing behavioral reactions, it may help to detect weak or noisy stimuli as well (McDonald *et al.*, 2000). Thus, besides a more accurate perception, with the help of another modality, the seemingly separated modalities can reveal more about an event than one single modality could and in a way that the modulating effect of the other modality remains hidden from the unified perception. The complex sensation of taste, for example, is a combination of taste, olfaction, tactile, and sometimes visual modalities. In hearing, speech perception happens in a similar way, which is well demonstrated in the McGurk effect. This describes an audiovisual, multimodal effect, where the visual stimulus /GA/ combined with the auditory stimulus /BA/ is often perceived as /DA/. Thus, in speech perception, we can state that visual stimuli may modulate auditory perception (McGurk & MacDonald, 1976). Similarly, when the speaking person’s face is seen, visual stimuli might augment the perceived voice by 15–20 dB (Sumbly, 1954), which improves speech perception. The sensations produced in this way shape behavior in a progressive way, for example, helping to find prey or to estimate the speed of an approaching object. Still, planning actions or organizing motor patterns raises the same challenges as in perception (Wickens *et al.*, 1994).

This produces a challenge for our mind: we have to be able to perceive the identity of an object, even if its features arrive through different sensory organs, like seeing or touching a cube. How does the cognitive system manage the simultaneous arrival of vast amounts of information from the surrounding world? As was mentioned above, different types of information, when coupled, may give a new, qualitatively different sensation. One of the greatest challenges is the manner in which individual features are integrated into one coherent percept (Livingstone & Hubel, 1988). During my work, I tried to look for an easy-to-use, well-operationalized tool to ensure a more accurate understanding of the topic. In the next part of the thesis, I give a brief overview of the theoretical background necessary, and I examine possible uses of the so-called flicker illusions for developing further research.

2. The two phases of perception

The process of recognizing an object can be divided into two steps: first, we have to separate it from others or from the background (individualize); second, we have to identify (Identification) it. To bind the features together, first, the group of features must be determined, which will be dealt with as an object. So individualization and identity are different things, and this distinction is supported by several studies (He *et al.*, 1997; Trick & Pylyshyn, 1994).

2.1 Individualization

The individualization of an object is described, on the basis of indexing an object, by the FINST system (Pylyshyn, 2001). The foundation of the theory is given by the “object index.” Pylyshyn’s FINST theory completes other theories by trying to describe the mechanism of the earliest representation of objects. He states that there exist visual indices (earlier called FINST, from FINgers of INSTantiation) that function as signals pointing to an object but do not contain any further information about the object itself – like a finger pointing to an object without telling whether it’s red, green, oval, small, and so on. This information has to be combined with the index in a special way and can be identified only later. This enables us to draw conclusions about the so-constructed “proto object” later, during visual processing. The model works

automatically and ignores changing features. Despite recognizing sometimes an object as a different one, we do know that we deal with the same object, like when someone is approaching in the hallway and we recognize her/him only at the last second as a friend. Even if the identity of an object suddenly changes, we know that we see the same object as the one we did not recognize a moment ago. The pointing signals are distributed in a rapid, pre-attentive way, but focused attention may have an effect on them.

The indexing system has limited capabilities; however, the limits are not really known. It is believed that it is limited to four items in infants and that it can be influenced by directed attention (Phyllysyn, 1989). The indices are mainly distributed for information about location. However, the index is not used to point to the location of the object in space, but only to the target in space. The rough indices would thus perform only an initial distinction of the object. Indexing the object allows connecting the features of the object that is, binding. If the goal is to recognize the objects or use them for some actions, the features have to be bound to each index (Phyllysyn, 2001).

2.2 Identification

Information from the objects thus separated from the background. According to one of the popular theories, visual information about objects is distributed on “feature maps” during processing (DeYoe & Van Essen, 1988). This, however, raises a question, namely, how the information will be built into a solid sensation during processing? This is called the binding problem (Treisman, 1996). Despite that some studies question the physiological relevance of the binding problem (Shadlen & Movshon, 1999), psychologists published results supporting the existence of it. One example might be the illusory conjunction (Treisman & Schmidt, 1982) when shapes and colors presented to the experimental subject appear to be wrongly bound. During the test, for example, the following characters appeared briefly on the monitor: red O, blue T, and yellow X. The subject tended to see, for example, a red T, yellow O, and blue X (Treisman, 1996). Other studies have pointed out that the effect is reinforced when subjects are distracted or when the stimuli are presented in the periphery where the spatial resolution is reduced (Prinzmetal *et al.*, 1986; Prinzmetal *et al.*, 2001) and have also excluded random guessing as a possible explanation for this phenomenon (Ashby *et al.*, 1996). An increasing number of clinical studies and psychophysical tests on healthy

individuals indicate that the binding problem does exist, even in everyday clinical practice (Robertson, 2003; Friedman-Hill *et al.*, 1995; Singer, 1993). In addition, various lesion studies also confirmed the relevance of the binding problem (Frens *et al.*, 1995; Robertson, 2003).

Feature binding may thus be the most important function in perception when producing reactions to sensory stimuli. But how do different systems know which features belong to which object? One option for the solution can be Treisman's attentional focus theory (Treisman, 1996). According to this theory, there is an automatic, quick processing, which deals only with the recognition of the visual characteristics of objects in the environment. These separate features, like color or shape, are represented independently in the mental maps. The perception of one feature does not require focused attention; however, the building of objects from the features does. Constructing a complex representation of the objects is made by binding the features coded in the mental maps. The theory compares attention to a searchlight with variable focus: while moving the light through the map of perception, it binds the separate features together on the "master map of locations." Stored knowledge may influence the combination of features (e.g., red - apple). In the absence of focused attention or relevant knowledge, the features are supposed to bind in a random way, producing illusory connections in a similar way as seen in the binding problem (Treisman, 1996). We also need to have some expectations about the objects. It is known, for example, that despite temporal changes, the objects remain the same. This, however, cannot be accomplished by the searchlight model since, when the object moves from one point to another, the freshly built composition of features falls apart. This model has to be completed with a memory function that stores the constructed representations as long as they are needed.

In the object file, theory information about the features is added to the active object representation later (Kahneman *et al.*, 1992). Originating from the feature integration theory of Treisman, this model supposes the existence of a hypothetical memory structure that codes different stimulus features in episodic combinations, and all the possible combinations are coded independently but in connection with the long-term memory, in a so called "object file." Building the object file is based on the given features and our previous knowledge about the object. Moderate changes to the object

file or changes related to the whole object result in updating the file, but no new file is constructed, and the system can handle changes in the object within certain limits. Large-scale changes result in building a new object file and new object identity (Kahneman *et al.*, 1992). Learning may play an important role in this skill (Xu & Carey, 1996). There are objects that might undergo considerable changes in their features without losing their identity, like growing trees or rotating objects. These changes will be interpreted as modification or rotation of the old object but not as an appearance of a new object. Explicit perception will happen when the object file is ready. During the recognition process, sensory description will be matched to the representations stored in long-term memory. In the case of a match, the identity of the object will be added to the file together with our previous knowledge. This information will be available for cognition and may alter our behavior as well (Kahneman *et al.*, 1992).

The physiological background of these multisensory integration is unclear. Many areas of the central nervous system have been found to be capable of processing multi-sensory stimulation (Kaposvari *et al.*, 2011; Benevento *et al.*, 1977; Desimone & Gross, 1979) ; Bruce (Bruce *et al.*, 1981; Rizzolatti *et al.*, 1981; Vaadia *et al.*, 1986; Baylis *et al.*, 1987; Hikosaka *et al.*, 1988). At the cellular level, multisensory processing is defined as the significant difference between responses given to the most effective unimodal stimulus and responses given to a combination of multimodal stimuli. Thus, multisensory integration might lead to an increase or decrease in neuronal responses, leading to an increased or decreased possibility of reacting to a stimulus (Stein & Stanford, 2008).

Where are these cells located? Schneider, based on his results with hamsters, came to the conclusion that there are two parallel pathways of visual processing in mammals (Schneider, 1969; Lennie, 1980). Based on his lesion studies, he developed his theory about the parallel geniculostriate and tectal coding of visual information. This type of processing is present in the whole *vertebrata subphylum*. The tectal pathway is used mainly by phylogenetically older species while younger animals show a preference for the geniculostriate pathway. Multimodal cells can be found in both. Later, other physiological and histological results confirmed these results (Wang *et al.*, 1998; Wang *et al.*, 2001).

3. SUPERIOR COLLICULUS

The most studied area where multisensory integration occurs is the superior colliculus (SC). The SC is an ancient component of the visual tectum. It can be found in most vertebrates (Maximino, 2008). The mammalian SC consists of seven alternating layers (Kanaseki & Sprague, 1974). These are separated into three parts, based on the histological characteristics and the afferent and efferent connections (Huerta, 1984). The cells in the superficial layers receive sensory information from the eye and other sensory organs. The deep layers have motor functions that initiate eye movements and goal-oriented limb movements. Intermediate layers have a mixture of cells with multisensory and motor functions (Wallace *et al.*, 1998).

3.1 The superficial layer

The superficial layer consists of “stratum zonale” (SZ), which consist of small marginal and horizontal cells. The “stratum griseum superficiale” (SGS; “superficial gray”) consists of various shapes and sizes neurons, and the “stratum opticum” (SO; “optic layer”) consists of axons coming from the optic tract. (Mohler & Wurtz, 1976; Huerta, 1984). The three superficial layers receive input mainly from the retina (retinocollicular), vision-related areas of the cerebral cortex (primarily from the visual cortex, area 17; corticotectal), and two tectal-related structures called the pretectum and *parabigeminal nucleus* (Hall & Lee, 1997).

On the surface of the cortex, the cells are grouped into columnar units (Hall & Lee, 1997) organized into around 100 honeycomb-shaped discrete columns (Chavalier & Mana, 2000); this columnar arrangement was later confirmed by physiological results (Behan & Appell, 1992). But the functional role of this columnar architecture is not known yet.

These neurons are involved in wakefulness and maintaining attention, via their connection with the thalamic neural networks (Kaas, 1988; Luppino *et al.*, 1988; Rafal & Posner, 1987), and they play a role in the control of attention (Robinson & Kertzman, 1995). Neurons in this area show response to somatosensory, visual, and auditory

stimuli (Stein *et al.*, 1993), with an increased responsiveness to reward (Goldberg & Wurtz, 1972). This effect disappears if the connection with the cortex is interrupted (Wickelgren & Sterling, 1969; Stein & Arigbede, 1972; Berman & Cynader, 1975; Stein *et al.*, 1975; Hardy & Stein, 1988).

3.2 The deep and intermediate layers

The deep layer consists of the following. The “stratum griseum profundum” (SGP) consists of loosely packed neurons (“deep gray”), and the “stratum album profundum” (SAP) consists entirely of fibers (“deep white”). The “stratum griseum intermedium” (SGI) is filled with many neurons of many sizes (“intermediate gray”), and the “stratum album intermedium” (SAI; “intermediate white”), consists mainly of fibers from various sources (Mohler & Wurtz, 1976). The retina and the striatum give only a few projections to the deep-lying neurons. The intermediate and deep layers receive inputs from a very diverse set of sensory and motor structures (Berson & McIlwain, 1982; Beckstead & Frankfurter, 1983). Most areas of the cerebral cortex project to these layers (Clemo & Stein, 1983), but their afferentation mainly comes from two places: the lateral suprasylvian area (Heath & Jones, 1971) and a polysensory area in the anterior ectosylvian sulcus (AES). Other afferents come from the brainstem (Harting, 1977; Wallace *et al.*, 1993).

These neurons, in addition to visual-space representation, contain the somatosensory representation of the body surface (Chalupa & Rhoades, 1977; Drager & Hubel, 1975; Meredith *et al.*, 1991; Stein *et al.*, 1976; Tiao & Blakemore, 1976 and the representation of auditory space (King & Palmer, 1983; Middlebrooks & Knudsen, 1984; Wise & Irvine, 1985). The area also has a motor representation (Peck *et al.*, 1995; Guitton & Munoz, 1991; Hartline *et al.*, 1995; Wurtz & Albano, 1980). Many of these cells are able to integrate the incoming signals (Jones & Powell, 1970). Integration in the SC is not simply a linear sum of the incoming signals. Cells perform an inverse summation, where incoming, very weak signals modulate better than the presumed sum, and clean and strong signals have a weaker modulatory effect than expected (the cells’ reaction can be several times larger than the sum of responses given to the two separate

stimuli; (Meredith & Stein, 1986). This form is known as the multisensory integration, and it seems to be found all throughout the nervous system (Stein & Stanford, 2008; Meredith & Stein, 1986; Perrault, Jr. *et al.*, 2003; Stanford *et al.*, 2005).

3.3 Receptive fields

The aforesaid cells that are capable of integration have also been found in several species, for example in cats (Gordon, 1973; Meredith & Stein, 1983; Peck *et al.*, 1995), in monkeys (Jay & Sparks, 1984), and in weasels (King & Palmer, 1985). A common feature of these multisensory neurons is that they have multiple receptive fields (for example, a bimodal multisensory, audiovisual neuron has a visual and an auditory receptive field.). The two layers work in close cooperation with each other, which is also suggested by the fact that there is a special correspondence between the sensory receptive fields of the deep neurons and the visual receptive fields of the neurons in the superficial layers above (Drager & Hubel, 1975; Chalupa & Rhoades, 1977). Also, stimulating the deep layers evokes saccadic eye movements, the direction and amplitude of which correspond to the visual maps in the superficial layers (Straschill & Hoffmann, 1970; Schiller & Stryker, 1972).

The location of the receptive fields depends on the role of the sensory receptive neuron. When the receptive fields are not located on the same spot in space, we can talk about spatial correlation. In this case, there is no word for a random arrangement. Despite the receptive fields not covering the same spatial area, they are connected to each other. For example, somatosensory stimuli may arrive from the posterior surface of the leg. This part of the leg, however, can be theoretically anywhere in the visual field. Still, obviously, there is no problem binding these maps together. Therefore, the tactile and visual receptive fields, although not located in the same space, are not arranged by chance in cases when the two receptive fields show spatial agreement. Thus, information from multiple modalities of neurons come from the same point, and we can talk about a spatial registry. Such cells are found in large numbers among the auditory and visual cells (Meredith & Stein, 1996). In this case, bimodal cells have a separate but overlapping RF for each preferred modality; thus, spatial location of the stimuli is of special importance for these cells. As long as stimuli arrive

from inside this RF, cells respond with increased cellular activity (Kadunce *et al.*, 2001). In addition, the sensory maps and SC premotor receptive fields overlap with each other (Roucoux & Crommelinck, 1976; Harris, 1980; Stein *et al.*, 1980; McIlwain, 1990). So, the multimodal information is directly translatable to orientation reactions (e.g., the sensory maps in general overlap with the eye movement motor map; (Hughes *et al.*, 1994; Frens *et al.*, 1995). Thus, the same factors that determine the multisensory integration at the level of neurons can also successfully modify the behavior (e.g., the detection of orientation and attention; Stein *et al.*, 1988; Stein *et al.*, 1989).

Although all visual, auditory, and somatosensory receptive fields have an excitatory area, not all of them have an inhibitory area. The auditory receptive fields often have inhibitory zones surrounding them, but the visual and somatosensory receptive fields rarely have such zones (Meredith & Stein, 1990; Wallace & Stein, 1994). If one of the stimuli happens to be on the periphery of the RF, it suppresses cellular activity, and if it is located outside the RF, the modulating effect will be totally missing (Meredith & Stein, 1996; Meredith & Stein, 1986). This explains the phenomenon of auditory stimulus often being hampered by the visual and somatosensory responses, but the reverse is rarely observed (Meredith & Stein, 1990). This mechanism eliminates the behavioral responses as well (Stein *et al.*, 1989; Wilkinson *et al.*, 1996). Much less often, but occasionally, cells can be found that do not have an overlapping audiovisual receptive field. In this case, the two receptive field stimulations result in a strong inhibition (Stein, 1998). This mechanism ensures that information about stimuli that are in different (non-related) space are inhibited. Thus, the temporal and spatial constraints work as a filter so that only a specific stimulus ensemble is treated. As long as stimuli arrive from inside this RF, cells in the SC consider them as originating from the same location (Kadunce *et al.*, 2001).

These RFs, however, change with changes in body position; thus, other modalities are organized into an eye-centered coordinate system, and auditory RFs follow eye movements. It means that the SC sets the position of the auditory RFs according to eye movements; moving the eye in a certain direction is followed by the translocation of the auditory receptive fields into the same direction and amplitude (Hartline *et al.*, 1995; Jay & Sparks, 1984). It seems to be self-explanatory that for the integration, stimuli must arrive within a certain time window, which can be surprisingly

long, even around a hundred ms. This enables the integration of different sensory modalities arriving with different latency times resulting from different conduction speed, processing, or stimulus character (Meredith *et al.*, 1987; Recanzone, 2003). These fields can be described by a wide spectrum of sizes. Towards the periphery, the visual receptive fields become larger, up to 120 to 180 degrees (Knudsen, 1982; Middlebrooks & Knudsen, 1984; Meredith & Stein, 1986; Wallace *et al.*, 1993). There are no innate abilities. The newborn monkey's SC multisensory neurons are not able to do normal multisensory integration (Wallace *et al.*, 1997). In the process by which the newborn's body gets to know its potential effect on the surrounding environment, these neurons develop. At the beginning, integration windows have to be very close in time; during aging the temporal relationship will be more permissive.

3.4 The role of the colliculus superior

As elsewhere in the brain, function results from structure. As mentioned above, the spatial location serving as a basis for attentional and orientational mechanisms might be the deep layers of the SC (Frens *et al.*, 1995; Hughes *et al.*, 1994). This assumption is confirmed by active electrode measurements, in which a micro-excitation induces saccadic eye movements in a very short latency. The direction and amplitude of the motion depends on the location within the SC-n (Mohler & Wurtz, 1976; Robinson, 1972; Schiller & Koerner, 1971; Schiller & Stryker, 1972; Sparks, 1978; Wurtz & Goldberg, 1972; Harting, 1977; Meredith & Stein, 1986; Meredith *et al.*, 1992). It seems reasonable to assume that those stimulus configurations that increase the induced response in the SC, strengthen the attentional orientation and behavioral response also, and those that reduce cellular response, involve the reverse effect. Cats in several experimental designs were trained to look at a target mark placed in front of them. First, they were allowed to immediately approach it. In some trials, they were trained to wait until they were allowed to approach the stimulus. When visual and auditory stimuli were at the same spatial location, the animals produced far more correct responses than they did when the stimuli were presented separately. In this case, the number of correct responses was significantly increased in all animals, regardless of the type of training. However, if the auditory and visual stimuli were presented at different spatial locations, in animals that were trained to delay the response to auditory stimuli, responses to

sound were suppressed, in contrast to those that had not been trained. It is true, in this case, the responses showed some weakening (Groh, 2002). So, we can assume that strengthening or inhibition in response to afferent neurons can play an important role in strengthening or inhibiting orientation behavior (Stein *et al.*, 1988). Thus, the area might play an important role in providing the availability of common motor systems among different sensory systems (Stein *et al.*, 1976; Jay & Sparks, 1987). Thus, it can be stated that, in general, the function of the SC is the directing of behavioral reactions towards an adequate stimulus in space. The most investigated field in this respect is the mammalian eye's movements: stimuli originating directly from the retina or cortical areas produce a local maximum on the tectal map, which, provided it is strong enough, initiates a goal-oriented saccadic eye movement. In addition, it also plays a role in target-oriented limb and head movements (Lunenburger *et al.*, 2001).

The SC does not need to “recognize” the objects – cats, following the destruction of their visual cortex, could not recognize objects but could still direct their attention towards the target and follow it, albeit much slower than before the lesion. After removing only one of the SCs, cats have an urge to turn towards the lesioned side and orient towards objects on this particular side and ignore objects on the other side. The effects of the lesion improve with time, but they never disappear completely, which suggests that the SC plays a fundamental role in orientation (Sprague, 1996). These results provide an excellent background for the indexing model of FINST, which makes it possible to index objects without any information about the object or its cognitive function and without building a representation of any kind (Phylyshyn, 2001; Phylyshyn & Annan, Jr., 2006).

The SC is only one of many central nervous system structures containing multisensor cells. Inputs from different sensory modalities (exteroceptive, interoceptive, or both) have been shown already: including those that converge cells in the cerebral cortex (Benevento *et al.*, 1977; Berman, 1961; Buser & Borenstein, 1959; Clemo & Stein, 1983; Dubner & Rutledge, 1964; Dubner & Rutledge, 1965; Fallon & Benevento, 1977; Fishman & Michael, 1973; Horn, 1965; Ito, 1982; Landgren *et al.*, 1967; Loe & Benevento, 1969; Robertson *et al.*, 1975; Rutledge, 1963; Schneider & Davis, 1974; Spinelli *et al.*, 1968; Thompson *et al.*, 1963; Toldi & Feher, 1984; Wester *et al.*, 1974;), in the thalamus (Borenstein *et al.*, 1959; Chalupa *et al.*, 1975; Huang & Lindsley,

1973;), in the hypothalamus (Dafny & Feldman, 1970), in the basal ganglia (Schneider *et al.*, 1982; Wilson *et al.*, 1983), in the hippocampus (Ranck, Jr., 1973), in the inferior colliculus (Aitkin *et al.*, 1978; Tawil *et al.*, 1983), in the reticular formation (Amassian & Devito, 1954; Bell *et al.*, 1964; Scheibel *et al.*, 1955, in the cerebellum (Amat *et al.*, 1984; Freeman, 1970), and in the primary sensory nucleus (Bricout-Berthout *et al.*, 1984; Jabbur *et al.*, 1971).

4. Cortex

4.1. Physiology of the multimodal areas

Information reaching the different sensory systems is processed by the various sensory cortical areas as if the cortical sensory regions were specialized to deal with a parallel flow of information. This idea of a special multi-stimuli processing area is confirmed by several results. Combining sensory information is needed not only for the different modalities, but also within modalities. Electrophysiological recordings from monkey brain cortices showed that different neurons in different areas responded with a different intensity to different features (Maurer & McNaughton, 2007). The classic view suggests that these primary sensory areas are unimodal and information is processed through highly specialized, strictly unimodal cortical areas in a serial way and information from different modalities may be combined only in the association areas. The visual percept is constructed through two parallel cortical systems. For fine details and colors, the ventral (What?) pathway is used, while for spatial attention and speed and direction of movement, the dorsal pathway (Where?) is relevant (Mishkin & Ungerleider, 1982). We are aware that the cortical streams are functionally not separated, but this oversimplified picture might serve as a good framework facilitating an understanding of the cortical network of visually active areas. Monkey electrophysiology has revealed that the different areas within the above-mentioned pathways react with different selectivity (preferences) to different features (Felleman & Van Essen, 1991). Hierarchically higher regions, such as the inferotemporal cortex, contain cortical modules that prefer stimuli that are similar to each other (Tanaka K., 1996). These observations are consistent with clinical findings of an isolated loss of a certain sensory feature (achromatopsia, etc.; Behrmann, 2001). In addition, these results are consistent with observations that are more than one hundred years old. Different

lesions are able to damage the relatively isolated areas, and thus develop specific deficits like achromatopsia or visual neglect (Friedman-Hill *et al.*, 1995).

Recent findings support the idea that this hierarchy in the cortex is not that strict. As knowledge has accumulated concerning the structure and function of these regions, it has become clear that the sensory regions previously regarded as uniform in fact involve subdivisions that process different features in that particular sensory domain (Pigarev, 1994; Stein & Stanford, 2008; Schiller, 1996), and more and more often these areas come from lower levels of the hierarchy (Ghazanfar & Schroeder, 2006). Some of these results might be attributed to top-down effects of higher multimodal areas, but this is unlikely. When analyzing electroencephalogram (EEG) studies (EEG recording analysis), the results are more likely due not only to feedback from higher-order areas, but also to feed-forward pathways, which form multisensory integration at a very early stage. In one of the EEG studies, shortly after auditory stimuli, a marked augmentation of signals was measured over the auditory areas, which became even bigger after tactile stimulation (Murray *et al.*, 2005). This cross-modal modulation was significant after 50 ms. A similar result was reported between auditory and visual stimuli, where less than 50 ms after stimulus presentation, a multimodal modulation was found (Giard & Peronnet, 1999). These interactions are too fast to originate from feedback effects; they can play an important role in multimodal binding and shed a different light on the functions of specific sensory areas (Foxye & Schroeder, 2005).

Multimodal neurons can fulfill a very wide range of functions, and discovering their anatomical and physiological background can reveal useful information, not only about perception but also about such higher order functions as attention or the organization of goal-oriented behavior. Besides that, discovering how our brain merges information arising from different modalities can give us important information about brain structure and function. In the following, we describe the widely accepted multisensory areas in the cortex. First, the cell's properties and functions in the multisensory areas will be described. Then we review the possible ways the information-coupling mechanism works.

4.2. Heteromodal and Multimodal cortex

In the following should clarify the difference between the Hetero and the multimodal areas. Several areas in the cortex are known where projections come from different modalities. These areas are called heteromodal areas (Chavis & Pandya, 1976; Mesulam & Mufson, 1982). In these areas, neurons are able to respond to stimuli from multiple modalities as well; in this case, these areas are called multimodal areas (Kaposvari *et al.*, 2011; Benevento *et al.*, 1977; Desimone & Gross, 1979; Bruce *et al.*, 1981; Rizzolatti *et al.*, 1981; Ito, 1982; Vaadia *et al.*, 1986; Baylis *et al.*, 1987; Hikosaka *et al.*, 1988;). The responses of these cells are similar to the response of SC neurons, but differences on important points can also be found (more on this characterization of the areas will be written). This, and the fact that connection to the SC is provided not by multisensory cortical cells but by unimodal cells (Wallace *et al.*, 1993) suggests that cortical neurons may play a different role in multisensory integration.

4.3. Multimodal areas

4.3.1. Frontal eye field

The function of the SC is closest to the frontal eye field (FEF). They are involved in generating the saccadic eye movements. The microelectrode stimulation of the FEF elicits saccadic eye movements, while combined lesions of the FEF and the SC completely eliminate the saccades (Groh, 2002). In primate experiments, the multimodal characteristics of the area were described. When monkeys have to respond to visual and auditory stimuli with saccadic eye movements, many cells of the area show responsiveness to visual stimuli, but somewhat fewer cells show responsiveness to auditory stimuli. Among these cells have been identified those that also respond to visual stimuli; these cells are multisensory neurons. The receptive fields of the two modalities overlap with each other, and eye movements also play a role (Russo & Bruce, 1994).

4.3.2. Posterior parietal cortex

The posterior parietal cortex is a really interesting area regarding the integration of stimuli from an object. This area provides a sort of framework, a basis for comparison, which is able to combine features from one or more modalities and to direct the focus of attention to different points in that frame (Robertson, 2003).

The role of the area may be best understood through its lesions (Fröhlich, 1996). Partial damage here causes a characteristic syndrome known as neglect syndrome. A special case is the hemispacial neglect, where one side of the space of attention is completely eliminated. In this case, the stimuli originating from the damaged area are not or are hardly perceived (Bisiach & Luzzatti, 1978). For example, when a patient suffering hemispacial neglect was given the task of imagining that he was standing in front of the cathedral (the Piazza del Duomo in Milan) and asked to tell everything that he could recall, the test subject named objects solely on the opposite side of the injury. When he was asked to imagine that he turned around in front of the cathedral, he was able to recall the other side of the object, but he was unable to describe the previously recalled items. The reason for the inability to recall is because of the absence of this frame and the attention dysfunction (Rafal & Posner, 1987). In this case, the attention can only be directed to one side. At this time, the stimulus, which is present on the other side, produces a high proportion of illusory conjunction (Cohan, 1991). In the case of bilateral parietal lobe lesions, we are talking about Balint's syndrome (Felleman & Van Essen, 1991). In this case, as described above, when the spatial information is almost completely eliminated, the patient behaved as if he would not have a spatial frame that different information from different systems can be placed in. This is best shown in Balint's syndrome, what we call simultaneous agnosia. Although, in this case, the patients are capable of detecting an object (but only one), they do not know where to find it, and their features are mixed. The patient otherwise is able to distinguish a feature such as color because each specific cortical area works like a feature detector, but they will be unable to connect them in an appropriate manner.

A good example is the case of the patient RM, who suffered nearly symmetrical lesions in the right and left hemispheres in the parietal occipital region due to a stroke. On both sides of the calcarine cortex, the temporal lobe and the somatosensory and motor cortex remained anatomically intact, and the supra marginal gyrus of the parietal

lobe as well (Friedman-Hill *et al.*, 1995). During a test, two colored letters were shown for 10 seconds, and RM was asked to tell what color and what kind of letters he saw. In the early test phases, he produced a 38% illusory linking of shapes and colors. It is worth noting that this high rate of false connections during a long exposure time is further evidence of the binding problem, especially when we consider that RM sat right before the screen and looked at it for 10 seconds while focusing on the task. RM showed a similar illusory binding ratio presented in similar circumstances, on movement-color and shape-size relationships (Friedman-Hill *et al.*, 1995; Robertson *et al.*, 1997). The ratio of increased illusory connections in Balint's syndrome has been confirmed in other cases (Humphreys *et al.*, 2000). The area was also found to be important for the development of saccadic eye movement, but it appears to play only a secondary role (Mazzoni *et al.*, 1996).

4.3.3. Intraparietal Sulcus

The lateral intraparietal cortex (LIP) area is involved in tasks related to visual working memory (Pesaran *et al.*, 2002). Although the largest portion of the area is dedicated to visual modality, it turned out also to have a role in tactile and auditory stimuli processing as well. Among these cells, multimodal cells were found too (Guipponi *et al.*, 2013). Several studies show that cortical cells do not always follow eye movements (Schlack A, 2005). Neural network simulations suggest that these cells are critical for transforming information from one coordinate system to another, as in the above-mentioned example, from an eye-centered into a head-centered one (Snyder, 2005). So, this cortex can combine spatial coordinate information between modalities; this is called "intermodality localization." Intermodal localization of spatial information is, for example, the ventriloquist illusion, where the major role is played by the intraparietal sulcus (IPS). It is responsible for two functions: for intermodal localization and intermodal spatial attention (Macaluso & Driver, 2001; McDonald *et al.*, 2001; Lewis *et al.*, 2000; Macaluso *et al.*, 2000). This phenomenon results presumably from the function of two separate systems, since intermodal attentional effects can be triggered in such a wide time window that it is certainly outside the time frame of multisensory integration (Meredith *et al.*, 1987).

4.3.4. Anterior ecto-sylvius sulcus

The Anterior ecto-sylvius sulcus (AES) of the cat brain cortex is currently the only known visual cortical area to which visual input entirely avoids the CGL and primary visual cortex (Harting *et al.*, 1992). The main source of visual information in the CS (Norita *et al.*, 1991), has already been demonstrated in morphological experiments (Rosenquist, 1985). It consists of several, anatomically connected, separate regions, and it processes auditory (FAES) or somatosensory information (SIV). It seems that the interaction between the regions is restricted to modulation; the areas cannot evoke a response in each other. More precisely, electrical stimulation of FAES affects SIV only when SIV cells are also stimulated simultaneously. In the opposite case, electrical stimuli on FAES cells attenuate activity in SIV (Stein & Stanford, 2008). Here, the visual neurons have extremely large receptive fields, and they are most sensitive to small visual stimuli moving fast in a certain direction. Retinotopic organization was not detected (Mucke *et al.*, 1982,).

AES inputs are important in the multi-sensory integration in CS (Wallace & Stein, 1994). But the cells from here do not send direct projection to the superior colliculus (Wallace *et al.*, 1993).

It has an important role in appropriately weighting of information reliability. (Wilkinson *et al.*, 1996), in an experiment, used the visual and auditory stimuli close to detectability threshold. During testing, the animal's task was to pay attention to the target stimulus. When the visual stimulus was blurred enough to be close to the detectability threshold, performance in orientation judging could be improved by presenting an auditory stimulus at the same spatial location. Pharmacological inactivation of the AES (lidocaine injected into the AES) prevented coupling of the stimuli to the visual stimuli presented in a modality orientation. These results suggest that the AES plays an important role in linking multisensory stimuli together. This is surprising because the projection of the AES to SC starts from the unimodal neurons and not in the area of multimodal neurons.

4.3.5. These were the best-known multisensory areas

We have started to know these areas more and more, but it seems that the binding of information can be explained rather by supposing a network of areas than by the function of the individual areas. Information about a certain dimension of an object, like shape or size, is available through several modalities; for example, we can learn about the shape of an object based on tactile or visual information (Held *et al.*, 2011). The problem of Molyneux was described by John Locke. That question was of a man who was born blind and learned to distinguish between objects by touch, for example, between a sphere and a cube. When he gets back his vision, will he be able to tell which is the cube and which is the sphere just based on the sight of those two objects? John Locke believed that he would not be able to do so because vision and touch have two independent detection methods.

This centuries-old idea already raises the question of how modalities represented in (multiple) networks complement each others' information across dimensions of an object. A good example of multimodal integration is the McGurk effect, where audiovisual information contributes to better speech comprehension (McGurk & MacDonald, 1976). According to the PET study of Banati and his colleagues, a whole cortical network is responsible for the coordination of intermodal activity (Banati *et al.*, 2000). This includes the inferior parietal lobes, the superior temporal sulcus (STS) on both sides, the anterior cingulum (A), the left dorsolateral prefrontal cortex (DLPF), and the insula-claustrum on the left side. The absence of sensory dominance in the fronto-temporal cortex indicates that different cortical areas support different integrative functions. The interactions of modality-specific information are suggested to be performed by delicate and flexible mechanisms that help process the least effective key stimulus (Giard & Peronnet, 1999), while fronto-temporal areas serve general integrative functions (Foxe *et al.*, 2000). A common area in these studies, the superior temporal sulcus, probably plays a very important role in the integration of complex properties (Allison *et al.*, 2000). Thus, the combination of information is interpreted in the light of what we intend to do with it (Kveraga *et al.*, 2007).

5. Possible mechanisms of feature integration

There are several ways features can be combined, each demanding different neurophysiological background, processing information with advantages and disadvantages.

5.1 Integration through convergence

Studies in lower animals, such as insects, reveal that a single neuron or a small group of neurons can represent a complex stimulus pattern (Hommel, 2004). These cells resemble the “grandmother cells”; they have a fixed connection pattern, and they can react to complicated feature patterns like determining the direction of flight from optic flow (Gross, 2002). Feature integration of this kind might be very rigid and expensive, or it can be very fast and capable of parallel processing with constant results.

The foundation of a system like that is a couple of coincidence detectors. This is a neurological unit, responding selectively to a given combination of features or stimulus patterns. The system is based on feature-selective detectors, which respond to, for example, a line segment having a particular orientation or length (De Valois & De Valois, 1980; Shapley & Lennie, 1985). A second layer of neurons, positioned on a higher level of the hierarchy, connects to these units playing the role of coincidence detectors and receiving converging input from the lower layer. Provided the coincidence detectors have a sufficiently high activation threshold, the activity of these cells indicates the presence of certain features in the environment (Singer & Gray, 1995). In order to operate this system, several conjunction neurons are needed, each of which monitors only a small section of space. A good conjunction can be achieved only if the feature arrives from a given location within a given time, and different objects will be stored in different registry fields. This makes the coding of complex objects possible.

Perception is continuous; thus, for accurate perception, the system has to be able to combine information in space and in time. Coupling sensory information separated in time can also be explained by the aforementioned, convergence-based system. Cells have been found which are able to represent temporal patterns to code an event in time. In the visual system, for example, a single cell may represent the speed and direction of movements (Newsome *et al.*, 1990). In the auditory system as well, cells have been found which code temporal patterns in a similar way, like the pitch of a sound (Scheich,

1991). Sensory and motor reactions are thus built from the sum of elementary parts. Different features form the sensory elements, combined in a solid representation of the object, while individual, spatially and temporally coordinated, separated, individual muscle fibers build motor responses.

In a system like this, cells have well-defined, fixed connections and probably use firing-rate coding to indicate the stimulus preference. Firing rate is related to stimulus preference – the better the stimulus “fits” the cell, the higher the response rate or baseline activity inhibition (Barlow, 1972). Neural systems like that can be found in higher animals, like primates, but are usually found on lower levels of the nervous system. This mechanism, however, cannot explain all the questions regarding perception. First of all, it is too rigid – learning might be possible but might be too slow and within narrow limits. Secondly, there are more things and features to code than neurons available to do the job. Last, besides face-recognizing neurons or special recognition skills due to special professions, neurons like this are difficult to identify (Baylis *et al.*, 1985) and might be extremely rare. It seems that complex constellations of features or motor responses are not determined by a single neuron. According to this, the mechanism just explained can represent different features (should they come from the same or different modalities) in perception only in the case of a group of highly important stimuli. It might be for stimulus constellations that we meet frequently, thus for which quick and reliable recognition is important for us. Naturally, the question arises, what other solutions might be available for solving the binding problem?

5.2 Integration through correlation

During electrophysiological measurements, such as the EEG, signals belong to different frequency bands. Despite these different wave activities, no clear cognitive processes were linked to EEG (Buzsaki, 2007). It is not yet clear whether causal relationship or correlation may be involved. The EEG studies have pointed out the following relationships.

- (i) Delta-band (1–4 Hz), large amplitude and a small oscillation frequency, dominant especially over the left temporal cortex. Generally, it is linked to the phase of deep NREM sleep (Timofeev & Steriade, 1996).
- (ii) Theta-band (4–7 Hz), often registered with the frontal electrodes. These oscillations are linked to the phase of encoding of spatial information in the hippocampus (Maurer & McNaughton, 2007) and have mnemonic neuronal connections (*Jensen et al., 2007*).
- (iii) Alpha-band: a fundamental wave in the waking state having a 8–12 Hz frequency, having usually higher amplitude over the occipital areas. The alpha rhythm is enhanced when the eyes are closed and at rest, and it is dominant above the occipital areas (Palva & Palva, 2007). It occurs in the waking state and is believed to be necessary to suppress stimuli that are not needed for problem-solving. Mu-wave (8–10 Hz) activity should also be mentioned within the alpha-wave activity. It is similar to the alpha activity; however, the mu wave is not desynchronized when the eyes are open, but when contralateral movements are performed. It is found mainly centrally, representing the resting state of the sensorimotor cortex.
- (iv) Beta-band: The normal range is between 18-25 Hz; the peak frequency rarely exceeds 30 Hz; it dominantly appears above the frontal cortex. Being awake with eyes open produces the main activity. It probably represents cognitive processes and is also linked to the development of motor response.
- (v) Gamma-band: oscillations have been found during feature binding (Singer & Gray, 1995) and attention or sensory selection (Fries *et al.*, 2002) or active attentional processes (Womelsdorf *et al.*, 2006; Fries *et al.*, 2001; Buschman & Miller, 2007).

Many people do not attach any special role to these different frequencies; they only link them to alertness. According to them, in general, it can be experienced during high vigilance associated with high-frequency EEG waves. During sleep, the EEG becomes slower and larger-amplitude delta waves dominate. So, there is no consensus on the role

of these waves (e.g., Ref. (Shadlen & Movshon, 1999). Nevertheless, their role emerges more and more at the level of the primary cortical areas (Schroeder & Lakatos, 2009; Lakatos *et al.*, 2007).

According to (Ettlinger & Wilson, 1990), the synthesis of information from different sensory modalities is achieved through synchronized activity between different cortical areas (see more later; cortical dynamics). The theory behind it dates back one hundred years: neuro-electrical oscillations reflect neuronal excitability (Bishop G, 1933).

The measurement of brain electrical activity using invasive methods is more precise than EEG. The invasive methods can measure the electrical activity of each of the six layers of the cortex with multielectrode arrays by local field potentials (LFP). These studies seem to support Bishop's theory. They found that "oscillations" originate from the inner and outer transmembrane currents measured in the supramarginal layer and show strong correlations with the multiunit activity (MUA; (Lakatos *et al.*, 2007). Systematic relationships between the oscillation phase and excitability were reserved for the very low frequency of 1 Hz and oscillations also (Steriade *et al.*, 1993; Contreras *et al.*, 1996; Sanchez-Vives & McCormick, 2000). Thus, several studies have supported the hypothesis that the registered wave activity is related to cell responsiveness (e.g., delta, theta, and gamma (Lakatos *et al.*, 2005). Since the wave oscillation phase represents the local excitability (see above), the current phase of the wave, wherein the stimuli reaches the processing system, determines that attenuation or amplification of the signal. In particular, if the input is close to the threshold (Fries *et al.*, 2002; Lakatos *et al.*, 2005; Womelsdorf *et al.*, 2006; Lakatos *et al.*, 2007) cells are synchronized to each other; thus, a functionally organized group is constructed.

In this model, the activity of the same neuron can participate in representing different objects at different times. Neurons, depending on the context, might form a code system that might change depending on the demands. There is no need for conjunction detectors like "grandmother cells" since the different constellations can be dynamically built from the existing features. A limited set of features can represent a wide range of complex objects. From a definite number of simple components, a system can be built, and it can represent unusual patterns or perspectives, and it can resist injuries or noise (Biederman, 1987). Unlike the previous model, this system requires connections capable of adapting. A great number of connections must be available,

since in this model, the number of connections determines the degree of freedom of the possible patterns. Processing the stimuli happens in three steps. Firstly, cells coding information from a given stimulus must be identified. Secondly, these cells must be organized into a pattern. Thirdly, these groups of neurons have to be separated from each other and also from active ones. This task can be managed by synchronizing the firing pattern of the neurons that code the same event/object (Milner, 1974).

5.2.1 Primary auditory cortical synchrony in multisensory signal processing

This multi-sensory stimulus processing was investigated in cats' primary sensory cortical area. During the research, two unimodal stimulations (auditory and somatosensory) and a multi-sensory stimulation (auditory and somatosensory stimulation at the same time) were used. Using the individual auditory stimulation, according to expectations, a classical feed-forward response from the fourth layer was found. Here, the cells greatly changed their firing rate to the auditory stimulation ("stimulus-evoked response"). In the same area, responses have been described for somatosensory stimuli, starting from the supramarginal layer. In this case, a barely measurable increase in firing rate was reported. To the combined ensemble of stimuli (auditory and somatosensory) in the MUA, a super-additive response was described as a multisensory cell response (Foxye *et al.*, 2000 ; Foxye & Schroeder, 2005). The higher firing rate observed in the multisensory stimulation can be explained as the ongoing oscillation and synchronization (phase-resetting) implemented by the modulation effect of somatosensory stimulation (Ghazanfar & Schroeder, 2006; Giard & Peronnet, 1999). Similar effects were found for visual input to auditory cortical processing of the primary and secondary auditory cortex (Gielen *et al.*, 1983). Not only the sensory system but also biological movements and vocalization have an explicit and predictable rhythmic pattern in processing, in which the neural responses can be arranged into oscillatory patterns (Lennie, 1980).

Following this line of thought, these results raise a question. If these oscillations play this role, what about those stimuli that conflict with their oscillation frequencies? In these highly unnatural conditions, as expected, when the task-relevant stimuli are in conflict with the low-frequency rhythms, it degrades the performance of subjects in the

task (Jones *et al.*, 2002; Praamstra *et al.*, 2006). This can be useful in the repression mechanism of distractor events and irrelevant stimuli associations.

5.2.2 Frequency ranges known to play a role in stimulus bidding

The role of different frequency ranges for the time being is still unknown; we can only make predictions and hypotheses. Well-supported data suggest that this wave synchronization helps, or is even critical for certain operations in the brain (Fries *et al.*, 2007; Fries *et al.*, 2007). It appears that the gamma-wave oscillations plays an important role in the information processing but metabolically are more demanding than low-frequency oscillations (Mukamel *et al.*, 2005; Niessing *et al.*, 2005). Therefore, long-sustained gamma activity is rarely observed; it is usually entrained into a lower-frequency delta or theta oscillation (Buzsaki & Draguhn, 2004; Canolty *et al.*, 2006; Lakatos *et al.*, 2005). Due to this connection, the information processing is characterized by distinctive features. Since this mechanism of gamma activity is “entrained,” in one moment it is augmented, in the other suppressed, depending on the lower frequency. So, when the lower frequency wave is in a high-excitability phase, practically explosive responses are expected of the currently incoming stimuli.

However, regarding areas responsible for synchronization in the central nervous system, there are only guesses. According to Etlinger (1986), the cortical synchronization is coordinated by a relay like the claustrum, which connects multiple sensory systems (Pearson *et al.*, 1982). But there are data supporting the role of the rhinal cortex as well (Murray & Mishkin, 1985). However, it should be mentioned that it is not certain, that one mechanism can explain the whole system. From several studies, it is possible to conclude that a variety of intermodality tasks may be based on quite different processes (Stein *et al.*, 1993; Radeau, 1994). Different task types and complexities of the stimuli may need different stimulus-processing mechanisms.

6. Designing an experiment: design of multisensory stimuli - Raising the problem

It is obvious by now that the multisensory integration covers multiple problems. Multisensory integration is when we try to combine the information of the same object perceived through several channels, if we separate the object from the background and if

we study the interaction of several information when one information has a profound impact on the processing of another one.

Visual stimuli, presented simultaneously can interfere with each other, even if they are positioned far away from the attended stimulus. Effects on the perception of the attended stimulus can also be demonstrated if the two stimuli belong to different modalities, for example, visual and auditory (Wilson, 1987), or even visual and haptic (Ernst *et al.*, 2000; Wozny *et al.*, 2008). A high-frequency visual flicker, for instance, may change the subjectively perceived pitch of a sound (it will seem to be higher; (Welch *et al.*, 1986; Gebhard & Mowbray, 1959).

Thus, the problem is complicated, and, according to this, a large arsenal of methods was used to answer several aspects of the topics. The results, however are difficult to compare and to interpret due to the different methods and stimuli used. The first step in my work was to choose a method, based on reviewing the literature. This should be easy to use and should enable one to study the widest range of problems by changing only one parameter. I choose the flicker illusions. In the next part of the thesis I give a brief overview of the unimodal and multimodal version of the illusion and describe what kind of research was performed in order to know whether this phenomenon can be used in the planned studies.

6.1 The multimodal double-flash illusion.

A simple flash presented simultaneously with several beeps leads to the illusion of several flashes (Shams *et al.*, 2000). When two flashes are presented with just one tone, the tone can induce the perception of two flashes fusing into one (Andersen *et al.*, 2004; Watkins *et al.*, 2007). This multimodal flicker illusion or double-flash illusion has triggered several studies. It has been demonstrated that the mechanism behind this illusion is not merely a bias in the criterion level (McCormick & Mamassian, 2008), and this finding has been supported by electrophysiological studies indicating that at least some of these illusions give rise to a percept of a real second flash.

Electroencephalogram (EEG studies have revealed that the illusion-induced extra activity can be detected over the primary visual cortex (Watkins *et al.*, 2006; Watkins *et al.*, 2007). EEG results of other studies have revealed significantly higher

oscillatory activity, induced gamma-band responses, and supra-additive audiovisual interactions during such illusions (Bhattacharya *et al.*, 2002). EEG and evoked-potential experiments have led to the findings that the perception activity is strongly modulated during the illusory flash, as is the latency in trials where the illusory flash was perceived (Shams *et al.*, 2001). The fact that the potentials observed after the illusory flash were similar to those observed after real flashes indicates that the underlying neuronal mechanism is similar in both cases and is a result of a very rapid interaction between auditory and visual areas initiated by the second sound (Mishra *et al.*, 2007; Mishra *et al.*, 2008). Magnetoencephalography (MEG) experiments have shown that the activity of cortical visual areas can be modulated with sound stimuli in occipital, parietal, and anterior regions (Shams *et al.*, 2005).

FMRI data have shown illusory-flash-related brain activity in the superior colliculus, the primary visual cortex, and in the right superior temporal sulcus (STS; (Watkins *et al.*, 2006; Watkins *et al.*, 2007). Also, another group found fusion-illusion-related activity in the superior temporal cortex (Mishra *et al.*, 2008). These studies suggest that such processing of bimodal information could be based on communication between the primary visual cortex, superior temporal sulcus (STS), and primary auditory cortex (Mishra *et al.*, 2008; Watkins *et al.*, 2006; Watkins *et al.*, 2007). Since these areas serve as a target for the cortical visual streams as well, it would be interesting to know how the two visual pathways contribute to the information exchange between the primary visual cortex and, for instance, the STS.

Multimodal stimuli – especially in a temporal context – are frequently used to get a better understanding of how different modalities can combine and influence the processing of each other. The double-flash and flash-fusion illusions are appropriate phenomena to investigate the temporal aspect of audio-visual integration. Still, it is not clear which mechanisms of the visual machinery contribute to these findings. The next logical step in understanding the neuronal background of the illusory-flash phenomenon could be an approach where we make a functional distinction between the (two) cortical pathways. We are aware of the fact that this distinction (especially at levels higher than the primary visual cortex) is less and less valid, but this might serve as a good working frame for collecting more data about the double flash and flash fusion and the underlying mechanisms.

In our laboratory, we investigated the role of the magnocellular (M) and parvocellular (P) pathways in the flicker illusion. The M pathway is known for processing achromatic, low-contrast stimuli very quickly (Bullier & Nowak, 1995; Maunsell *et al.*, 1990; Merigan & Maunsell, 1993; Shapley, 1990). The M-pathway can be selectively stimulated with stimuli having low spatial frequency and low contrast; however, these weak stimuli cannot drive this pathway to the full extent (Derrington & Lennie, 1984; Kaplan & Shapley, 1986; Lee *et al.*, 1995; Leonards & Singer, 1997). According to a recent theory, the M pathway can send information into the inferotemporal cortex through the orbitofrontal areas, thus preparing it for the incoming, slower activation through the P pathway (Kveraga *et al.*, 2007).

In contrast, the P pathway conducts information about colors and high spatial frequencies with a much slower speed and needs much higher contrast (about 8% at least) when detecting achromatic stimuli (Hicks *et al.*, 1983; Tootell *et al.*, 1988). The parvocellular pathway has worse temporal resolution (Derrington & Lennie, 1984) as compared to the M pathway. (The magnocellular units in the macaque lateral geniculate body have the highest sensitivity for stimuli modulated at temporal frequencies close to 20 Hz, while the optimum for parvocellular units is close to 10 Hz.) Stimuli containing high spatial frequencies can drive this system selectively. Since the P pathway is responsible for coding color information, it can also be selectively stimulated with isoluminant color stimuli (Tobimatsu *et al.*, 1996).

The interaction-related activity of the superior colliculus (Watkins *et al.*, 2006) shows that the M-pathway is involved in audiovisual interaction. This is in accordance with observations suggesting that the enhanced visual detection can be attributed to the magnocellular system (Jaekl & Soto-Faraco, 2010; Meredith, 2002). Whether the P pathway or ventral stream contributes to the double-flash and flash-fusion illusions is unknown. In our study, we investigated the contribution of magno- and parvocellular pathways to the development of the double-flash and flash-fusion illusions.

We used pathway-specific visual stimuli. We designed stimuli that are matched to the sensitivity of the different pathways (P and M). However, we have to note that

entirely selective stimulation of the M or P pathway is not possible. High-contrast stimuli can drive both pathways strongly. Low-contrast stimuli can drive the M pathway separately, but this kind of stimulus is quite weak, so it cannot drive the whole pathway to its full extent. Both the subjective and the physical isoluminant stimuli contain color information; thus, they can drive the P pathway. In addition, the subjective isoluminant stimuli are known to be selective for the P pathway.

To separate the pathways better, we used central and peripheral stimulation. The M pathway receives information mainly from the non-central retina through the M ganglion cells. On the other hand, the P pathway receives information from the whole retina through the P ganglion cells, but the density of P ganglion cells decreases towards the periphery of the retina. Thus, the central stimulation facilitates processing through the P pathway, while peripheral stimulation drives both pathways. We used a pure, meaningless tone as input for the integration processes.

We hypothesized that the parallel pathways, in accordance with their temporal resolution, play different roles in the illusions. We found significant differences for the double-flash illusion in high contrast conditions with central and peripheral stimulations, which is consistent with previous studies. We also found a strong double-flash illusion in the pathway-specific conditions. This indicates that the incongruently added second tone can modulate the visual processing through M and P pathways and evokes the illusory perception of a second flash. In the case of the double flash, we did not find dependence on the two pathways, although this could be explained by the robustness of this illusion. The condition, which does not subserve the double-flash illusion, might be more sensitive for the differences (Kaposvari *et al.*, 2014).

With peripheral stimulation, we found a strong significance for fusion in the physically isoluminant and in the high-contrast conditions. In the high-contrast conditions, the incidence of the flash fusion is not surprising, since it can vary as described earlier, depending on the given group of participants (Mishra *et al.*, 2008). With stimuli optimized for the M pathway, we could not induce the fusion illusion. Although we did not find a significant fusion illusion in the subjectively isoluminant condition peripherally, the difference between the fusion that was found in physical

isoluminant condition and the d' level in low contrast condition was supported also by the variance analysis.

In conclusion, we found that the robust double-flash illusion can be induced in both M and P pathways. The fusion illusion can be induced in the P pathway, while the M pathway does not support it. Although the difference could be observed only at the peripheral condition, the incidence of flash fusion seems to be pathway-specific, depending on the temporal resolution of the given pathway.

6.2 Unimodal illusion

A similar phenomenon can be observed during the processing of unimodal information. In the unimodal illusory-flash effect, the perceived number of flashes of a target stimulus can be increased by an inducer flashing nearby (Chatterjee *et al.*, 2011). Such illusions are especially suited for the investigation of the temporal binding of information. The above-mentioned, so-called unimodal flicker illusion has been less researched in contrast with the illusion where two different modalities interact (double-flash illusion; (Shams *et al.*, 2001). During the flicker illusion, the inducer triggers the illusory percept. The psychophysical and neurological background is not yet clear and raises the question whether it is caused merely by the more liberal criterion answering “yes” in the presence of more than one inducer. This itself might result in more correct hits (Green, 1966). The key novelty in our paper is that we calculated the individual criterion level for each subject and determined whether the illusion appears in subsequent perceptions.

We set out to investigate the possible mechanisms and principles subserving the flicker illusion. We first clarify whether a sound is the source of a simple disturbing signal or whether it really triggers a perceived flash similar to a real flash. We then attempt to shed light on the mechanisms subserving the illusory flashes.

7. . Experiments and Methods

Experiment I

The first experiment was designed to confirm that our method could elicit an illusion; we then checked whether the triggered illusion was more than a change in the criterion level.

Methods

Participants

Eleven volunteer university students (mean age: 23.7 years, six males) with normal or corrected to normal vision participated in the experiment. All data originating from every person in every experiment was evaluated.

Setup

In all experiments stimuli were generated on an Apple MacBook Pro laptop computer (Apple, Cupertino,) in a dark room and were presented using a ViewSonic CRT monitor (21-inch, 800×600 pixel resolution, 60-Hz refresh rate; ViewSonic, Walnut,). Subjects were seated with their eyes 57 cm away from the screen to cover 1° area on the retina with the stimuli; their heads were supported by a chin rest. The experiments were run in MATLAB (MathWorks, Natick, M) using the Psychophysics Toolbox extensions (Brainard, 1997;Pelli, 1997).

Stimuli

Stimuli were high-contrast light spots of circles (diameter 1°) on a 33 cd/m^2 gray background. The subjects were asked to fixate the stimulus in the middle of the screen (target stimulus); the inducer was the other spot of circle, placed at 7° horizontally, on the periphery, to the right (Figure 2). Fixation mark was not displayed on the screen (Shams *et al.*, 2000; Chatterjee *et al.*, 2011). The target stimulus was first presented once for the duration of one frame (16 ms); the first flash of the inducer was timed simultaneously with the target onset, but a further second, third, or fourth inducer flash could be presented to induce the illusory flashes of the target stimulus. Between two flashes, only the gray background was visible for four frames (interstimulus interval, 64

ms). Depending on the number of inducer flashes (one to four), four stimulus types were used, which were presented 30 times each giving a total of 120 trials, presented in a pseudorandom order.

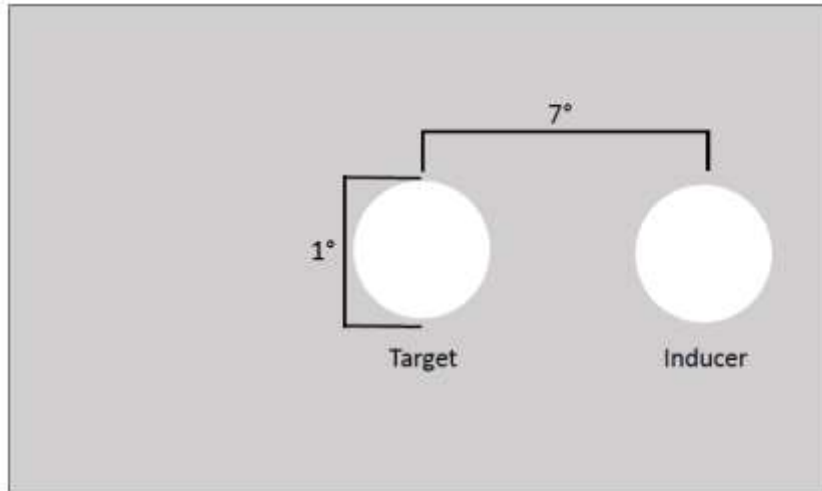


Figure 2.: Stimulus arrangement. The target stimulus on the left, located in the middle on the screen, also serves as a fixation point. The inducer (on the right) is situated 7° away, in the periphery. The diameter of both stimuli is 1°. The background is a 25% gray. Please note, that for clarity the stimulus size is largely exaggerated.

Thus, in Experiment I the following stimuli were presented: type 1, both the target and the inducer flashed once; type 2, the target flashed once, while the inducer flashed twice; type 3, the target flashed once, while the inducer flashed three times, and so forth. The task of the participants was to indicate by pressing the keyboard keys the number of perceived flashes, which could vary between one and four. The session continued, and a new trial started only once a response was given (i.e., a keyboard press was detected by the program). There was no feedback given about the correctness of the response.

Depending on the aim, the stimuli were modified in Experiments II and III, forming further conditions (see the corresponding Method sections).

In this study, the illusion presented a situation in which the subjects indicated the presence of a nonexistent stimulus (a false-positive response). In terms of signal

detection theory, this corresponds to a false alarm (F). We calculated the mean numbers of FAs in the categories for every stimulus type across subjects (FA1–4). FAs may originate from a dysfunction or “noise” in the perceptual system or from perceiving the illusory flashes of the targets. We therefore classified the FAs into two main groups. The first group contained trials in which both the target and the inducer flashed only once; there was no illusion (FA1). The second group contained trials in which the target flashed once and the inducer two, three, or four times. There were illusions in this group (FA2, FA3, and FA4). The first group was used to set a baseline for subtraction from the data on illusory groups; in this way the estimated number of illusions, phantom delta, was determined; for example, $\Delta 2 = \text{FA2} - \text{FA1}$.

Due to interindividual differences an experimental subject might be more or less susceptible to seeing an illusory flash (d'). The name d' , however, comes from signal detection theory and is used to describe the *sensitivity* (Green, 1966). In order to follow the logic of signal detection theory, we used the term sensitivity in our study, although the term *susceptibility* would have perhaps been a more appropriate expression.

Signal detection analysis was applied to calculate the sensitivity (d') and the criterion level. Criterion level calculation was based on the ration of correct hits and false alarms as described in the literature (Gardner R.M., 1984) and d' was calculated from the hit rate (H) and the distribution of the FAs via the formula $d' = z(F) - z(H)$ where z stands for the z -score. The more sensitive the system is to a signal, the higher the absolute value of d' . This allowed us to figure out what appears in the percept. The extent to which the subject tended to give a false-positive response to a nonexisting stimulus was defined by the value of c , determined from the distribution of the false-positive responses.

Throughout the study, one-way repeated measurement ANOVA with the Greenhouse–Geisser correction (Geisser S, 1958) and Dunnett's multiple comparisons tests were used (Dunnett C.W, 1955), in which the flashes of the inducers served as the main factor and the mean number of perceived flashes as the dependent variable.

Results and discussion

The method proved to be a suitable means for eliciting an illusion and in cases when an illusion was present, both c and d' seemed to decrease. A higher number of FAs was detected when the inducer flashed only once as compared to when it flashed several times; flashing the inducer twice resulted in a relatively low number of phantom flashes ($\Delta_2 = 0.187$), while three inducer flashes resulted in a considerable increase ($\Delta_3 = 0.627$; Figure 3). ANOVA indicated $F(1.549, 13.94) = 40.44$ ($p < 0.0001$) that whereas two flashes did not evoke an illusion, three and four flashes did so in about 62% of the trials. Considerable changes were detected in both d' and c if the number of inducer flashes was varied (for type 1, d' was 0.93; for type 2, d' was -0.03 , and for type 3, d' was -1.55), while the corresponding values of c were 0.47, 0, and -3.18 , respectively, demonstrating that change in c played a substantial role in the number of reported flashes. Accordingly, our method was capable of inducing illusory flashes. The fact that several flashes of the inducer resulted in changes in both c and d' suggested that the perception of several flashes of the target stimulus cannot be explained solely by the more “liberal” tendency to report more than one flash.

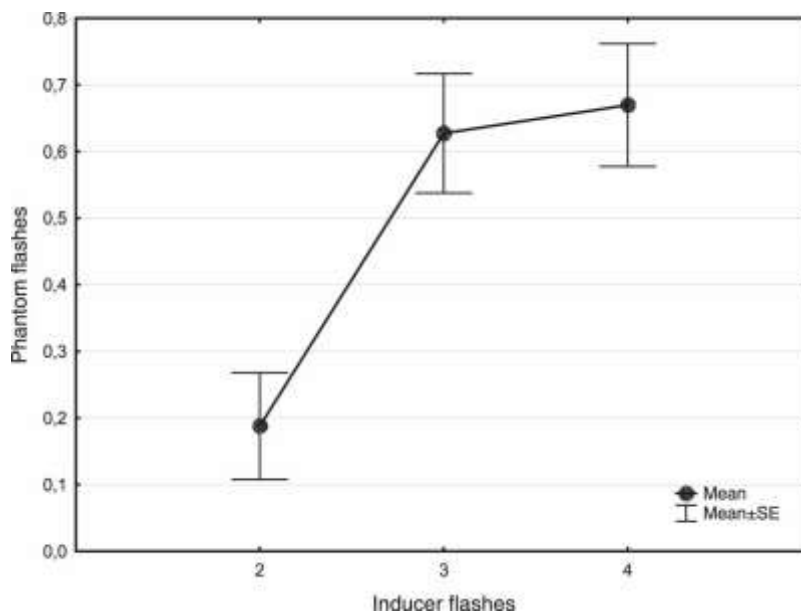


Figure 3.: The mean number of phantom flashes as a function of the number of inducer flashes. Ordinate: mean number of phantom flashes (Δ). Abscissa: number of inducer flashes. Data points are means \pm SEM.

Experiment II

In Experiment I we checked whether the target and the flicker illusion produced the same perceptual experience. Next we investigated whether the illusory flashes had the same or opposite polarity as the preceding (target) stimulus. Polarity in this case meant a difference in brightness relative to the background (Figure 3).

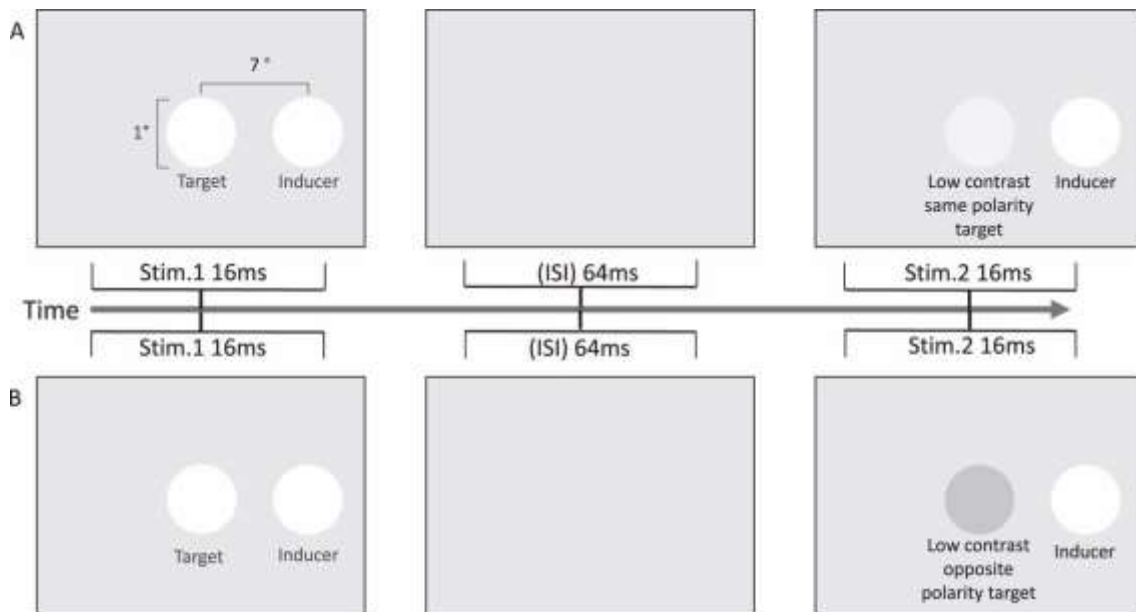


Figure 4.: Stimulus arrangement in Experiment II. The figure shows the stimuli used in the light condition, in which the first stimulus was a light spot of circle with high contrast. Please note, that for clarity the stimulus size is largely exaggerated. The two subconditions show the same-polarity subcondition (A) and the opposite polarity subcondition (B). Time scale shows timing of the first stimulus, the target, simultaneously with the inducer (stimulus 1). Both were presented for 16 ms (one frame). This is followed by the interstimulus interval (ISI), which lasted for 64 ms (four frames). Stimulus 2 (target and the inducer) was presented for 16 ms (one frame). Stimulus 2 either consists of a low-contrast target, having the same polarity as the high-contrast target (A), or the opposite polarity (B). Depending on the stimulus (i.e., how many low contrast flashes are presented after the high contrast flash), stimulus 2 can be presented zero to three times.

In sensory integration one stimulus frequently predominates over the other one; this predominance is probably also present in the case of congruent stimuli, but the phenomenon is usually investigated for incongruent stimuli (Stein & Stanford, 2008). Stimuli can be modified in such a way that, after the first flash of the target, the target continues to flash simultaneously with the inducers. If illusory flashes have the same polarity as the target stimuli, then a second, (low-contrast) target stimulus that matches the polarity of the first, high-contrast stimulus may be supported by the illusory flash, while a second, (low-contrast) target stimulus with the opposite polarity might be attenuated by the illusory flash.

Experiment II was designed so that the first high-contrast target stimulus was followed by low-contrast flashes of the same target stimulus that had either the same (same-polarity subcondition) or the opposite polarity (opposite-polarity subcondition), while the inducer was used to trigger the illusion as described previously (Figure 4). It is important to note that in this experiment Δ depended not only on the phantom flashes but additionally on the existing, low-contrast flashes as well. Thus, similar to the previous experiment, significant differences between the stimulus types proved that the low-contrast value of the target flashes had been successfully set around the perceptual threshold. According to our hypothesis, the perception induction of the illusion would differ under the same-polarity and opposite-polarity subconditions.

Methods

Participants

Ten new volunteer subjects, university students (mean age: 23.9 years, four males) with normal or corrected to normal vision participated in the study. All subjects and all results were included in the statistics.

Stimuli

The stimuli used in Experiment I were modified: after the first flash of the target, the target continued to flash on its original location simultaneously with the inducers, but it was changed to have a lower contrast.

Two conditions were produced this way. If the first flash of the target was physically brighter than the background, the condition was called bright, and if it was darker than the background, it was called dark. In terms of Weber's law, in the first condition the stimulus had a positive contrast value, while in the second it had a negative contrast value.

Each of the conditions had two subconditions. Depending on whether flashes following the first flash of the target had the same polarity (i.e., in the bright condition, they were still brighter than the background) or not, they were called same-polarity and opposite-polarity subcondition, respectively.

Thus, in the first (bright) condition the first, high-contrast “target” (lighter than the background) flash was followed by low-contrast target flashes, with either the same (same-polarity subcondition) or the opposite (opposite-polarity subcondition, Figure 3) polarity as compared to the first target flash.

In the second (dark) condition, the first, high-contrast (darker than the background) flash was followed by a low-contrast flash, with either the same (same-polarity subcondition) or the opposite polarity (opposite-polarity subcondition). Depending on the number of inducer flashes each of the subconditions contained four stimulus types, as described in Experiment I and were presented in a pseudorandom order.

Stimuli having a high contrast are easy to separate from the background (ceiling effect), while success rate in separating stimuli having a low contrast is only 79.37% (KingdomA.A.F, 2009). For every participant, contrast values were individually determined in a pilot experiment, for both the light and the dark conditions. In this test, the participants had to report when the target stimulus flashed more than once. When the contrast was determined, the high-contrast target stimulus and the peripheral inducer were always flashed; in 50% of the trials, a second stimulus was flashed at the location of the target stimulus the parameters of this second stimulus varying with the performance of the participants. In this way, the contrast value of the second flash stimulus was determined for both the light and dark, same-polarity conditions. Inducers were flashed one to four times. The inducer was not modified in this experiment.

Results and discussion

While evaluating the results, we investigated the detectability of low-contrast flashes, with the same or opposite polarity following the high-contrast flashes.

In the light condition, in which the first flash was brighter than the background, in the same-polarity subcondition one flash of the inducer resulted in $\Delta = 0.163$, two flashes resulted in $\Delta = 0.521$, three flashes resulted in $\Delta = 0.957$, and four flashes resulted in $\Delta = 0.963$ phantom flashes, respectively. The numbers of phantom flashes were significantly different when compared to the one-flash case, $F(1.544, 13.90) = 77.22, p < 0.0001$. In the subcondition involving opposite polarities, one, two, three, and four flashes of the inducer resulted in $\Delta = 0.147, \Delta = 0.421, \Delta = 0.521,$ and $\Delta = 0.731$ perceived flashes, respectively. The latter three values of perceived flashes were significantly different from that in the type 1 condition, $F(2.554, 22.99) = 23.88, p < 0.0001$. Our results confirm the literature claim (Chatterjee *et al.*, 2011) that statistically verified illusory flashes were likely to occur when the inducer is flashed three times. Figure 5 shows the separation of the lines illustrating the number of phantom flashes starting from the type 3 condition.

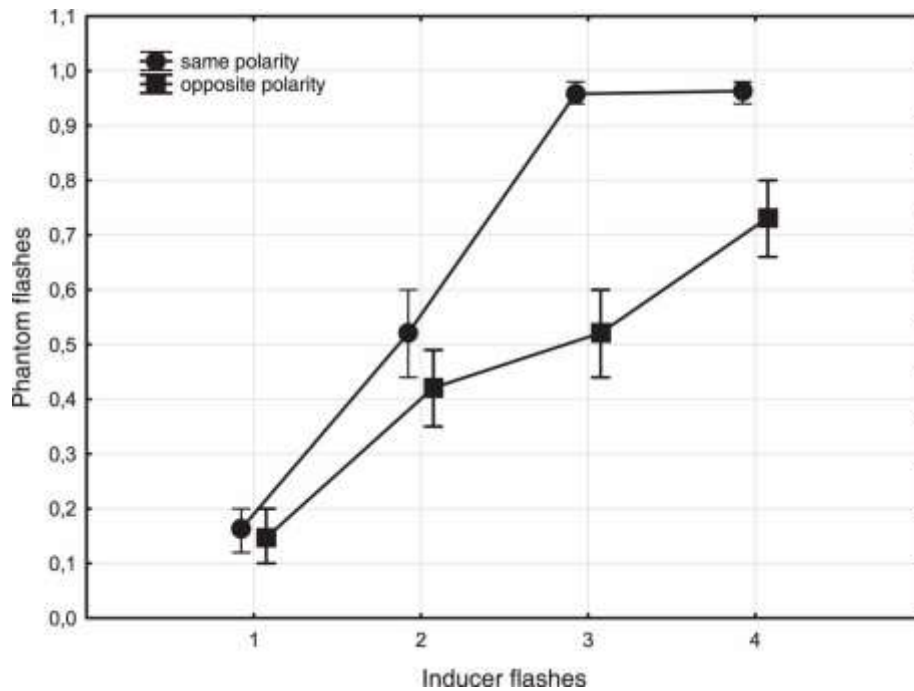


Figure 5.: The mean number of phantom flashes as a function of the number of inducer flashes in the light condition. The line with the circles relates to the subcondition in which the contrast polarity was the same as that of the flash of the target stimulus. The line with the squares relates to the subcondition in which the contrast polarity was the opposite of that of the flash of the target stimulus. Data points are means \pm SEM.

In the opposite-polarity subcondition, the detectability of the target stimulus did not change when the inducer flashed three times, but a moderate increase was seen in the case of four flashes, $F(2.554, 22.99) = 23.88, p < 0.0001$. On the other hand, in the same-polarity subcondition the number of perceived flashes in the case of three inducer flashes was significantly higher than when the inducer flashed only twice, $F(1.544, 13.90) = 77.22, p < 0.0001$. There was statistically no significant difference in the perception between the type 1 stimuli of the opposite-polarity subcondition and the same-polarity subcondition (mean difference = 0.015). Neither was there significant difference in the perception between the type 2 stimuli of the same subconditions (mean difference = 0.257). In the same subconditions, using the type 3 stimuli, however, we found significant differences (mean difference = -0.357). This was to be expected since previous results in this study indicated the emerging of the illusory flashes. Further, using the type 4 stimuli in the same subconditions resulted in significant differences as

well (mean difference = -0.568), ANOVA $F(3,72) = 4.833$, $p = 0.004$. We therefore hypothesize that the illusory flash is perceptually similar to a real flash.

In the dark condition (Figure 6), one flash of the inducer in the opposite-polarity subcondition resulted in $\Delta = 0.238$; two flashes in $\Delta = 0.691$; three flashes in $\Delta = 0.957$; and four flashes in $\Delta = 0.946$ perceived flashes. The latter three numbers of perceived flashes were significantly different from that in the one-flash condition, $F(1.714, 15.42) = 44.18$, $p < 0.0001$. In the same-polarity subcondition, one flash of the inducer resulted in $\Delta = 0.163$; two flashes in $\Delta = 0.466$; three flashes in $\Delta = 0.893$; and four flashes in $\Delta = 0.925$ perceived flashes. The latter three numbers of perceived flashes were once again significantly different from that in the one-flash case, $F(1.472, 13.25) = 42.63$, $p < 0.0001$. There was no significant difference (interaction) between the subconditions, $F(3, 72) = 1.021$, $p = 0.3885$. Since the results obtained in the two subconditions did not differ significantly, we concluded that an illusory flash was not induced in this condition, and therefore no further analysis was performed.

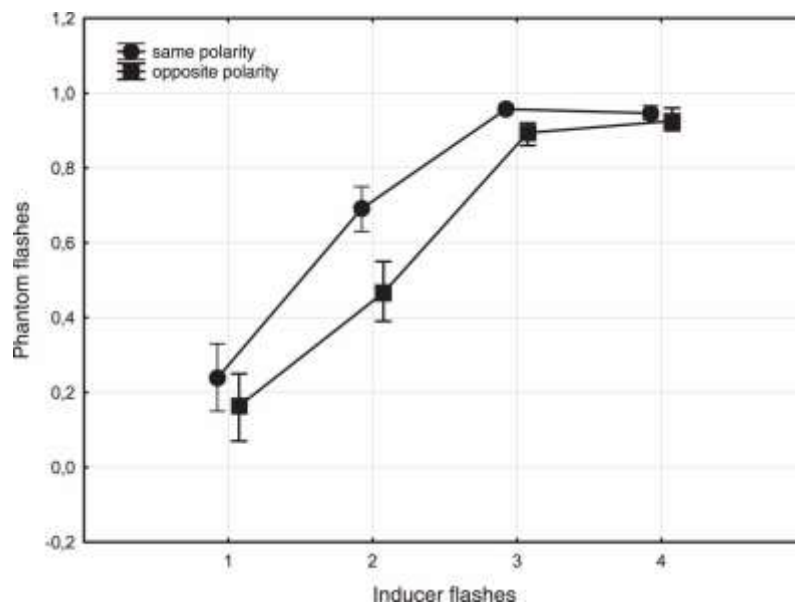


Figure 6.: The mean number of phantom flashes as a function of the number of inducer flashes in the dark condition. The line with the circles relates to the subcondition in which the contrast polarity was the same as that of the flash of the target stimulus. The line with the squares relates to the subcondition in which the contrast polarity was the opposite of that of the flash of the target stimulus. Data points are means \pm SEM.

Experiment III

This experiment was designed to determine the logic of processing behind the phenomenon. There are several potential explanations as to how one stimulus can influence the perception of another. While the modality appropriateness hypothesis explains the dominance from the receptor side, the information reliability hypothesis and the discontinuity hypothesis do so from the stimulus side (Hove *et al.*, 2013). To decide what principle is involved, we performed a factorial experiment to test these three hypotheses.

Modality appropriateness

The characteristics of the visual areas that process a particular stimulus can clearly influence the processing (Schwartz J.L., 2014). A good example in multimodal stimulus perception is when the better temporal resolution of hearing complements the processing of visual stimuli in the temporal domain (double flash illusion), or, in the opposite case, when the better spatial resolution of visual processing complements the perception of auditory stimuli (ventriloquism). In these cases, the particular modality that dominates in the given situation is usually the one with the better resolving power. According to this logic, illusions triggered in both the fovea and the periphery of the retina could argue against this hypothesis; the triggering of an illusion at the periphery of the visual field by flashes in the center would argue against the idea that better temporal resolution at the periphery promotes predominance of the center.

Information reliability

Modality predominance can also be explained by the quality of the stimuli. A predominant modality is determined not only by the more precise processing capability, but also by the reliability of the information (Welch & Warren, 1980). This is naturally closely related to the previous hypothesis, since the more accurate the processing of a given dimension in a modality, the more reliable the information will be, even if it is ambivalent. As described previously a 79.37% threshold was determined overall for the peripheral stimuli, and this was used as low-contrast stimulus for the tests. Theory predicts several changes. First, the use of a low-contrast inducer should result in a weaker central illusion. Further, the illusion should also be present in the periphery

when low-contrast flashes are used, since the stimulus coming from here is less reliable if a high-contrast stimulus is used at the same time, in the center.

Discontinuity

Another explanation could be the discontinuity hypothesis (Shams *et al.*, 2002), which emphasizes the temporal parameters of the stimulus rather than the strength of the double flash illusion. According to this idea, discontinuous stimuli (individual flashes in our case) predominate in interactions, as do peripheral flashes over foveal flashes. In other words, a periodic modality has a larger impact on the sensory systems than a continuous one. This hypothesis could explain the robustness of the illusion, for an illusion should be expected at the periphery, too. If illusions follow this logic, we could expect this independent of the retinal location; several flashes on the fovea should induce illusory flashes on the periphery, and fusion should not be observed.

Methods

Participants

A new group of 10 volunteer university students (mean age: 24.1 years, four males) with normal or corrected to normal vision participated in this study. As in the previous experiments, no subjects and no data were excluded.

Stimuli

As in the previous experiments, the participants were asked to detect flashes of the target stimulus (flashed once only) in the presence of one to four flashes of the inducer. They were requested to fixate the central stimulus; the target could be the central or the peripheral stimulus. The experiment had two conditions. In the first, both the central and the peripheral stimuli had high contrasts (high-contrast condition). In the second, the peripheral stimuli had the previously individually determined contrast (low-contrast condition).

Results and discussion

The number of illusory flashes was determined as in Experiment I. To obtain the phantom flash Δ , the number of FAs under the nonillusory conditions was subtracted from that under the illusory conditions. In the first condition, type 2 stimuli resulted in $\Delta = 0.131$, type 3 stimuli in $\Delta = 0.426$, and type 4 stimuli in $\Delta = 0.442$, $F(2.244, 20.19) = 25.34$, $p < 0.0001$. Two flashes triggered flicker illusion (Figure 7A). When the target stimulus was positioned in the periphery, the illusion became weaker, but did not disappear. Two flashes resulted in $\Delta = 0.326$, three flashes in $\Delta = 0.368$, and four flashes in $\Delta = 0.315$, $F(1.977, 17.79) = 12.09$, $p = 0.0005$ (Figure 7B). In the second condition, where the target was at the center, low-contrast peripheral flashes did not induce the illusory flash ($\Delta = 0.115$), $F(1.571, 14.14) = 2.562$, $p = 0.1207$ (Figure 7C). Feedback derived from the responses of the participants to flashes at the periphery indicated that a central stimulus elicited a weak illusory flash. Two flashes resulted in $\Delta = 0.147$, three flashes in $\Delta = 0.336$, and four flashes $\Delta = 0.347$, $F(1.977, 17.79) = 12.09$, $p = 0.0005$. The low-contrast target was flashing at the periphery, and the high-contrast inducer at the center (Figure 7D). The illusion was induced both at the center and at the periphery, which supports the discontinuity hypothesis. Even though the illusion was not present when the low-contrast inducer was used, the peripherally presented, low-contrast target stimulus with the central low-contrast inducer did induce the illusion. This supports the information reliability hypothesis. The modality appropriateness hypothesis can be excluded since illusions were successfully triggered in the periphery.

To check the discontinuity hypothesis, we created a fused condition in which four flashes of the target stimulus were linked to zero to four flashes of the inducer. In accordance with an earlier report (Andersen *et al.*, 2004), we did not observe any fusion effect, $F(1, 9) = 0.008876$, $p = 0.9270$.

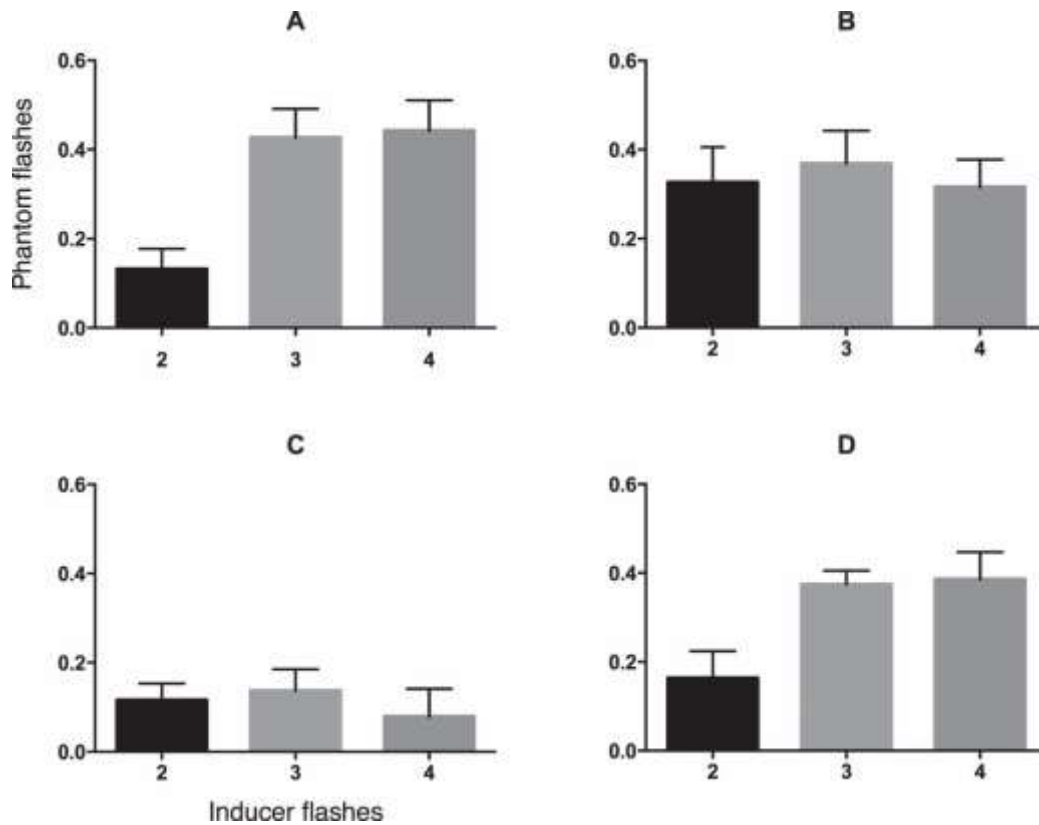


Figure 7.: The mean number of phantom flashes as a function of the number of inducer flashes in Experiment III. Columns show means \pm SEM. (A) High-contrast central target, high-contrast peripheral inducer. (B) High-contrast central inducer, high-contrast peripheral target. (C) High-contrast central target and low-contrast peripheral inducer. (D) High-contrast central inducer, low-contrast peripheral target.

8. Conclusion

Different senses collect information from different dimensions of the outside world. Vision uses light, an electromagnetic radiation that can be seen by the human eye and spreads rapidly in a straight line. Hearing uses sounds mediated by the vibrations of air. The sense of smell detects airborne chemical particles, and so on. Each sensor has different advantages and disadvantages; each of them is able to describe an object in another way.

There are permanent features of objects. There is so-called invariant information. This is a “general characteristic, such as intensity, spatial position, speed,

rhythm, texture, size, and so on. This information can be made independent of the detection system and can be interpreted in any system (Lewkowicz, 2000). The invariance of sensory modalities appears in early detection during development (Lewkowicz, 1994). In contrast, associations between intermodalities defining the object properties are not so obvious. There is no consistency between information from the various dimensions of the object, for example, without prior experience. In addition, if you have learned associations between the unimodal characteristics, it does not give any information about the other external relations. The rose's smell has no information on the visual appearance of the flower (Lewkowicz, 2000). From these different dimensions and bits of information, the picture is put together. Doing so may not only make it possible to eliminate the others' deficiencies but also can form a better picture quality, thus blurring the boundaries between the senses, as was written above already, at the level of the primary cortex. However, this does not necessarily abolish the existence the unisensory areas. Think again some more! The backbone of processing such information is in the areas of the corresponding senses. Other sensory experiences or opportunities for action or intentions only modulate these areas in the operation, even if it is substantial. It simply draws attention to the need to think with much more variability.

It is obvious from what has been spoken of above that multi-sensory stimulus processing can be modified by a great many factors. In this case, if we are unable to control the key variables or at least take them into account, it is easy to observe artifacts or misunderstand the results of others.

Studies on integration are showing more and more results. It is still difficult to see a bigger picture, due to the use of a large variability of stimulus packages. We have to consider, for example, that stimuli and tasks cannot be neglected. An important example is the complexity of the task. The more complex the task to be performed, the more complex the response expected, and the higher the latency, and the multisensory integration window also shows an increase (Karns *et al.*, 2012).

In my work, I wanted to find a tool with which the different hypotheses can be examined step by step, changing only one variable at a time. I expect that a more transparent set of experiments can be set up. The choice fell on the flicker illusions described above. In order to properly use this illusion, some basic research was needed.

In the unimodal form of the illusion, not surprisingly, and in accordance with our hypothesis, we experienced a substantial change in the responses; that is, an increase in the number of flashes of the inducers resulted in an increased probability of the indication of several flashes by the participants (McCormick & Mamassian, 2008). Moreover, our results led us to the conclusion that the increase in the number of perceived flashes in the illusory condition were based, at least partly, on a real perceptual phenomenon (a visually based decision), as in the case of multimodal, audiovisual (Shams *et al.*, 2002) and haptic visual illusion studies (Violentyev *et al.*, 2005).

Since the subcondition involving the same polarity increased the perceived number of flashes in the light condition, while the opposite polarity decreased it, we hypothesize that the illusion has a real polarity that matches the preceding flash. We may therefore reject the hypothesis of a decreased sensitivity of negative after-images behind the multiple flashes. If this were the case, the perceived number of flashes would have been increased with low-contrast flashes that had the opposite polarity to that of the high-contrast flashes.

The mechanism of the illusion might be explained by the results of the third experiment. Centrally evoked successful illusions at the periphery disprove the theory of modality appropriateness and support the information reliability theory. This seems to be in accord with the finding that the probability of inducing the illusion is clearly dependent on the reliability of the target and inducer stimuli. Stimulus reliability seems to be a factor that influences the degree of predominance in forming the percept. These results also support the stimulus discontinuity effect as a possible factor elevating the predominance of a particular stimulus, especially since we failed to detect a fusion effect. Thus, we consider that it is the stimulus continuity and reliability rather than the better temporal resolution of the periphery that lies behind the phenomenon.

Nonetheless, it must be noted, that the picture is far from complete. Attention directed to the periphery may well be a more difficult task. The components of our paradigm that were not targeted to the control of attention may have caused bias. In this case, we could not control the attentional effects.

It is well known that stimuli presented simultaneously tend to be perceived as arriving from the same source (Watanabe & Shimojo, 2001), and that stimuli processed in a parallel fashion may be linked together in a rather long temporal window (Stein & Meredith, 1990). Our illusions might rest on perceiving the stimuli from the same source. This effect is not random: faced with an ambiguous or conflicting situation, the system will build the percept based on the most reliable information.

The character of the results might also suppose the participation of subcortical structures, such as the SC, but the cause is more likely a link within the primary sensory cortex. For a better understanding of the mechanism and the neurophysiological background, EEG and single-cell recordings, currently underway in our laboratory, may be informative.

In the multimodal form of the illusion, we found that the robust double-flash illusion can be induced in both M and P pathways. The flash-fusion illusion can be induced in the P pathway, while the M pathway does not support it. Although the difference could be observed only at the peripheral condition, the incidence of flash fusion seems to be pathway-specific, depending on the temporal resolution of the given pathway. Thus the origins of activity related to the flash-fusion and double-flash illusions in the STS seem to not be identical, and it presumes different mechanisms of integration.

According to the latest results of MRI studies, the flicker illusion could produce physiological results that also draw distinct processing according to P and M pathways (during edition). Research on this topic at the moment is being conducted at the institute. The results show that the flicker illusion can be used in the field of information connection.

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