The relationship between visually guided motor behavior and visual perception

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Abstract

Neuropsychological studies prompted the hypothesis that visual information is processed in two anatomical and functional distinct streams in the primate brain. The perception versus action hypothesis states that the dorsal stream transforms visual information for the guidance of motor actions while the ventral stream uses visual information for object recognition and conscious perception (Goodale & Milner, 1992; Milner & Goodale, 1995).

Critical evidence in healthy observers was reported by Aglioti, DeSouza, and Goodale (1995). They found that grasping is not, or only little affected by visual illusions. In their study, the Ebbinghaus Illusion deceived perceptual judgments of size, but only marginally influenced the size estimates used in grasping the same objects. This dissociation between perceiving the size of an object and grasping it was interpreted as strong evidence for the perception versus action hypothesis because it assumes that mainly the ventral stream is affected by visual illusions, but not the dorsal stream.

In the present study this claim is tested extensively. A mathematical model is formulated that explicitly states the assumptions that are needed to compare the effects of visual illusions on perception and on grasping. Experiments show that the Ebbinghaus Illusion, the Müller–Lyer Illusion, and the Parallel–Lines Illusion affect maximum preshape aperture in grasping. In the Ebbinghaus Illusion there is a very good match between the perceptual effect and the grasping effect. In the Müller–Lyer Illusion the grasping effect is larger than the perceptual effect and in the Parallel–Lines Illusion it is smaller. Further experiments show that these differences can be attributed to problems in matching the perceptual task and the grasping task. Furthermore, it is shown that the larger perceptual effect that was found in previous studies for the Ebbinghaus Illusion (e.g., Aglioti et al., 1995) was most likely caused by a non–additive effect that selectively increased the effect of the illusion on perception.

The literature on the effects of visual illusions on grasping is reviewed and it is concluded that grasping reliably is affected by visual illusions. In particular, there is no evidence that grasping is *less* deceived by visual illusion than perception. This contradicts the predictions of the perception versus action hypothesis and is compatible with the more parsimonious account that the same visual signals that are used for object recognition and conscious perception are also used to guide motor actions.

Contents

Chapter 1

Introduction

Recent developments in neuroscience led to the hypothesis that visual information is processed very differently if it is used to guide motor acts than if it is used for object recognition and visual perception (Goodale & Milner, 1992; Milner & Goodale, 1995). The perception versus action hypothesis states that this division of labor in the primate brain is fundamental and can be observed in normal, healthy humans. Surprisingly, the motor system might not — or only little — be deceived by visual illusions which affect our conscious perception. For example, Aglioti, DeSouza, and Goodale (1995) reported that the effect of the Ebbinghaus Illusion was largely diminished if observers did not judge the size of an object, but grasped it. This result is consistent with the notion that the motor system "sees" something different than the perceptual system and has been counted as strong evidence for the perception versus action hypothesis. Based on the evidence presented in this study, I will argue against the existence of such a dissociation between perceiving the size of an object and grasping it.

In chapter 2 the perception versus action hypothesis and preceding hypotheses will be described. The perception versus action hypothesis assumes that visual information is processed in two anatomically and functionally distinct streams. One stream, the dorsal stream, is assumed to be specialized for transformations that are used to guide motor behavior. The other stream, the ventral stream, is assumed to be specialized for computations that are needed for object recognition and visual perception. Goodale and Milner assume that the way in which visual information is processed in the dorsal stream makes it resistant to visual illusions, while the ventral stream is affected by visual illusions.

Chapter 3 will focus on the methodological question how it is possible to compare the effects of visual illusions on grasping and on perception. To do so, one has to compare two different dependent variables, one being a measure for the motor effect of the illusion and the other being a measure for the perceptual effect. This is different from the "standard" experimental design employed in psychological research. In this "standard" design the effects of different experimental conditions on *the same* dependent variable are compared. For example, the long tradition of research on reaction times (e.g., Donders, 1862) has followed this rationale: The experimental conditions were varied and the effects on one single dependent variable were observed. Here it is shown that two different dependent variables can be compared given that some preconditions are met. A model will be formulated, the Common Representation Model, that allows this comparison.

In the chapters 4, 5, and 6, experiments will be described that were performed to investigate the Ebbinghaus Illusion, the Müller–Lyer Illusion and the Parallel–Lines Illusion. In chapter 7 the findings will be discussed in the light of other studies and consequences for the perception versus action hypothesis will be derived.

The main result of this study is that grasping is affected by visual illusions. This was found for the Ebbinghaus Illusion, the Müller–Lyer Illusion and the Parallel–Lines Illusion. The motor effects of the illusions were equal to the perceptual effects in the Ebbinghaus Illusion, larger in the Müller–Lyer Illusion and smaller in the Parallel–Lines Illusion. Further experiments show that these differences can be attributed to problems in matching the perceptual task and the grasping task. Also, it is shown that the larger perceptual effect that was reported by other studies for the Ebbinghaus Illusion (e.g., Aglioti et al., 1995) can be attributed to an incomplete match between perceptual task and motor task. An overview of the literature shows that (a) the motor system clearly is affected by visual illusions and (b) currently there is no convincing evidence that visual illusions affect the motor system *less* than the perceptual system. This outcome challenges the perception versus action hypothesis and rejects one critical piece of evidence that is usually counted in favor of this hypothesis (e.g., Milner & Goodale, 1995; Jackson & Husain, 1997).

Chapter 2

Two visual systems in the primate brain

There is a long tradition of theories assuming a functional subdivision of the visual system in the primate brain. Early theories (e.g., Trevarthen, 1968; Schneider, 1969) focused on a distinction between the phylogenetically older pathway from the retina to the superior colliculus and the more recently evolved geniculostriate system which proceeds from the retina via the lateral geniculate nucleus to the striate cortex (cf. Figure 2.1). For example, Schneider (1969) suggested that the retinal projections to the superior colliculus are used for localization of stimuli (“where”) while the geniculostriate system is used for identification (“what”). Later theorizing has questioned such a prominent role of the superior colliculus and has focused more on a dichotomy that takes place in the cortex, while the superior colliculus pathway plays only a subsidiary role. The most prominent of those later theories is the account of Ungerleider and Mishkin (1982).

2.1 Ungerleider & Mishkin: “What” versus “where”

Ungerleider and Mishkin (1982) reviewed a large body of evidence from neuropsychological, behavioral, electrophysiological, and anatomical studies mainly performed with rhesus monkeys (*Macaca mulatta*). They derived a theory that locates both, localization of stimuli (“where”) and identification (“what”) in cortical areas. They distinguished a dorsal stream that computes the spatial aspects of visual stimuli and a ventral stream that

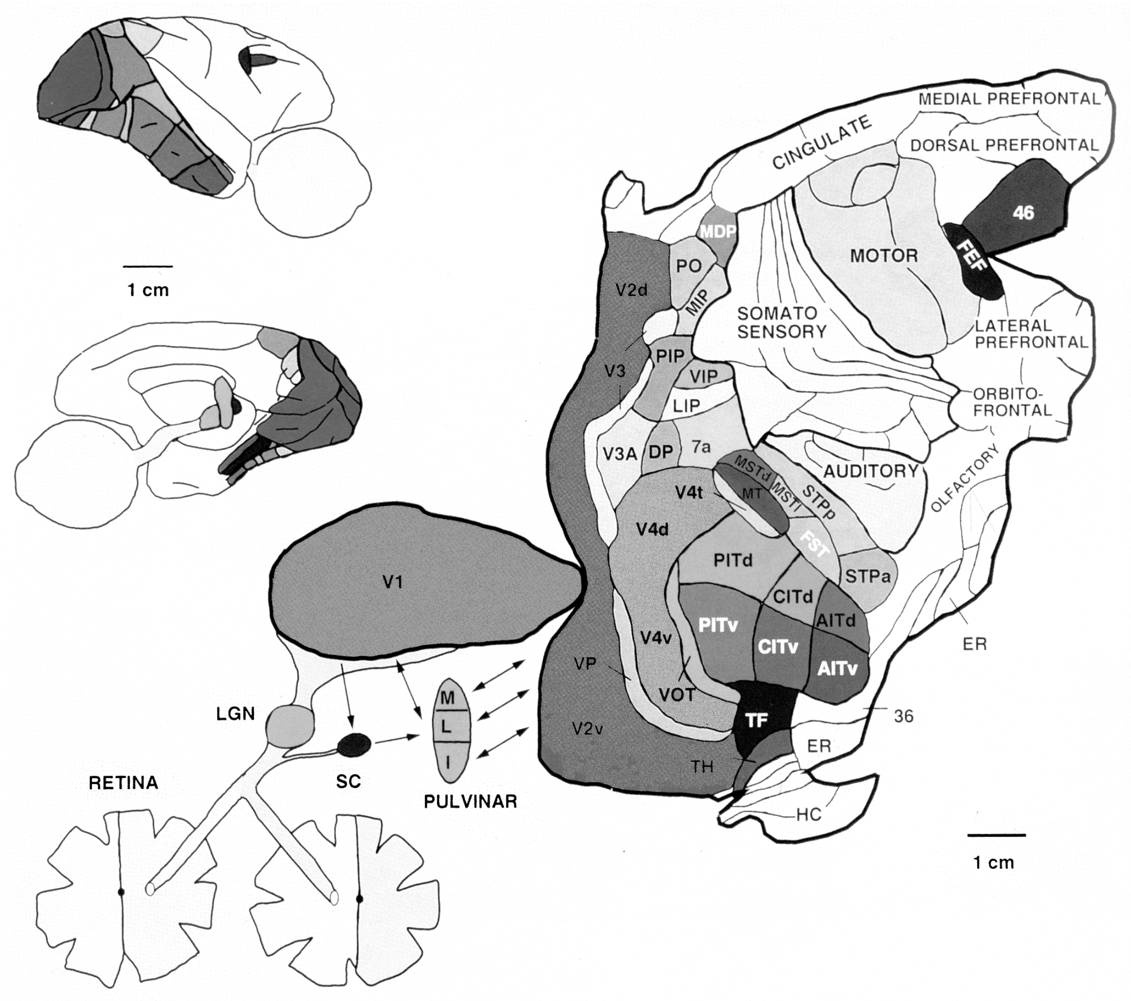

Figure 2.1: Overview of the macaque visual system. In the upper left is a lateral and a medial view of the right hemisphere. The large picture is an unfolded representation of the cerebral cortex and major subcortical visual centers. LGN, lateral geniculate nucleus; SC superior colliculus. Reprinted from Van Essen, Anderson, & Felleman (1992).

serves object recognition. The dorsal stream connects the primary visual cortex (striate cortex, or V1) with the posterior parietal cortex, while the ventral stream connects the primary visual cortex with the inferior temporal cortex (Figure 2.2). The main findings they used for their theory will be sketched in the following.

Electrophysiological experiments using single cell recordings had shown that neurons in the inferior temporal cortex respond to visual stimuli (Gross, Rocha-Miranda, & Bender, 1972) — just like neurons in the striate and prestriate cortex (Hubel & Wiesel, 1968, 1970). However, the optimal trigger features of neurons in the inferior temporal

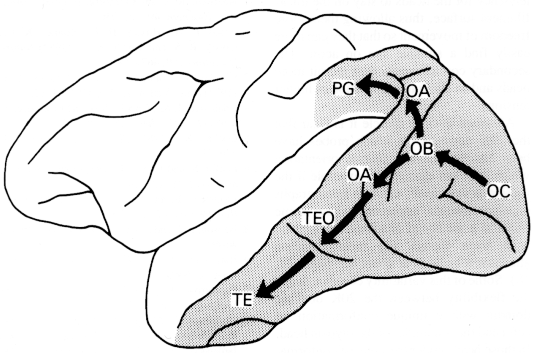

Figure 2.2: Lateral view of the left hemisphere of a rhesus monkey. Arrows indicate the dorsal and the ventral stream, as proposed by Ungerleider & Mishkin, 1982. The streams originate in the striate cortex (area OC) and diverge in the prestriate cortex (areas OB and OA). The ventral stream proceeds to the inferior temporal cortex (areas TEO and TE), while the dorsal stream terminates in the posterior parietal cortex (area PG). Reprinted from Mishkin, Ungerleider, & Macko (1983).

cortex, are much more complex and the receptive fields of these neurons are very large compared to neurons in striate and prestriate cortex. Also, studies that combined ablation of the striate cortex with single–cell recordings showed that visual responsive neurons in the inferior temporal cortex are exclusively dependent on input from the striate cortex. The pathway from the retina via the superior colliculus to the cortex turned out to be less important for these neurons (Rocha-Miranda, Bender, Gross, & Mishkin, 1975).

It has been known since early reports of Brown and Schäfer (1888) and of Klüver and Bucy (1939) that lesions to the temporal cortex of monkeys cause impairments in object recognition. Later research showed that damage restricted to inferotemporal cortex is sufficient to cause a pattern of deficit that is similar to what is known in humans as visual agnosia: An inability to recognize or discriminate objects despite of largely spared “low–level” visual abilities as flicker detection, visual acuity, visual field, and light thresholds (for review see Gross, 1973).

Gross and Mishkin (1977) argued that the very large receptive fields in the inferior temporal cortex might be the neuronal basis for a “stimulus equivalence” mechanism. This mechanism would provide the ability to recognize an object as the same — independent of its retinal position or (more general) its position in space. Of course, the drawback of such a mechanism would be a loss of information about the spatial location of the object. A second mechanism would be needed that extracted the spatial locations of the objects from the visual input. Ungerleider and Mishkin (1982) proposed that the posterior parietal cortex fulfills this function.

This hypothesis has been derived from a series of lesion studies on monkeys that showed a dissociation of visual deficits after inferior temporal and posterior parietal lesions. In an initial study, Pohl (1973) investigated rhesus monkeys after posterior parietal, inferior temporal and frontal lesions (the frontal lesions are not of interest here). After applying the lesions, he tested the monkeys in an object discrimination task and in a landmark discrimination task. In the object discrimination task, the monkeys were rewarded for choosing one object out of two objects (a red cylinder with vertical white stripes and a silver cube) which were placed randomly left or right. After they met a learning criterion, the other object was rewarded and they had to relearn the reward contingencies. In the landmark discrimination task, the monkeys were confronted with two plaques and had to choose the plaque that was closer to a landmark (the red cylinder with vertical white stripes). Again, after they met the learning criterion the reward contingencies were reversed and they had to choose the plaque that was further away from the landmark. In both tasks, reward contingencies were reversed seven times. The monkeys with inferior temporal lesions showed severe impairment in the object discrimination task and performed much worse than the monkeys with posterior parietal lesions. In contrast, the monkeys with posterior parietal lesions performed (on average) worse in the landmark discrimination task than the monkeys with inferior temporal lesions. (Note, however, that the monkeys with temporal lesions were as impaired as those with parietal lesions in the initial learning of the landmark discrimination task. The difference between the two groups appeared only after the second reversal of the reward contingencies). While in these tasks initial learning was tested, Pohl also tested re–learning after the lesion. A different group of monkeys had already learned a more difficult landmark discrimination task in which the landmark had been moved more and more to the center between the two plaques. After the lesion, the monkeys were tested in re–learning the task. Again, the parietal lesioned monkeys made much more errors than the temporal lesioned monkeys.

The results of this and a series of similar studies were interpreted as evidence that the inferior temporal cortex is mainly involved in remembering and evaluating the qualities of an object — independent of its position in space. In contrast, the posterior parietal cortex was seen to be involved in the perception of the spatial relations among objects and not in their intrinsic properties (cf. Figure 2.3, Mishkin, 1972).

The deficits caused by lesions to the posterior parietal cortex are not restricted to deficits in visual spatial orientation. The classical symptoms are misreaching, contralateral neglect of auditory, tactile and visual stimuli and impairments of tactile discrimination. This led to the hypothesis that the function of the posterior parietal cortex is to construct supramodal spatial information out of converging inputs from all sensory

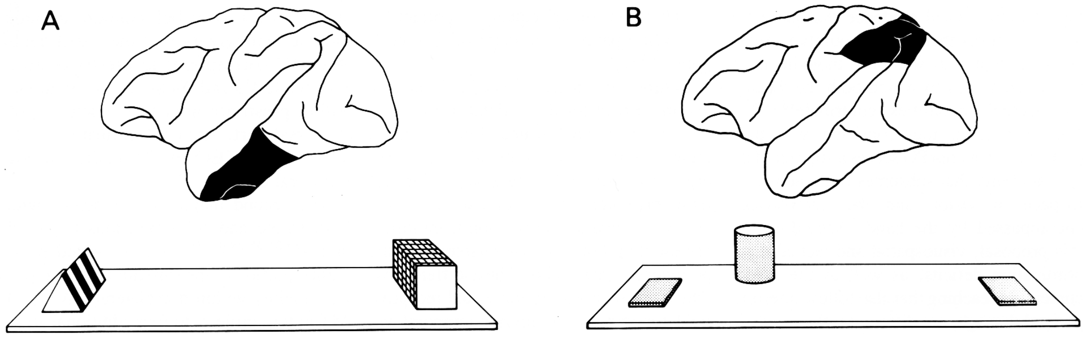

Figure 2.3: Schematic diagram of behavioral tasks that were summarized by Ungerleider & Mishkin (1982) to be sensitive to lesions to the inferior temporal cortex (A) and the posterior parietal cortex (B) in monkeys. **A.** Object discrimination task. The monkey is first familiarized with one object in a central position and then has to choose the non–matching object in the test phase. Only the test phase is shown. **B.** Landmark discrimination. The monkey is rewarded for choosing the plaque closer to the landmark (the cylinder). Reprinted from Mishkin, Ungerleider, & Macko (1983).

modalities — with a significant contribution of vision (Ungerleider & Mishkin, 1982).

The results from lesion studies on rhesus monkeys are similar to the impairments found in humans with lesions to temporal or parietal cortex. Patients with lesions to parietal cortex often show hemifield neglect and a disruption of visuomotor abilities, generally called optic ataxia (Bálint, 1909; Holmes, 1919). Patients with lesions to temporal regions frequently show difficulties in form discrimination, object recognition and problems with visual memory — a pattern of deficits that is usually called visual agnosia. An early account of the phenomenon distinguished between an apperceptive agnosia and an associative agnosia (Lissauer, 1890). Patients with associative agnosia were thought to be able to achieve a percept of an object (e.g., by copying a drawing), however are unable to recognize the object. While patients with apperceptive agnosia were thought to be unable to achieve even a coherent percept of the object. Given the similarities between the pattern of deficits in monkeys and in humans it seemed parsimonious to integrate the human data into the framework of the Ungerleider and Mishkin account (e.g., Grüsser & Landis, 1991).

Another aspect of the Ungerleider and Mishkin (1982) hypothesis is that the information about object identity ("what") and object location ("where") has to be reintegrated at some point. Mishkin et al. (1983) stressed this fact and left the question where this might happen to future research (speculating that possible candidates are the frontal lobe and the limbic system).

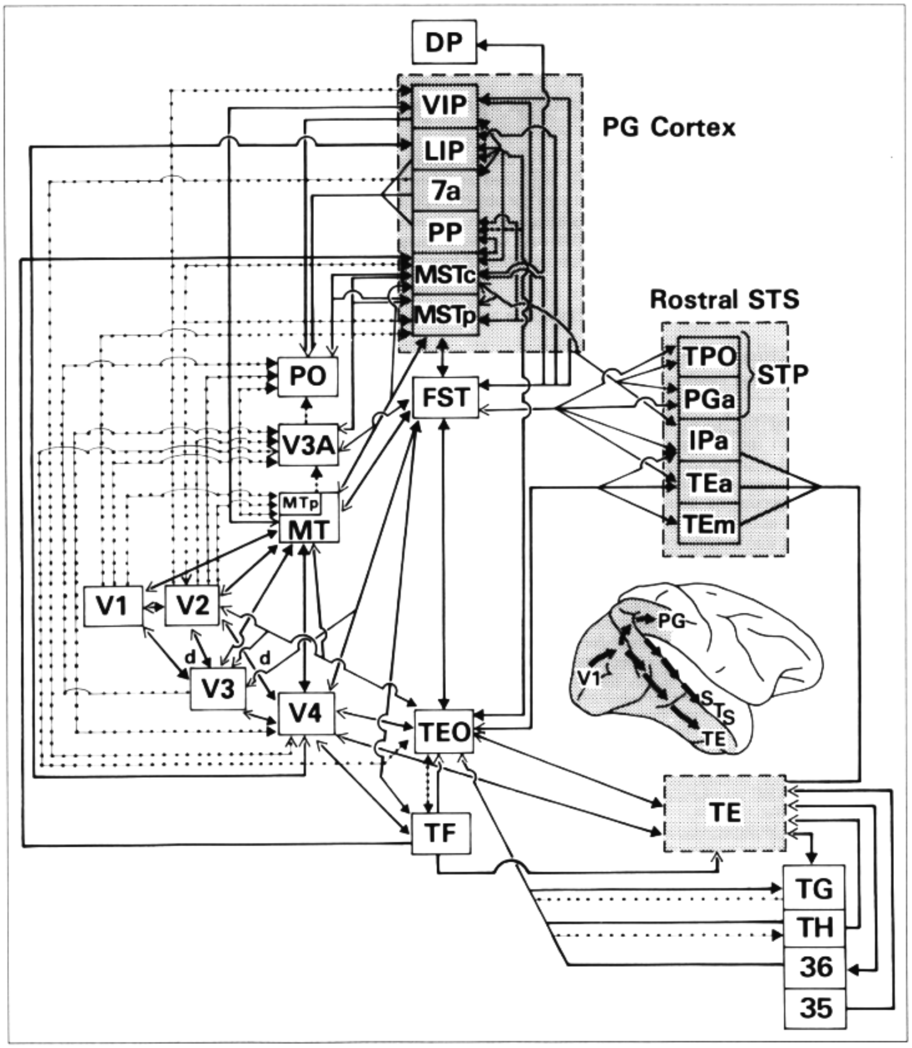

Figure 2.4: Summary diagram of the visual cortical hierarchy, as proposed by Distler, Boussaoud, Desimone, & Ungerleider, 1993. Solid lines indicate connections originating from both central and peripheral visual field representations, while dotted lines indicate connections restricted to peripheral field representations. Solid arrowheads indicate feedforward connections, open arrowhead feedback connections and reciprocal solid arrowheads intermediate type connections. Distler and coworkers proposed that the dorsal stream terminates in posterior parietal cortex (PG), and the ventral stream in the inferior temporal cortex (TE). They suggested that the rostral superior temporal sulcus (STS) might be a possible site for interactions between the two streams. Reprinted from Distler, Boussaoud, Desimone, & Ungerleider (1993).

In summary, Ungerleider and Mishkin (1982) argued that the computational reason for the evolution of two functionally distinct streams is that both streams need to fulfill different computational requirements. The ventral stream is assumed to perform computations that are needed for object recognition. Object recognition must be invariant to retinal translations in order to recognize a stimulus as the same regardless of its spatial position. Therefore the computations in the ventral stream should abstract from spatial information. The complementary computation of spatial locations is assumed to be performed in the dorsal stream.

The hypothesis of Ungerleider and Mishkin has been very influential in neuroscience. And, it has been advanced and refined. For example, the version shown in Figure 2.4 is already an elaborated version of the hypothesis, proposed by Distler et al. (1993). It should be noted, however, that the behavioral observations are not as equivocal as one might suspect from the prominence of the theory. Studies that compared parietal and temporal lesions in monkeys did not replicate the effects found by Pohl. Ungerleider and Brody (1977) tested acquisition of the landmark task after parietal and temporal lesions and found, contrary to Pohl (1973), a greater impairment in monkeys with temporal lesions. Other groups did not find a deficit in the landmark task after posterior parietal lesions (Petrides & Iversen, 1979; Ridley & Ettlinger, 1975). The discrepant results might be explained by differences in the testing methods, or in the precise location of the lesions. Nevertheless, they indicate some uncertainty in the behavioral observations (for review see Merigan & Maunsell, 1993).

In an ambitious account, the hypothesis of Ungerleider and Mishkin has been extended even further. Livingstone and Hubel (1988) proposed that the dichotomy between the dorsal and the ventral stream can be traced all the way back to the retina and the LGN, the lateral geniculate nucleus, which is the main relay station between the retina and the primary visual cortex.

2.2 Livingstone & Hubel: Magno– versus parvo–system

Livingstone and Hubel (1988) proposed that there exist at least two distinct systems in the primate brain, a magno–system and a parvo–system which separate already at the level of the retina. The systems were assumed to be optimized for different tasks, which can be roughly mapped to the “where” (magno) and “what” (parvo) distinction proposed by Ungerleider and Mishkin (1982). To appreciate this proposal, a description of the physiological properties of the geniculostriate system is needed.

The main input to the primary visual cortex (or striate cortex) stems from the LGN (lateral geniculate nucleus) which receives its input from the retinal ganglion cells. This geniculostriate pathway is divided into distinct subsystems. Already the retinal ganglion

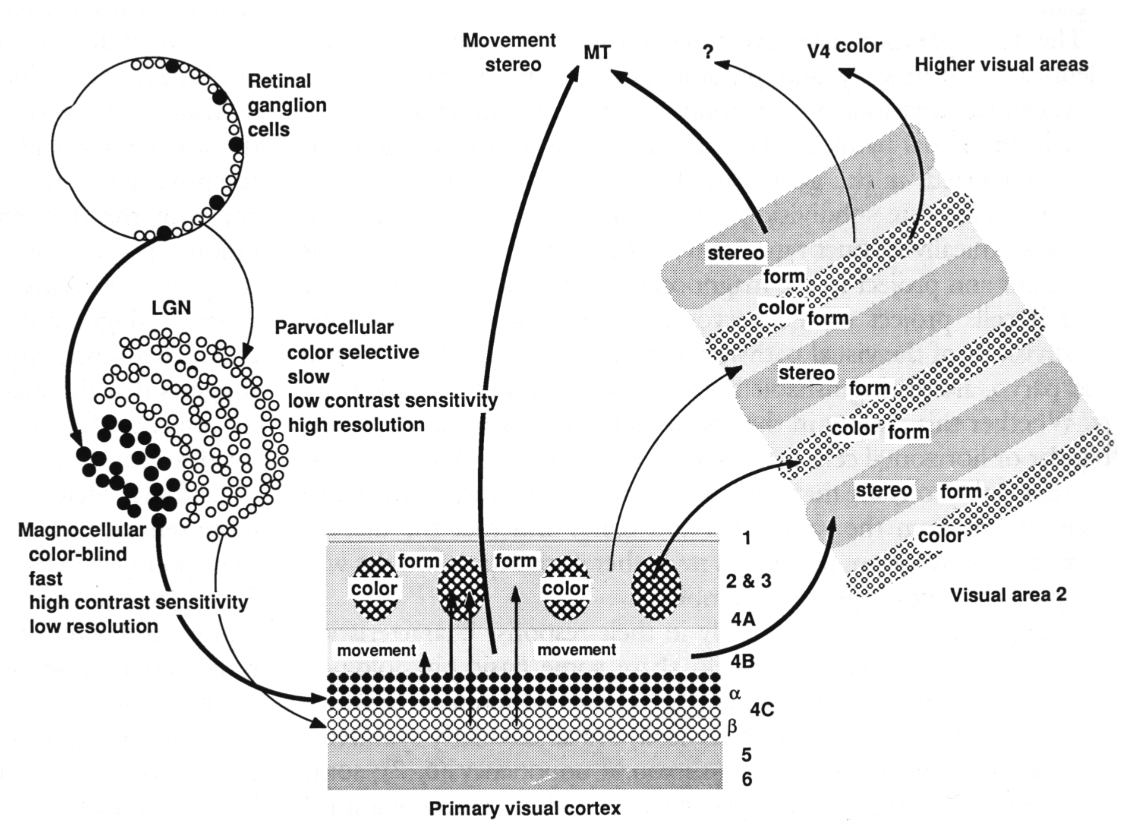

Figure 2.5: Schematic diagram of the functional segregation of the primate visual system as proposed by Livingstone & Hubel (1988). The stripes in V2 are (starting at the bottom): thin, inter, and thick stripes. LGN, lateral geniculate nucleus; MT middle temporal lobe. Reprinted from Livingstone & Hubel (1988).

cells consist of two major classes of cells: M–cells and P–cells (Shapley & Perry, 1986). These cells project to the two magnocellular layers and the four parvocellular layers of the LGN, respectively. The magnocellular (large–cell) and parvocellular (small–cell) layers of the LGN project separately to the layers 4Cα and 4Cβ of the striate cortex (cf. Figure 2.5). There are also other projections of the magno– and parvocellular layers of the LGN to the layer 6 (Hubel & Wiesel, 1972), which are even reciprocal (Lund, Lund, Hendrickson, Bunt, & Fuchs, 1975), however do not play a prominent role in the model proposed by Livingstone and Hubel.

Recently, a further pathway (besides the magnocellular and the parvocellular) was described in the macaque, the koniocellular pathway which projects from the LGN to the layers 2 and 3 of the primary visual cortex (Hendry & Yoshioka, 1994). The koniocellular neurons occupy regions ventral to each of the magnocellular and parvocellular layers such that six regions of koniocellular neurons exist in the LGN of macaques. The koniocellular neurons have generally very small somata and they seem to receive input from the superior colliculus and the retina (cf. Hendry & Calkins, 1998; van Essen & DeYoe, 1995). The function of the koniocellular pathway is not yet well understood. However, some information about this pathway is available and it will be described where appropriate. Note, that this pathway was not known to Livingstone and Hubel and therefore is not part of their model.

The magno–cells as well as the parvo–cells of the LGN have roughly circular receptive fields and show center–surround opponency. That is, they are excited (or inhibited) by the adequate illumination of a small retinal region and inhibited (or excited) by adequate illumination of a larger surrounding region. They differ in their response properties in the following ways (cf. Livingstone & Hubel, 1988).

Most of the parvo–cells (which comprise about 80% of the cells in the geniculostriate system) are sensitive to color. Also, the koniocellular neurons (about 10% of the cells) are believed to be sensitive to color (Hendry & Calkins, 1998), while the magno–cells (about 10% of the cells) generally show little sensitivity to color. For example, a parvo–cell might be excited by red light in its center, while it is inhibited by green light in its surround (single–opponent neuron). In contrast, a magno–cell might be excited by light of any wavelength in its center and inhibited by light of any wavelength in its surround (broadband neuron). This behavior origins in the different ways in which the signals from the retinal cones are combined. In humans and old world anthropoids as the macaque monkeys there exist three different types of cones, S, M, and L cones. These cones are most responsive to short, medium and long wavelengths, respectively. Often they are also called “blue”, “green”, and “red” cones. However, this is slightly misleading because the wavelengths at which the cones are most responsive do not exactly match the common expectation for these colors. For parvo–cells the cones are typically combined in such a way that they are red–green opponent or blue–yellow opponent (yellow is achieved by summing the input of M and L-cones). The magno–cells typically receive a weighted sum of the input of all three cone types and therefore respond to overall changes in intensity. The koniocellular neurons are believed to be mainly blue–yellow opponent (Martin, White, Goodchild, Wilder, & Sefton, 1997; Silveira et al., 1999).

Further differences arise from the fact that parvo–cells have smaller receptive fields than magno–cells (by a factor of 2–3), providing higher visual acuity than magno–cells. Also, they respond slower and more sustained than magno–cells and are less sensitive to low–contrast stimuli.

In the early 1980s most of this was already well known. However, considerable progress was achieved in knowledge about the physiology of the visual cortex. Staining for the mitochondrial enzyme cytochrome oxidase had shown blob–like structures in the primary visual cortex of primates (Horton & Hubel, 1981). The "blobs" are most prominent in the upper layers (layers 2 and 3), but can also be seen in the lower layers (layers 4B, 5 and 6). Electrophysiological recordings showed that the neurons in the blobs did mainly respond to color and had circular receptive fields, while the neurons between the blobs showed the already known orientation selectivity. These findings suggested that the blobs provide a separate color system in the primate cortex (Livingstone & Hubel, 1984, but see Leventhal, Thompson, Liu, Zhou, & Ault, 1995).

Note, that the neurons in the blobs only receive indirect input from the magno–cells and parvo–cells of the LGN (cf. Figure 2.5). In contrast, the koniocellular neurons seem to provide a direct route from the retina to the blobs of V1 (Hendry & Yoshioka, 1994).

Similar to the primary visual cortex (or V1) there is also a characteristic pattern in the adjacent visual area (V2) if stained for cytochrome oxidase. The pattern consists of alternating thick and thin stripes, separated by interstripe regions and running perpendicular to the V1–V2 border (Livingstone & Hubel, 1983). Livingstone and Hubel established the connections between the two areas by injecting horseradish peroxidase (which travels along the axons of neurons in both, anterograde and retrograde direction). These investigations showed that the interblob regions of V1 mainly connect to the interstripe regions of V2, the blobs of V1 to the thin stripes of V2, and layer 4B of V1 to the thick stripes of V2 (Livingstone & Hubel, 1984, 1987a).

Livingstone and Hubel combined their findings with further anatomical and functional findings and the "where" versus "what" distinction of Ungerleider and Mishkin. They suggested that the separation of magno– and parvocellular pathways proceeds to higher visual areas, namely the areas V4 and the middle temporal area, generally called MT or V5 (Livingstone & Hubel, 1987b, 1988). These areas had been investigated by Zeki and colleagues using single cell recordings. They had proposed that V4 mainly processes color (Zeki, 1978), while MT mainly processes motion and binocular disparity (Dubner & Zeki, 1971; Zeki, 1973).

In short, Livingstone and Hubel (1988) suggested that the primate visual system is segregated into a magno–system and a parvo–system. The magno–system was seen to mainly process motion and binocular disparity (i.e., depth information). The parvo–system was seen to be divided in two subsystems, one processing color and the other processing form and shape information. In the higher visual areas, the parvo–system was seen to correspond to the ventral "what" stream of Ungerleider and Mishkin (1982), and the magno–system to the dorsal "where" stream.

The appeal of this proposal was that it fitted very well with the psychophysical data know at that time. It seemed that the response properties of the magno–cells and of the parvo–cells directly determine the way we perceive the world — mainly in the domains of color perception, motion perception and perception of stereoscopic depth. Livingstone and Hubel (1987b) compiled a large number of psychophysical demonstrations in favor of their proposal. Most of the evidence was based on the fact that some perceptual function that was attributed to the magno–system was comprised at equiluminance.

Two stimuli are equiluminant if they show only a difference in color, but not in luminance (note that both, color as well as luminance are psychophysical quantities that describe a relationship between physical properties of the stimulus and the experience of an observer). Equiluminance can be determined by heterochromatic flicker photometry: In a simple design, two light sources of different color are alternately displayed at a rate of 20 Hz or above. The participant adjusts the intensity of the lights until the perception of flicker disappears or is minimized (e.g., Wyszecki & Stiles, 1982). Clearly, many different wavelength distributions can lead to the same luminance. Most of these (but not all) will be perceived as different in color. If flicker photometry is performed with one of the stimuli being white (containing all wavelengths of the visible spectrum at the same intensity) and the other stimulus being monochromatic light (containing only one wavelength), it is possible to determine the relative efficiency of each wavelength in eliciting luminance. The resulting curve, the spectral luminosity $V(\lambda)$, is the basis for a standard defined by the Commission International de l'Eclairage (C.I.E.) in 1924. Note, that the spectral luminosity is solely defined via perception — independent of any physiological correlate of luminance. The more it is interesting that the spectral luminosity curve corresponds quite well to the sum of the spectral sensitivities of the M and L cones, if the L cones are weighted by a factor of two (Figure 2.6). This summation is similar to the way in which the retinal M–ganglion cells (belonging to the magno–system) sum their cone inputs (Smith & Pokorny, 1975).

Based on findings like this, Livingstone and Hubel assumed the magno–system to be only sensitive to differences in luminance and not to differences in color (broadband neurons). Therefore, they predicted that functions of the magno–system should be comprised at equiluminance. Livingstone and Hubel reported that motion perception, depth perception from stereopsis, depth perception from motion parallax, depth perception from perspective, and visual illusions[1] are severely impaired at equiluminance.

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[1] Livingstone and Hubel interpreted visual illusions, as for example the Müller–Lyer Illusion, as a deception of the size constancy mechanism which is intimately linked with depth perception (Gregory, 1963). Therefore, they located the source of visual illusions in the dorsal "where" stream. It might be confusing

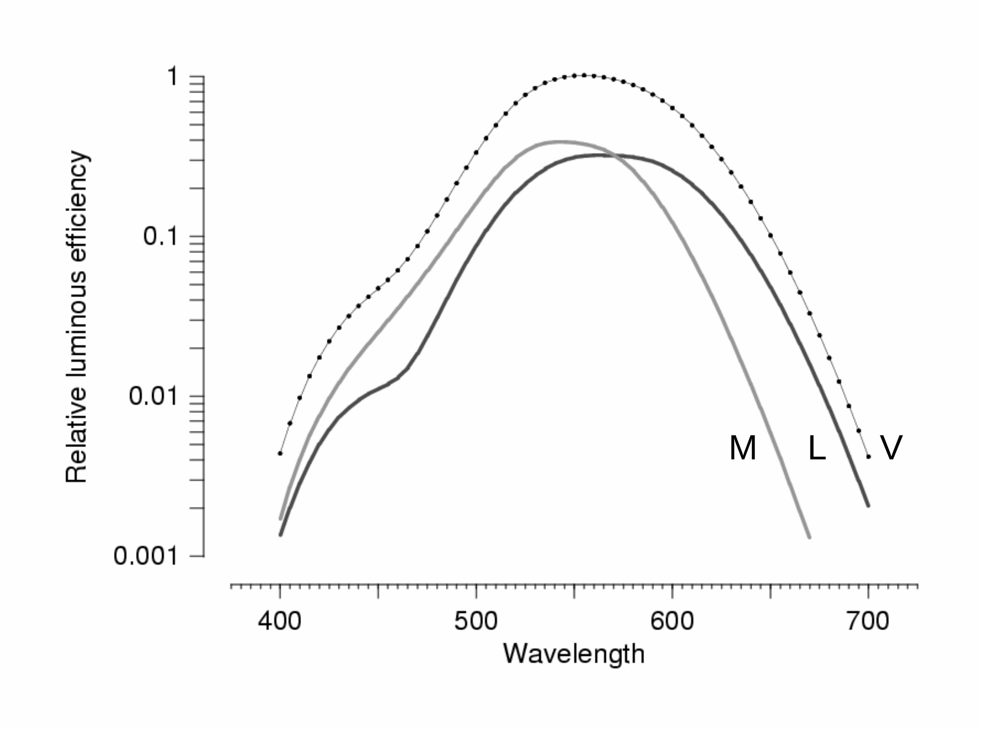

Figure 2.6: Human luminous efficiency $V(\lambda)$ and cone spectral sensitivities as functions of the wavelength (λ) of light. $V(\lambda)$ is the relative luminous efficiency as defined by the Commission Internationale de l'Eclairage (C.I.E.) in 1924 for a small field (2°) observer. The L and M curves show the relative cone spectral sensitivities for the L and the M cones. They are scaled at an L:M ratio of 2:1, so that their sum closely approximates the $V(\lambda)$ curve. Adapted from Gegenfurtner & Hawken (1996).

For example, Ramachandran and Gregory (1978) found a decrease in apparent motion at equiluminance. They alternately presented two randomly textured patterns (Julesz, 1971). The patterns consisted of red and green areas and were identical, except that in one pattern a squared region was offset to the right. With stimulus durations of 100 ms and an inter stimulus interval of 50 ms, observers perceive the square oscillating back and forth horizontally. As the green luminance was gradually reduced to equiluminance the perception of apparent motion disappeared despite the individual elements of the pattern were still clearly visible. Ramachandran and Gregory concluded — as did later Livingstone and Hubel — that color and motion are handled separately by the human visual system.

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that Milner and Goodale (1995) assumed the same illusions to be generated in the ventral stream (section 2.5.3). This is due to the fact that Milner and Goodale distinguished between allocentric and egocentric coding of distance information and assumed that visual illusions are generated by a deception of allocentric coding — which they located in the ventral stream. See section 2.3 for details.

The hypothesis of Livingstone and Hubel gained wide acceptance and was highly influential. However, it seems clear today that the proposal in its strong original form cannot be held up (for reviews see Schiller & Logothetis, 1990, Merigan & Maunsell, 1993, and Gegenfurtner & Hawken, 1996). The reasons will be sketched in the following.

Different researcher groups investigated the effects of discrete lesions to the LGN. Small injections of, for example lidocaine or GABA can selectively block transmission through the magnocellular or parvocellular layers of the LGN. Maunsell, Nealey, and DePriest (1990) found in single cell recordings that responses in area MT were almost always greatly reduced by blocks of the magnocellular layers, while few MT neurons were affected by parvocellular blocks. While this result conforms to the predictions of Livingstone and Hubel, this is not true for the area V4. Ferrera, Nealey, and Maunsell (1994) found that blocks to parvocellular as well as to magnocellular layers affected responses in area V4 in a similar way. The results suggest that at least the ventral pathway receives input from both, parvocellular as well as magnocellular layers of the LGN.

Schiller, Logothetis, and Charles (1990) also applied chemical–lesions to the LGN of rhesus monkeys. In behavioral tests they found that some results conformed to the predictions of the hypothesis (e.g., color perception was impaired after parvocellular lesions and motion perception after magnocellular lesions). However, the results regarding stereo perception did not conform to the hypothesis: Magnocellular lesions did not produce any deficit, while parvocellular lesions produced a deficit with high spatial frequencies, but not with low spatial frequencies.

Electrophysiological studies in the intact visual system of monkeys showed that there is much more convergence as early as in V1 and V2 than has been originally thought. For example, Leventhal et al. (1995) investigated the receptive field properties of neurons in the layers 2, 3, and 4 of anesthetized rhesus monkeys. Different from Livingstone and Hubel (1984) they did not find a relationship between the degree of orientation sensitivity and the degree of color sensitivity. Also, color sensitive neurons were not restricted to the blob regions and orientation sensitive cells were not restricted to the interblob regions.

Gegenfurtner, Kiper, and Fenstemaker (1996) investigated in anesthetized monkeys (*Macaca fascicularis*) the selectivity of cells in V2 to direction, orientation, color, and size. They found that neurons generally respond to more than one stimulus attribute and that it is not possible to classify cells as being solely tuned to one of the attributes. Also, despite there was a tendency for more color sensitive cells in the thin stripes, they did not find a clear segregation in responsiveness between the different regions. In all three regions there were color sensitive cells. Similar results were reported by Peterhans and Heydt (1993) for awake rhesus monkeys (however, this study did not investigate the chromatic properties of the cells).

In a similar study, Gegenfurtner et al. (1994) reported results for area MT which were in much better agreement with the hypothesis of Livingstone and Hubel. Gegenfurtner et al. investigated the responsiveness of neurons in area MT to moving gratings. The gratings were either modulated in luminance, in chromatic contrast, or in both. They found that responses of single neurons in area MT were almost completely determined by the luminance modulation. Interestingly, most neurons in MT were unresponsive to gratings near equiluminance, despite of color contrast. Because these planes of the "null" responses varied slightly, the averaged population response did show a residual sensitivity to color contrast. Also very few cells showed signs of color–opponent input.

In conclusion, anatomical and physiological studies provided evidence that: (a) there is a strong interconnectivity at very early cortical stages, as early as the areas V1 and V2; (b) the area V4 which is seen to belong to the ventral stream receives input from both, parvo– as well as magno–cells in the LGN; (c) input to area MT seems to originate mainly in the magnocellular layer of LGN. Residual sensitivity to color might be caused by slight variations in the equiluminance planes of magno–cells, as well as by (minor) input of parvo–cells.

What about the psychophysical data that suggested that perception of (mainly) motion is comprised at equiluminance? Contrary to the original belief, a number of studies showed that equiluminant stimuli can affect motion perception. For example, equiluminant stimuli can induce a motion after–effect on luminance stimuli (Cavanagh & Favreau, 1985; Derrington & Badcock, 1985; Mullen & Baker, 1985). Also, equiluminant stimuli can cancel the motion of luminance stimuli drifting in the opposite direction (Chichilnisky, Heeger, & Wandell, 1993).

One problem with some of the early studies was that the cone contrasts of luminance stimuli were not matched to the cone contrasts of equiluminant stimuli (cf. Gegenfurtner & Hawken, 1996). The cone contrast of a stimulus is defined via the difference the stimulus causes in cone excitation (ΔS,ΔM,ΔL) relative to the current adaptive state of the cones (S, M, L). The ratios $\Delta S/S$, $\Delta M/M$, and $\Delta L/L$ define a point in a (local) three–dimensional space, the cone contrast space. The cone contrast of two stimuli is the euclidian distance between the two corresponding points in the cone contrast space. For motion perception the S cones can be neglected because their contribution to motion perception is relatively small. Therefore, cone contrast space can be reduced to a two–dimensional space that takes only the M and L cones into account. Chromatic cone contrast is limited to a smaller range than luminance cone contrast because the absorption spectra of the M and L cones overlap. This problem is even more pronounced on a standard CRT monitor which is limited in the range of wavelength distributions it can generate.

Studies investigating stimuli that were matched for cone contrast suggested to make a distinction between slow moving and fast moving stimuli. A slow moving stimulus could, for example, be a sine wave grating that moves at a speed of 1 cycle per second, while a fast moving grating would move at a speed of 8 cycle per second. Hawken, Gegenfurtner, and Tang (1994) found that the perceived speed of slow equiluminant gratings was strongly dependent on cone contrast. Speed was strongly underestimated with low contrast. The perceived speed of slow luminance gratings also depended on cone contrast but to a much lower degree. In contrast, the perceived speed of fast moving gratings was close to veridical. It did neither depend on cone contrast nor was there a difference between equiluminant stimuli and luminance stimuli.

Experiments that determined psychophysical thresholds also showed a difference between slow moving and fast moving stimuli. For fast equiluminant gratings there was a lower sensitivity than for fast luminance gratings, both in detecting motion and identifying its direction. For slow equiluminant gratings, however, the sensitivity was higher than for slow luminance gratings especially in detecting the motion (Gegenfurtner & Hawken, 1995).

From these and similar findings Gegenfurtner and Hawken concluded that fast moving stimuli as well as slow moving luminance stimuli are processed together. This could happen in a mostly magnocellular pathway, including area MT. Additionally, they assumed that slow moving equiluminant stimuli are processed by a different mechanism which is color opponent and is sensitive to the direction of motion but is impaired in processing the speed of motion.

In summary, the proposal of Livingstone and Hubel has been very influential and still provides a framework for ongoing research. However, it seems clear today that the functions in the visual cortex are not as neatly segregated as has been originally thought. Area V4 clearly receives input from magno– as well as from parvo–cellular layers of the LGN and area MT shows some sensitivity to color, though its input seems to be dominated by the magnocellular pathway. Also, there seems to exist an additional color–opponent process which reacts to motion. Finally, it should be noted that if the strong predictions are removed from the Livingstone and Hubel model, the differences between this approach and the model of Ungerleider and Mishkin are attenuated and the approach might be seen as just a variant of the Ungerleider and Mishkin model.

2.3 Goodale & Milner: Perception versus action

Goodale and Milner criticized the Ungerleider and Mishkin model on empirical and on theoretical grounds (Goodale & Milner, 1992; Milner & Goodale, 1995). They argued that the Ungerleider and Mishkin model, despite assuming parallel streams, would be still in a tradition of thinking that sees the construction of one uniform percept as the final goal of the processing of visual information. They argued that, for example, there is ample evidence in vertebrates for the existence of highly specialized and distinct visuomotor systems that transform visual information for the purposes of certain motor actions. In their view this contradicts the notion that there exists one central representation of the world that can be used to guide just any motor act. Milner and Goodale see this view as a theoretical prejudice that has led vision research to focus solely on the input–characteristics of visual stimuli. For example, in a typical discrimination task an animal or human is asked to discriminate different visual stimuli and to respond with different actions to them. Milner and Goodale argued that in these tasks it is generally abstracted from the nature of the response, be it picking up an object, pressing a lever, jumping from one platform to another — or whatever responses are employed in these tasks. To the contrary, they suggested to explicitly investigate the relationship between motor outputs and visual inputs — assuming that there exist specialized visual systems that are exclusively designed to guide certain motor acts. These motor acts might, for example, be the guidance of eye movements, the guidance of grasping, or visual perception[2].

Milner and Goodale proposed that the function of the dorsal stream is the direct guidance of motor actions, while the ventral stream is only indirectly linked to action via cognitive processes, as object recognition and (more generally) conscious perception (Figure 2.7). They argued that the streams are optimized to fulfill contradictory requirements: To guide actions computations have to be fast, they only need a short term memory because the position of the object can change quickly and they have to code the position of the object relative to the effector (egocentric coding). In contrast, they argued that computations for object recognition do not need to be as fast (but see Thorpe, Fize, & Marlot, 1996) and should provide a long term memory to allow, for example, object constancy. Also, for object recognition it is not as important to code an object relative to an effector

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[2] Milner and Goodale (1995) distinguished between two uses of the term "perception": One refers to any processing of sensory input. The other is more restricted and refers to "a process which allows one to assign meaning and significance to external objects and events" (page 2). This use of the word "tends to be identified with one's phenomenological experience of the world" (page 2). It is this second use that is meant when Milner and Goodale speak about perception.

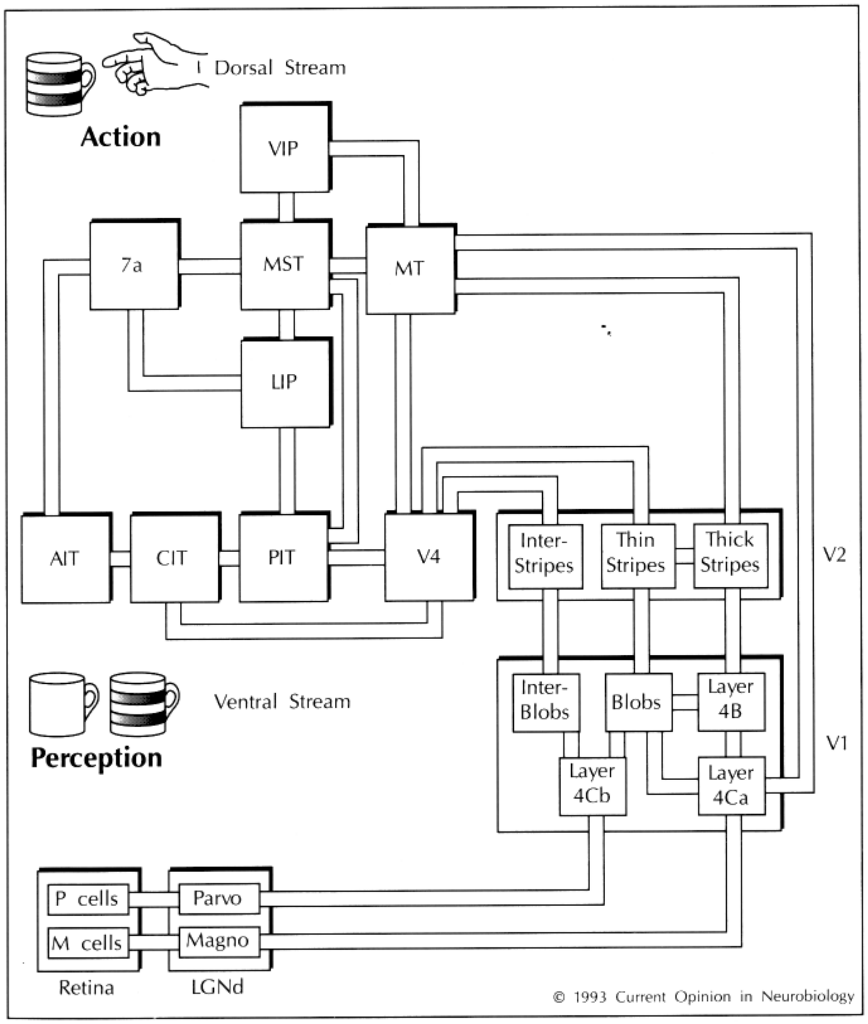

Figure 2.7: Schematic diagram of the visual cortical hierarchy, as proposed by Goodale (1993). Magno– and parvo–pathways are heavily intermingled after they reach V1. Also, even though two main streams of processing can be identified, they are believed to be heavily interconnected. AIT, anterior inferotemporal cortex; CIT, central inferotemporal cortex; LIP, lateral intraparietal sulcus; PIT, posterior inferotemporal cortex; VIP, ventral intraparietal sulcus. Reprinted from Goodale (1993).

but the object should be coded relative to other objects (allocentric coding).

The most prominent evidence for this theory is a double dissociation between visual perception and visual guided motor behavior that was found in the patients D.F. and R.V..

2.4 The patients D.F. and R.V. — a double dissociation between perception and action.

Goodale, Milner, Jakobson, and Carey (1991) described a dissociation in the patient D.F. between perceiving objects and grasping them. D.F. was then a 35–year–old woman who had suffered from a carbon monoxide poisoning as a result of a faulty gas water heater (15 month before the testing). She showed a profound visual form agnosia: poor perception of shape and orientation, while having relatively intact basic visual abilities (Milner et al., 1991). Despite this deficit she performed quite normal if she was asked for actions that required to take into account the shape or orientation of objects.

Goodale et al. (1991) tested D.F.'s ability to report the orientation of a slot of 12.5 x 3.8 cm which was cut in a disc. They found that she was not able to report the orientation of the slot neither verbally nor by manually orienting a card to match the direction of the slot (cf. Milner et al., 1991). However, if she was asked to reach out and place her hand (or a hand–held card) in the slot she performed quite well.

In another test, she was confronted with a set of Efron rectangles (Efron, 1969), solid plaques that all have the same surface area, however, differ in the ratio of their length and width. In discriminating the rectangles she performed on chance level. Also, if she was asked to indicate manually the front–to–back extent of the objects, she performed poorly. However, if she was asked to reach out and pick up the objects, her grasp was appropriately scaled to the size of the objects (more specifically, her maximum preshape aperture was scaled to the size of the object, cf. section 2.5.3).

In a later study, Goodale et al. (1994) presented specially formed shapes to D.F. requiring a precise placement of thumb and index finger in grasping (the shapes had been designed to investigate algorithms for the control of grasping in two–fingered robots, Blake, 1992). D.F. was not able to discriminate the shapes in a same / different task — nevertheless she performed normal in grasping the shapes.

In summary, D.F. showed no difficulty in using information about shape or size to guide her movements in grasping. However, she had a severe visual form agnosia which made it impossible for her to use the same information to distinguish one object from the other, or to indicate the object's shape or size perceptually. This dissociation between being able to use visual information for the guidance of action and being unable to use it for perception fits perfectly to the functional distinction between the dorsal stream and the ventral stream proposed by Milner and Goodale. Consequently, the damage caused by the anoxia should be in early parts of the human homologue of the ventral stream. Of course, as Milner and Goodale stress, only tentative conclusions are possible because brain damage caused by anoxia is not clearly localized. Given this caveats, they report that MRI scans support their interpretation because the major focus of cortical damage seems to be in the ventrolateral region of the occipital cortex, an area that is assumed to be the human homologue of the ventral stream. Also, the primary visual cortex, which provides input for both the dorsal and the ventral stream, seems to be largely intact. This indicates that the dorsal stream still can receive cortical visual input.

For a double dissociation it is necessary to find deficits that reverse the deficits found in D.F.. That is, to find patients in whom the human homologue of the dorsal stream is impaired while the ventral stream is intact. Such a pattern of deficits can be found in patients with bilateral lesions of the posterior parietal cortex (e.g., Perenin & Vighetto, 1988; Jakobson, Archibald, Carey, & Goodale, 1991). These patients often show an optic ataxia: They are unable to grasp objects appropriately or to orient their hand when reaching for the objects. Nevertheless, they are usually well able to use the size or orientation of the objects in a perceptual task.

Goodale et al. (1994) directly compared the behavior of an ataxic patient with that of D.F.. The patient R.V. was then a 55–year old woman who had an optic ataxia after strokes that caused large bilateral lesions of the occipitoparietal cortex — lesions that can be attributed to the dorsal stream. She showed clear visuomotor deficits in grasping and in pointing to objects while her visual acuity was in a normal range and she was not apraxic (i.e., she could show how she would perform certain movements, for example eating with a spoon). She had normal hand strength and finger–tapping abilities. When R.V. was asked to discriminate the shapes of Blake (1992), she showed only little impairment compared to a control participant. However, if R.V. was asked to grasp the shapes in a precision grip (using only thumb and index finger), she performed poorly choosing unstable grasp points. Only after having made contact with the objects and receiving haptic feedback of the object her manipulation appeared essentially normal.

The disabilities of R.V. have an opposite pattern to the disabilities found for D.F., showing a double dissociation between perceiving the shape of an object and using this information to guide the fingers in grasping. A double dissociation between two functions is usually interpreted as evidence in favor of two separate neuronal systems that can be impaired independently. In fact, this is what Milner and Goodale inferred: The existence of two independent systems that use visual information in quite different ways. The ventral stream to enable visual perception and the dorsal stream to enable visually guided motor behavior.

Of course, there are caveats to this conclusion. As mentioned above, the diffuse nature of the brain damage of D.F. requires some caution in drawing strong conclusions. Also, plasticity and learning might have changed the pattern of deficits such that straightforward interpretations can be problematic. Finally, it is clear that a dissociation between perception and action is not the only possible cause for the pattern of deficits in D.F. and R.V.. The deficits could, for example, as well be caused by a damage to one of two output systems that both origin in one single representation of object size (cf. Smeets & Brenner, 1995).

It would provide strong support for the theory if one found a dissociation between perception and action in the healthy visual system. In fact, this is a necessary condition because Milner and Goodale assume that the two streams create different representations of an object due to different output requirements for motor acts and visual perception. If the output behavior does not reflect a difference in the representations, then the assumed cause for the existence of the two systems is in doubt. In consequence, Milner and Goodale discussed a number of psychophysical studies on healthy participants that they counted as evidence for their interpretation.

2.5 Psychophysical evidence for a dissociation between perception and action in healthy participants

Milner and Goodale (1995) compiled evidence from psychophysical experiments on healthy participants that support their hypothesis. The most important lines of evidence will be described and one of the most striking psychophysical findings, a dissociation between perceiving a visual illusion and grasping it, will be put to empirical test in the remaining chapters.

2.5.1 Pointing and not–perceived changes in position

Goodale, Pélisson, and Prablanc (1986) showed that displacing an object during a saccade can influence an ongoing pointing movement. Participants were asked to point to a target that appeared suddenly in their peripheral visual field. In half of the trials, the target was shifted even further during the first saccade that was made towards the target. In the other half of the trials, the target remained stationary. Participants were able to smoothly incorporate the shift of the target in their pointing movement as well as in their second saccade (the “correction saccade” which usually occurs if one does look at a new target). Pointing to the shifted target was as accurate as to a stationary target and the time needed for the pointing movement was not increased more than can be expected by the larger amplitude of the movement. Goodale and colleagues interpreted this in the way that the motor system always does a fine–tuning after the first saccade. They argued that this fine tuning determines the amplitude of the correction saccade as well as the final amplitude of the pointing movement. This fine–tuning is sufficient to incorporate the deviation introduced by the shift of the target, as long as the shift is not too large.

Despite this high sensitivity of the visuomotor system to a change in location, Goodale and coworkers reported that none of the four participants realized that the target sometimes jumped to a new location. Testing this in additional forced–choice experiments, they found that the participants were unable to detect the shift of the target.

A similar result was obtained in earlier work of Bridgeman and coworkers (Bridgeman, Lewis, Heit, & Nagle, 1979). They reported that participants were not able to detect the displacement of a target if it occurred near the time of a saccadic eye movement. Nevertheless, participants were still able to accurately point to the new position of the target (to avoid that participants used simple visual feedback while moving the hand towards the target, either the pointing device or the target were made invisible during the pointing task: the pointing movement was performed "open–loop").

In another study, Bridgeman, Kirch, and Sperling (1981) used induced motion to further investigate this phenomenon (see also Wong & Mack, 1981). A frame surrounding a fixed target was displaced, creating the illusion that the target had jumped in the opposite direction. Target and frame were then extinguished, and the participants pointed open–loop to the last position of the target. Similar to the previous studies, pointing was not influenced by the induced motion. In another condition, the induced motion was canceled out by a corrective displacement of the target, such that now the target was perceived as being stationary despite it was moving. Pointing, again, was not deceived by the illusion and reflected the veridical position of the target.

All these results can be interpreted as strong evidence for a dissociation between perception and action (Bridgeman et al., 1981; Goodale & Milner, 1992; Milner & Goodale, 1995). They fit well with the framework of the perception versus action hypothesis because they do not only show a different behavior of the perceptual measure and of the motor measure, but also do conform with the notion that the motor system operates in egocentric coordinates (being mainly concerned with the position of an object relative to the effector), while the perceptual system operates in allocentric coordinates (being mainly concerned with the position of an object relative to other objects).

However, there also has been critique. Smeets and Brenner (1995) argued that in the perceptual tasks of the studies performed by Bridgeman and coworkers participants had to detect a *change in position* (i.e., a velocity) of the target object. In the motor task, on the other side, participants had to indicate only the *position* of the target. Smeets and Brenner argued that the different results in these tasks might simply indicate different processing of velocity information and of position information, independent of the question whether a perceptual response or a motor response was required. In consequence it should be possible to find the same difference that was found by Bridgeman and coworkers between the perceptual task and the motor task in purely perceptual tasks or in purely motor tasks.

Smeets and Brenner (1995) tested this idea by presenting running spiders (sic!) on a computer monitor. The target spiders moved for a short time across the screen and then disappeared. In the perceptual task, participants were asked to match either the velocity or the position of a comparison spider with that of the target spider. The comparison spider appeared 500 ms after the target spider had disappeared. Varying the velocity of the background, Smeets and Brenner found that the induced motion that was caused by the moving background did only influence the velocity judgment, but not the position judgment. In the motor task participants hit the running spiders in order to “squash” (sic!) them. The position at which participants hit the spiders was not influenced by the background motion. Nevertheless, reaction time, movement time and the velocity profiles of the hand showed effects of the moving background. The results indicate that (a) a perceptual judgment of position is unaffected by a moving background, (b) a perceptual judgment of velocity is affected by a moving background, (c) the position at which participants hit a moving target is unaffected by a moving background, and (d) other components of the motor response are affected by a moving background. These results fits well with the notion that the task demands (i.e., whether velocity information or position information is required to fulfill the task) are responsible for the different effects found by Bridgeman et al. (1981) — and not the nature of the response (i.e., whether it is a perceptual or a motor response).

Similar results were obtained in an earlier study: Abrams and Landgraf (1990) presented a target that underwent a combination of real movement and induced motion. As in the studies of Bridgeman et al. (1981) and of Smeets and Brenner (1995), open–loop reaching to the final location of the target was little influenced by induced motion. However, induced motion did influence open–loop arm movements that were performed to reflect the extent of the target movement.

2.5.2 Pointing and visual illusions

The main critique against the studies described in the previous section is that in the perceptual task participants judged target velocity, while in the motor task they reacted to target position (Smeets & Brenner, 1995). A series of studies avoided this problem by presenting stationary stimuli that formed a visual illusion.

Mack, Heuer, Villardi, and Chambers (1985) and Gentilucci, Chieffi, Daprati, Saetti, and Toni (1996) asked participants to point to the vertices of the Müller–Lyer Illusion (Figure 2.8a) and also to perform perceptual judgments of the length of the shaft of the figure. Despite a strong perceptual illusion, Mack and colleagues did not find an effect of the illusion on pointing if full vision of the illusion during the pointing response was allowed. Similarly, Gentilucci and colleagues did find only a small effect of the illusion on pointing in the full vision condition. In both studies the effect of the illusion on pointing increased if either the illusion configuration was only flashed for a short time (183 ms, Mack et al.) or if first, vision of the hand was suppressed and second, a delay was introduced between vision of the illusion–configuration and performance of the pointing response (5 sec, Gentilucci et al.).

A similar result was obtained by Bridgeman, Peery, and Anand (1997). They investigated the Roelofs effect: A target inside an off–center frame appears biased opposite the direction of the frame (Figure 2.8b). In the perceptual task participant judged the position of the target (e.g., by classifying the target to be in one out of five possible positions). In the motor task they pointed to the target with an unseen pointer. Consistent with the previous studies, Bridgeman et al. found that all participants were significantly deceived in the perceptual task ($N = 10$), but only half of the participants in the motor task. If a delay was introduced between stimulus offset and the response (4 sec), the difference between the tasks was diminished.

Again, the results were counted as strong evidence for a dissociation between perception and action (Bridgeman et al., 1997; Goodale & Haffenden, 1998). The interpretation is straightforward: Pointing was not affected by the illusions because for pointing visual information is processed in egocentric coordinates and because the illusions were created by special arrangements of objects. This should not affect egocentric coordinates. In contrast, the perceptual system is assumed to work in allocentric coordinates and therefore should be deceived by the illusions. An interesting additional effect is the observation that the influence of the visual illusions on pointing did increase with prolonged delay between presentation of the stimulus configuration and performance of the task. This was interpreted as reflecting the fast decay of the egocentric representation. The egocentric information is no longer available and the motor system has to use the less adequate perceptual information of the ventral stream to guide action.

However, this interpretation has also been criticized. Post and Welch (1996) argued: (a) Only open–loop conditions should be considered as valid tests for the perception

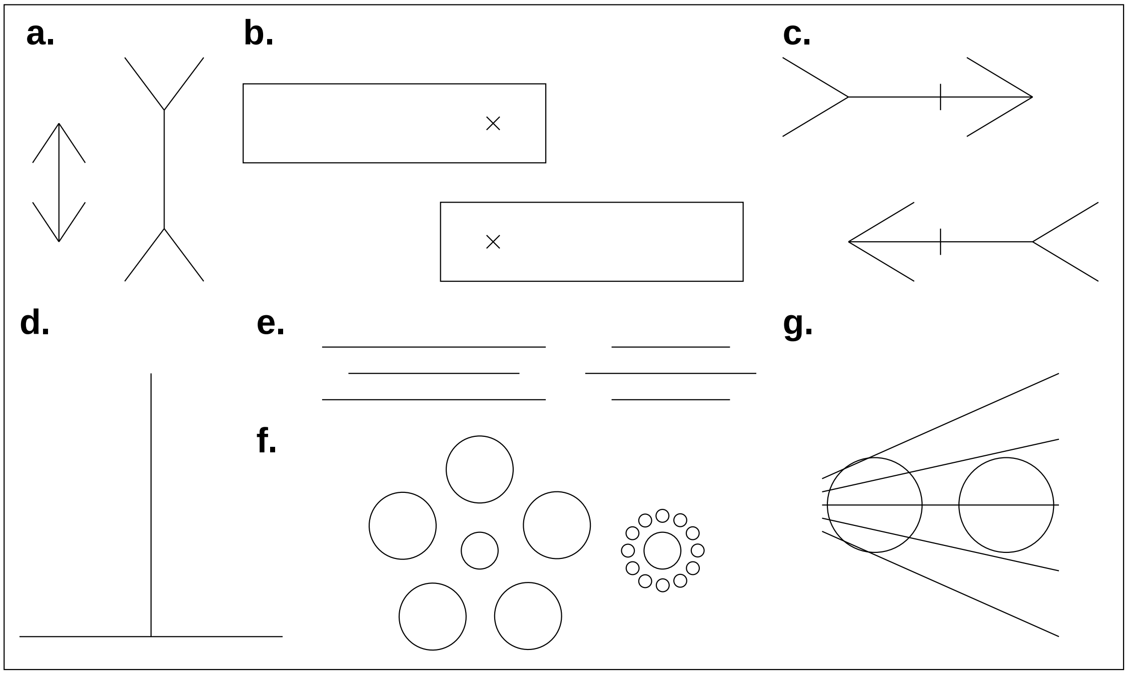

Figure 2.8: Visual illusions that were employed by the studies described in the text. **a.** Müller–Lyer Illusion (Müller–Lyer, 1889). The shafts have the same length, but the shaft with the outward pointing fins appears larger. **b.** Roelofs effect (Roelofs, 1935). The crosses are vertically aligned, but the frame offset to the left makes the cross appear farther to the right. **c.** Judd Illusion (Judd, 1899). Both marks bisect the shafts, but appear displaced relative to the shaft in the direction in which the arrows point. **d.** Horizontal–Vertical Illusion (Fick, 1851). The horizontal line and the vertical line have the same length, but the vertical line appears longer. **e.** Parallel–Lines Illusion (Wundt, 1898). The central lines have the same length, but the line between the long lines appears longer than the line between the short lines (assimilation effect). With a larger separation between the central lines and the context lines this effect can also be reversed, such that the line between the long lines appears shorter than the line between the short lines (contrast effect, cf. Jordan & Schiano, 1986) **f.** Ebbinghaus Illusion (Ebbinghaus, 1902). The central circles have the same diameter, but the central circle surrounded by large context circles appears smaller. **g.** Ponzo Illusion (Titchener, 1901). The circles have the same diameter, but the circle which is closer to the (theoretical) apex appears larger.

versus action hypothesis because in full–vision conditions the participants could simply match the visual image of the limb with the image of the target. In consequence the conditions with the smallest illusion effect in the study of Gentilucci et al. (1996) cannot be counted in favor of the perception versus action hypothesis. (b) The perceptual tasks in the studies of Mack et al. and Gentilucci et al. required to compute an extent (i.e., the length of the Müller–Lyer shaft), while the motor task required to compute a location (i.e., the vertices of the Müller–Lyer figure). Post and Welch suggested that the dissociation is not between perception and action, but between estimating extent and location. They demonstrated this in two motor tasks on the Judd illusion (Figure 2.8c). In both tasks participants were asked to indicate the midpoint of the shaft of the Judd figure by pointing open–loop to it. In the extent–estimation task there was no mark present in the middle of the shaft while in the location–estimation task the mark was present. This manipulation sufficed to differentially influence pointing: Pointing was affected by the illusion in the extent–estimation task, while it was unaffected in the location–estimation task.

2.5.3 Grasping and visual illusions

In the light of the psychophysical studies described so far the status of the perception versus action hypothesis is ambiguous. There is a wealth of empirical findings that are counted in favor of the theory but there is also serious criticism on the validity of these conclusions. In this situation a finding of Aglioti et al. (1995) employing a visual illusion has drawn considerable interest because it seemed to support the perception versus action hypothesis in an ideal way.

Visual size illusions are often induced by a special arrangement of objects. For example, the Ebbinghaus (or Titchener) Illusion consists of one central circle that is surrounded by a number of context circles. If the context circles are larger as the central circle then the central circle is perceived smaller than without context circles. Conversely, if the context circles are smaller then the central circle is perceived enlarged (Figure 2.8f). The Ebbinghaus Illusion is a typical size–contrast illusion: The size difference between the central circle and the context circles is amplified. Size differences can also be attenuated, a process which is often called assimilation (cf. Coren & Girgus, 1978). An example for assimilation is the Parallel–Lines Illusion (Figure 2.8e). In this illusion, the longer context lines cause the central line to be perceived as being longer, while the shorter context lines cause the central line to be perceived as being shorter.

The question which mechanisms are involved in visual illusions has been subject to considerable debate (e.g. Gregory, 1963; Day, 1972; Coren & Girgus, 1973). It seems clear today that a size–constancy mechanism is involved. The mechanism normally enables us to compensate for differences in retinal image size which are caused if an object is viewed at different distances (e.g., Holway & Boring, 1941). The mechanism has to integrate a number of different depth cues and can be deceived by misleading cues provided by visual illusions. However, is also seems clear today, that size–constancy cannot be the only mechanism responsible for visual illusions. For example, lateral inhibition might play an important role, independent of size–constancy (for review see Coren & Girgus, 1978).

With respect to the perception versus action hypothesis the interesting fact is that in the Ebbinghaus Illusion the context elements exert an influence on the central circle. In the framework of the perception versus action hypothesis, this influence could be created in the ventral stream because this stream operates in allocentric coordinates (an object is coded relative to other objects in the field). In contrast, the dorsal stream is believed to operate in egocentric coordinates and consequently could be unaffected by the illusion. Therefore, it seemed likely that motor actions directed at the central element of the Ebbinghaus Illusion are unaffected by the illusion.

Aglioti et al. (1995) tested this idea by presenting the Ebbinghaus Illusion with a thin disc ("poker–chip", 3 mm thick) instead of the central circle. This was done to enable the participants to grasp the discs. While reaching to grasp an object the index finger and thumb open to a maximum aperture that is already linearly related to the object's size (Figure 2.9, cf. Jeannerod, 1981, 1984). This maximum preshape aperture (MPA) is formed well before the hand has any contact with the object. Therefore, it reflects an early size estimate that is used by the motor system. If no other than visual cues are available then this estimate must have been computed from the visual input. Due to the linear relationship between the MPA and the size of the object it is possible to determine whether the illusion affected this size estimate that is used by the motor system.

Of course, some precautions have to be taken that no other sources of information about the true size of the object are available for the participant. For example, Post and Welch (1996) suggested that reaching and grasping should be performed without seeing the hand (open–loop) to avoid online adjustments during the movement.

In order to test whether grasping is affected by the Ebbinghaus Illusion, Aglioti and coworkers used a "titration" paradigm. The main idea of this procedure is to find ("titrate") a pair of discs that is perceived as being equal in size if presented in the illusion (Figure 2.10). If grasping is affected to the same amount by the illusion as perception, then the MPA while grasping the discs should be equal (see Appendix B.2 for a formal deduction of this prediction). If, on the other side, grasping is not affected by the illusion then the MPA should reflect the physical size difference between the two discs.

To implement this idea, Aglioti and coworkers selected in a pre–test for each participant a pair of discs which appeared to the participant as being equal in size if presented in the Ebbinghaus Illusion. For most participants this required a size difference of 2 mm (e.g., diameters of 28 mm and 30 mm). For ease of presentation these discs will be called

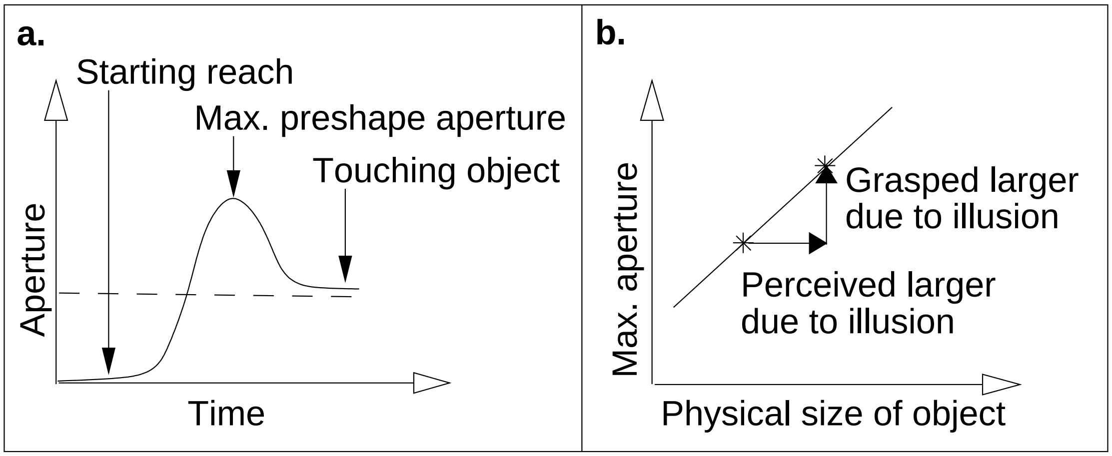

Figure 2.9: Maximum preshape aperture (MPA). **a.** Typical time course of the aperture between index finger and thumb during the transport component of a prehension movement. After about 70% of movement time a maximum is reached, the maximum preshape aperture. **b.** For intermediate object sizes (app. 2 cm to 6 cm) the MPA is linearly related to the physical size of the object. This allows to predict the effect that a visual illusion should exert on MPA— given that grasping and perception share the same internal representation of object size.

S (small) and L (large) disc in the following.

During testing, the S and L discs were presented inside the Ebbinghaus figures in various combinations. Aglioti and coworkers distinguished between two trial types (see Appendix C for a detailed description and discussion of the trial types). In “perceptually different” trials, either two S discs or two L discs were presented (top panel of Figure 2.10). In “perceptually same” trials, the S disc was presented within small context circles and the L disc within large context circles, just as had been done during the pre–test (lower panel of Figure 2.10). The whole display could be rotated such that for each participant in half of the trials the large context circles were on the left and in half of the trials they were on the right.

Each trial was prepared by the experimenter in the dark. Then the light went on for 3 sec. Half of the participants had received the instruction: “if you think the two discs are the same size, pick up the one on the left; if you think they are different in size, pick up the one on the right” (Aglioti et al., 1995, p. 681). The other half of the participants received instructions with the left–right assignments being reversed. The participants grasped while the light was on, then the light went off, and the experimenter prepared the next trial.

The critical condition was the “perceptually same” condition in which the two discs

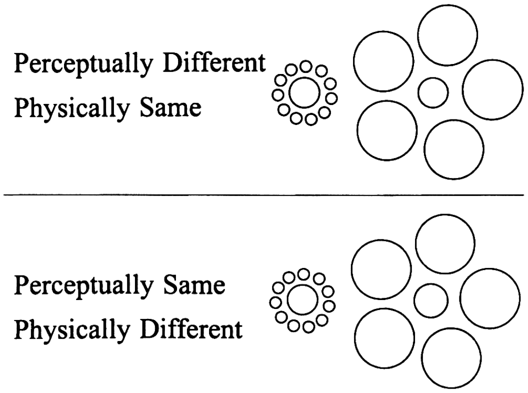

Figure 2.10: The two major classes of trial types in the Aglioti paradigm (Aglioti et al. 1995). In the top figure the two central circles are of the same physical size, but appear different; in the bottom figure the circle surrounded by large context circle is slightly larger in order to appear approximately equal in size to the other central circle. In the actual experiment of Aglioti et al. (1995), the central circle was replaced by a plastic disc that was grasped by the participants. Reprinted from Milner & Goodale (1995).

were perceived as being equal in size though they were physically different. Results showed that, despite being perceived as equal in size, the MPA in grasping differed between the two discs. Clearly, this seemed to show that grasping is not (or only little) affected by visual illusions.

The study was replicated by Marotta, DeSouza, Haffenden, and Goodale (1998) using the same design (which will be called in the following Aglioti paradigm). Marotta et al. (1998) also found that the MPA in grasping was different between two discs that were perceived as being equal in size (however, this was only true if the participants viewed the objects binocularly, with monocular viewing there was no significant difference in grasping between the two discs).

A second replication, again using the Aglioti paradigm, was performed by Haffenden and Goodale (1998). Again, the MPA was different between two discs that were perceived as being equal in size. In this study, grasping was performed “open–loop” (participants could not see their hand during grasping), eliminating critique that could be raised against the study of Aglioti et al. and of Marotta et al. (e.g., Post & Welch, 1996). Haffenden and Goodale (1998) did also add a second task to the Aglioti paradigm. In this task, participants did exactly the same as in the grasping task, but instead of grasping one of the discs they indicated the size of the disc by opening index finger and thumb (without seeing hand or stimulus). After this, they grasped the disc (this was done to provide the same amount of haptic feedback as in the grasping task). Haffenden and Goodale interpreted this "manual estimation" task as being perceptual in nature and therefore tapping the ventral stream. They assumed that this task requires totally different control structures as grasping and that participants do a kind of manual "read–out" of what they perceive (Haffenden & Goodale, 1998, p. 125). This view was supported by the finding of Goodale et al. (1991) that the patient D.F. scaled MPA normally to the size of objects (interpreted as reflecting the intact dorsal stream), while she was not able to indicate the size of the objects using index finger and thumb (interpreted as reflecting the impaired ventral stream). The advantage of using the manual estimation task was, of course, that now the whole procedure was as similar as possible between the motor task (grasping) and the perceptual task (manual estimation). The results of the manual estimation task seemed to support the original finding of Aglioti et al. (1995) in an ideal way: While grasping showed a difference between two discs that were perceived as being equal, manual estimation did not.

Taken together, the results of all three studies seemed to suggested a straightforward interpretation: "Size–contrast illusions deceive the eye but not the hand" (Aglioti et al., 1995, title of the study). It seemed that visual illusions provide an elegant way to show the different processing characteristics of the dorsal and the ventral stream in healthy humans.

Nevertheless, there remained some questions open. The titration procedure allows only a binary interpretation of the results. Either, one can conclude that grasping is affected by the illusion (if in the "perceptually same" condition there is no difference between the two discs in grasping), or one can conclude that grasping is not affected by the illusion (if there is a difference in grasping). However, it could very well be that grasping is *less* affected by visual illusions than perception. For example, Daprati and Gentilucci (1997) suggested this possibility. To solve questions like this, one needs to estimate the size of the effects the illusion exerts on grasping and on perception. Clearly, this is possible. One simply has to compute the difference between one disc being grasped if it is surrounded by large context circles versus the same disc being grasped if it is surrounded by small context circles.

This computation is also possible in the Aglioti paradigm (see Appendix C for a detailed description). Aglioti et al. (1995) reported these results, but not Haffenden and Goodale (1998) and Marotta et al. (1998). Aglioti et al. (1995) found (a) a clear effect of the illusion on grasping and (b) the absolute size of the effect (in mm) was significantly smaller than the effect on perception (cf. Figure 4.4b on page 46). A. Haffenden computed the corresponding values for her study (cf. Figure 4.4c), and the values were similar to the results of Aglioti et al., but the grasping effect was not significant (personal communication, August, 1998).

This aspect of the data does not fit to the notion that grasping is not affected by visual illusion. However, because the grasping effect was smaller than the perceptual effect, Aglioti et al. argued that the grasping effect might be due to a residual influence of the ventral stream and therefore reconciled the data with the perception versus action hypothesis.

In the following years further studies were performed that employed other visual illusions (Brenner & Smeets, 1996; Daprati & Gentilucci, 1997). All of these studies reported estimates for the grasping illusion and for the perceptual illusion. And in all of these studies, the grasping effect seemed to be smaller than the perceptual effect. These results did not only strongly support the perception versus action hypothesis but also influenced theorizing in such different fields of neuroscience as, for example, visual awareness (Koch & Braun, 1996), cognitive representation of space (Jackson & Husain, 1997), early visual processing (Marendaz, 1998), memory (Creem & Proffitt, 1998), and neuropathology (Milner, 1997).

Because of this theoretical importance, the findings of Aglioti et al. (1995) were tested extensively in the present study. Before describing the experiments, however, a methodological issue needs to be addressed. This is related to the question, whether it is possible at all to validly compare the illusion effects on grasping and on perception.

Chapter 3

Separate Representation Model versus Common Representation Model

Currently, three possibilities are discussed how visual illusions might influence grasping. The first is that grasping is not at all influenced by visual illusions. This is the *strong* version of the perception versus action hypothesis (Milner & Goodale, 1995). In the following this model will be called the strong Separate Representation Model because it assumes two different representations of object size, one for perception and one for action. It is easy to test this model. One just has to probe whether MPA is affected by visual illusions.

The second model allows for some crosstalk between the two representations (Aglioti et al., 1995; Milner & Goodale, 1995; Daprati & Gentilucci, 1997). This crosstalk leads to the *weak* version of the Separate Representation Model. Specifically, it is assumed that two separate representations of object size exist for the purposes of perception and action, respectively, and that there is some small effect of the perceptual representation on the motor representation. The model predicts that the motor illusion is decreased, compared to the case where one representation of object size exists. Naturally, this leaves the problem of predicting the size of the full motor illusion for a common representation of object size.

Most of the previous studies have solved this problem by predicting that the full motor illusion should have the same numerical magnitude as the perceptual illusion (e.g., if

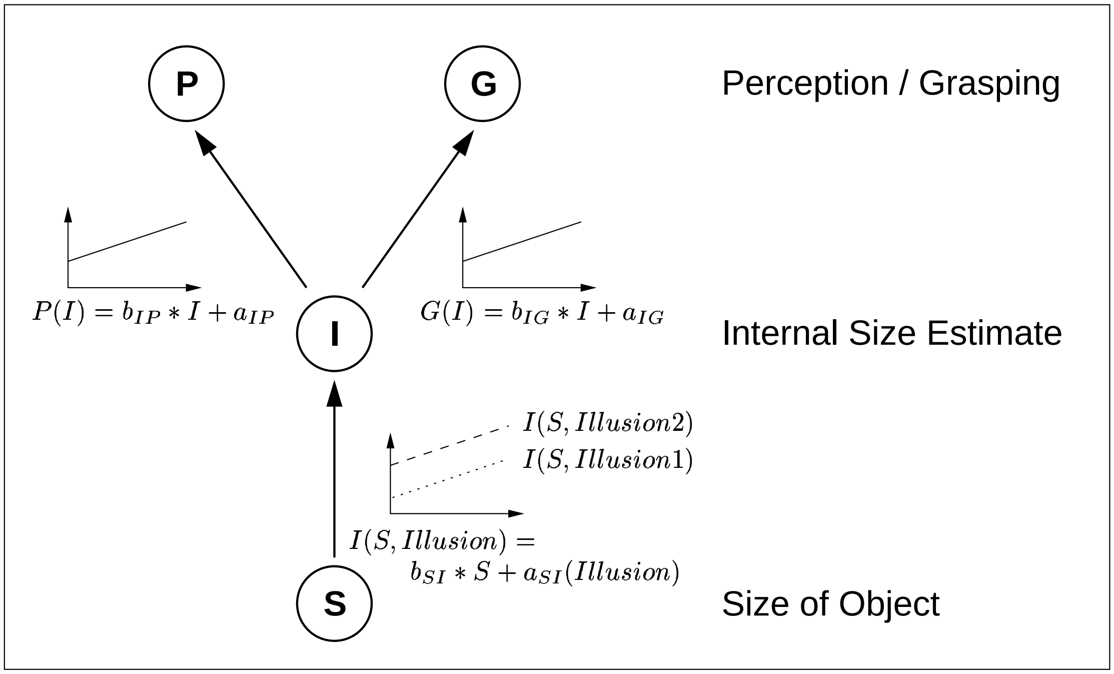

Figure 3.1: An explicit version of the Common Representation Model. See the text and the Appendix B for more details on this model.

perception were deceived by 1 mm the full motor illusion would be predicted to be also 1 mm). While this prediction is valid in the end, it is not at all obvious. To justify it one needs some (plausible) assumptions and the fact that MPA is a very well–behaved dependent variable. In the following these assumptions shall be made as explicit as possible.

The Common Representation Model assumes that only a single representation of object size exists. This representation is influenced by the visual illusion and is used to generate the percept of size as well as to guide grasping. Given that both, MPA as well as perceived size depend linearly on physical size it is possible to use a linear model which can be tested easily (Figure 3.1). In this model the visual information is assumed to be transformed linearly into an internal representation of object size. This internal representation is influenced by the illusion. This influence is modelled by shifting the linear function that relates physical size to the internal representation by a fixed amount. The internal representation is then transformed linearly either to the perception of object size (i.e., to the response in the perceptual task) or to MPA (the response in the grasping task). Given this very simple model, it is possible to calculate the influence that the visual illusion has on MPA from the influence it has on the perceptual measure (see Appendix B.1):

$$\Delta_G = \frac{b_G}{b_P} * \Delta_P \qquad (3.1)$$

(Where Δ_G stands for the grasping illusion, Δ_P for the perceptual illusion, b_G for the slope with which the grasp–measure depends on physical size and b_P for the slope with which the perceptual measure depends on physical size). This relation can be even further simplified because the slopes b_G and b_P are usually similar — at least for standard perceptual measures (cf. the Experiments 1, 5, and 8). This simplifies the formula to:

$$\Delta_G = \Delta_P \tag{3.2}$$

This means that the explicit version of the Common Representation Model comes to the same prediction as was used in most previous studies (i.e., the motor illusion should equal the perceptual illusion). However, the prediction depends on the condition that the perceptual measure as well as MPA are linearly related to physical size with the same slopes. Therefore, it is necessary to test this condition by varying the physical size of the objects — especially if unusual (perceptual) measures are used.

Another fact that can be exploited to distinguish between the different models is that participants show inter–individual differences in the strength of the perceptual illusion and of the motor illusion. The question arises whether these differences are correlated across participants, for example whether a participant showing a large perceptual effect also shows a large motor effect. The strong version of the Separate Representation Model predicts that there is no correlation between the perceptual illusion and the motor illusion across participants — because the model does not predict any motor illusion at all. The Common Representation Model, on the other hand, clearly predicts an across-participants correlation between the motor illusion and the perceptual illusion. But, how big should this correlation be? This question is important for the interpretation of small and non–significant correlations. Are these correlations not significant because of a lack of statistical power — or can they be taken as evidence against the Common Representation Model? The problem here is that the inter–individual differences can be small compared to the overall noise–level.

Fortunately, it is possible to derive an upper bound for the expected value of the correlation. The idea is as follows. Assume that the perceptual measure would measure the internal representation without any noise. In this case, the perceptual measure would perfectly reflect the inter–individual differences between participants. The MPA would suffer from some noise that is added between internal representation and grasping (this assumption is necessary to account for the larger variance of the motor data). Given this model, the expected correlation between perceptual illusion and motor illusion equals the ratio of their standard deviations (see Appendix B.3):

$$\rho_{\Delta_P,\Delta_G} = \frac{\sigma_{\Delta_P}}{\sigma_{\Delta_G}} \tag{3.3}$$

Table 3.1: Optimal sample sizes for product moment correlations.

Correlation	$\beta = .20$	$\beta = .05$
.30	68	116
.40	37	63
.50	22	39
.60	15	25

Note. Given are the optimal sample sizes for a one–tailed test with a significance level of $\alpha = .05$. β is the Type II error. The power equals $1 - \beta$. For example, assume the expected value (the "true" value) of an across–participants correlation in the population was $\rho = .40$. Using a sample of $N = 37$ participants, the probability to obtain a significant outcome in a statistical test with $H_0 : \rho \leq 0$ and $H_1 : \rho > 0$ would be $1 - \beta = .80$. That is, (only) 4 out of 5 studies would come to the correct conclusion that there exists a correlation in the population. To improve this ratio, the sample size had to be increased even further. Data are from Cohen (1988).

Of course, this is an idealized model. Most importantly it is assumed that no noise is added in the transformation from the internal representation to the perceptual measure. Any such noise will reduce the expected value of the correlation. Therefore, the value will be called the Idealized Expected Correlation in the following. Note, that the Idealized Expected Correlation is — statistically speaking — a population parameter. That is, the measured values in a sample will fluctuate around the Idealized Expected Correlation and can — according to the laws of probability — very well be larger than the Idealized Expected Correlation.

The Idealized Expected Correlation gives a rough idea of the correlation size that can be expected and what sample sizes are required to provide enough statistical power to reliably detect this correlation. For example, in the experiment on the Ebbinghaus Illusion (Experiment 1), there was an Idealized Expected Correlation of $\rho = .32$ while the empirical correlation was $\rho = .34$. Expecting a similar relationship in future research, one can calculate the optimal sample sizes to reliably detect such an effect. Cohen (1988) gives an optimal sample size of $N = 68$ for an expected correlation of $\rho = .30$ and of $N = 37$ for $\rho = .40$ (one–tailed test, $\alpha = .05$, $\beta = .20$). This shows that, in general, large sample–sizes are needed — at least to show that there is no correlation between perceptual effect and grasping effect (typically, studies used smaller sample sizes of eight to eighteen participants, cf. Table 7.1 on page 86). Table 3.1 gives an overview of the optimal sample sizes.

Table 3.2: Predictions of the competing models.

Model	Illusion effects	Across–participants correlation
strong Separate Representation Model	$\Delta_G = 0$	$\rho_{\Delta_P,\Delta_G} = 0$
weak Separate Representation Model	$0 < \Delta_G < \Delta_P$	$0 < \rho_{\Delta_P,\Delta_G} \ll \frac{\sigma_{\Delta_P}}{\sigma_{\Delta_G}}$
Common Representation Model	$\Delta_G = \Delta_P$	$0 < \rho_{\Delta_P,\Delta_G} \leq \frac{\sigma_{\Delta_P}}{\sigma_{\Delta_G}}$

Note. The predictions rest on specific assumptions that are described in the text and in the Appendix B. Δ_G stands for the grasping illusion, Δ_P for the perceptual illusion. $\frac{\sigma_{\Delta_P}}{\sigma_{\Delta_G}}$ is the Idealized Expected Correlation.

Since the Idealized Expected Correlation is only an upper bound for the expected value of the correlation, the measured correlation can hardly be used to discriminate between the weak Separate Representation Model and the Common Representation Model. Both models predict a smaller correlation than the Idealized Expected Correlation. The Common Representation Model does so because there will be noise in the perceptual system and the Separate Representation Model because of the incomplete crosstalk between the perceptual representation and the motor representation. Nevertheless, the correlation can be used to discriminate between the strong Separate Representation Model on one side and the weak Separate Representation Model and the Common Representation Model on the other side.

In summary, two relationships were described that can be used to distinguish between the models (see Table 3.2): (a) The sizes of the perceptual illusion and of the motor illusion discriminate between the strong Separate Representation Model, the weak Separate Representation Model, and the Common Representation Model. The strong Separate Representation Model predicts that there is no motor illusion at all. The Common Representation Model predicts that the motor illusion equals the perceptual illusion and the weak Separate Representation Model predicts that the motor illusion is smaller than the perceptual illusion. (b) The across–participants correlation between the perceptual illusion and the motor illusion can give some insights about the validity of the strong Separate Representation Model versus the weak Separate Representation Model and the Common Representation Model. The strong Separate Representation Model predicts no correlation between the perceptual illusion and the motor illusion (because it predicts no motor illusion at all). The weak Separate Representation Model as well as the Common Representation Model both predict a positive correlation. For these models it is possible to give an upper bound for the correlation, the Idealized Expected Correlation.

In the following these two relationships between perception and grasping will be used to evaluate the Ebbinghaus Illusion, the Müller–Lyer Illusion and the Parallel–Lines Illusion. Also, control experiments will be reported ensuring that the perceptual task and the motor task were adequately matched.

Chapter 4

Ebbinghaus Illusion

The first and most influential study investigating the existence of a dissociation between perception and grasping in visual illusions was performed by Aglioti et al. (1995) and was replicated by Haffenden and Goodale (1998)[1]. These *original studies* used the Ebbinghaus (or Titchener) Illusion: a central circle surrounded by large circles appears smaller than when surrounded by small circles (cf. Figure 2.8f on page 26). To determine the influence on grasping, the central circle was replaced with a disc which was grasped by the participants. Results showed a larger effect of the illusion on perception than on MPA. This was interpreted as strong evidence for the perception versus action hypothesis of Milner and Goodale (1995).

Several problems in the original studies encouraged a replication using an improved and simplified design. First, even though the effect on perception was larger, the original studies also found influences on grasping — as did other investigators (cf. Table 7.1 on page 86). It is difficult to draw clear conclusions from these studies, because some reported a statistically significant motor illusion while in others the effect of the illusion on grasping failed to reach significance. To resolve this apparent conflict a larger sample size was used in the present experiment.

Second, the original studies compared the influence of the illusion on the perceptual measures directly with the influence on MPA. For example, Aglioti et al. (1995) found an influence of 2.5 mm on perception and of 1.6 mm on grasping (cf. Figure 4.4b on page 46). Due to the statistically significant difference between these values ($p < .02$,

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[1] The study of Marotta et al. (1998) is not discussed here, because no estimates for the illusion effects in this study are available; cf. section 2.5.3.

$N = 14$), they concluded that the influence of the illusion on the motor system was dissociated from the influence on perception. However, this conclusion is only valid if the functions relating MPA to physical size and relating perceived size to physical size have the same slopes. If this is not the case, then one has to correct for the difference in slopes — as was argued in chapter 3 and is shown in equation 3.1 on page 34. To obtain a good estimate of these slopes, a wider range of disc sizes was used in the present study.

Third, in order to make the perceptual and motor tasks as similar as possible, only one Ebbinghaus figure was presented at a time: A central disc was surrounded by either large or small context circles (*single–context versions*, Figure 4.1a). In the perceptual task, participants indicated the size of the central disc by adjusting the radius of an isolated circle which was displayed on a monitor (Coren & Girgus, 1972b; Pressey, 1977). In the grasping task, participants grasped the central disc. This is different from the original studies in the following way. These studies used the *composite version* of the illusion (Figure 4.1b): Two Ebbinghaus figures, having different context circles, were presented simultaneously. In the perceptual task, participants directly compared the two central discs. In the grasping task, however, participants grasped only one of the discs on each trial. The overall effect of the illusion on grasping was then determined by adding the effects each context had on grasping. Note the asymmetry in this procedure. In grasping, participants operated on only one Ebbinghaus figure at a time, while in the perceptual task they operated on both figures simultaneously. A perceptual task that is more similar to the grasping task of the original studies is shown in Figure 4.1c: On each trial, participants compare an isolated circle to one of the central discs and the overall effect of the illusion on perception is then determined by adding the effects of the two separate comparisons. In using the direct comparison instead, the original studies implicitly rely on an additivity assumption: It is assumed that the perceptual effects of the two Ebbinghaus figures simply add up to yield the effect obtained by the direct comparison. The Experiments 3 and 4 will show that this is not the case. A direct comparison between two Ebbinghaus figures (Figure 4.1b) yields a larger effect than if the perceptual effects are determined for each figure separately and then added (Figure 4.1c).

Using the described simplified and improved design, Experiment 1 investigated whether grasping is affected by the Ebbinghaus Illusion.

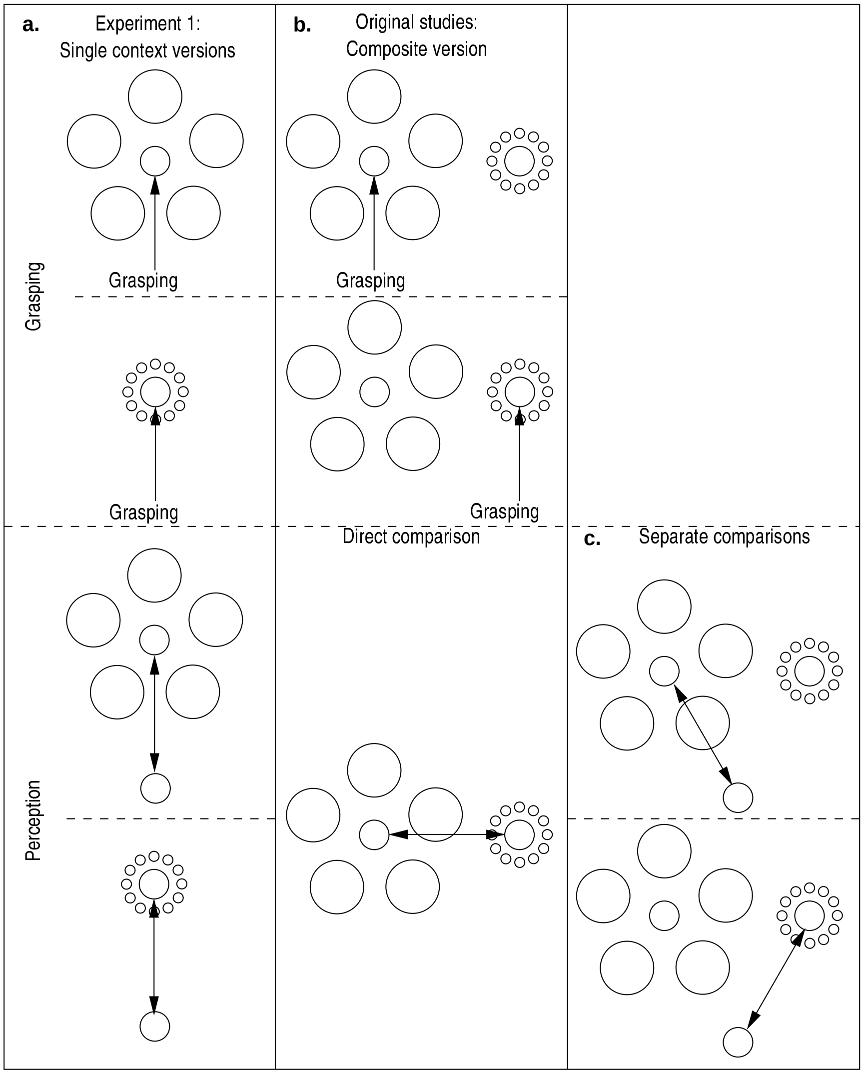

Figure 4.1: Stimuli used in the present experiments and in the original studies. **a.** In Experiment 1 participants operated on only one Ebbinghaus figure at a time (single–context versions). **b.** In the original studies of Aglioti et al. (1995) and of Haffenden & Goodale (1998) asymmetric measures were used: To perform the grasping task, participants had to calculate only the size of one of the central discs. In the perceptual task, participants had to compare the two central discs directly, both being subjected to the illusion at the same time. **c.** A perceptual task that is more similar to the grasping task of the original studies.

4.1 Experiment 1: Grasping the Illusion

In this experiment the effects of the Ebbinghaus Illusion on grasping and on perception were investigated and compared. The geometry of the Ebbinghaus figures was similar to the geometry used in the original studies of Aglioti et al., 1995 and Haffenden & Goodale, 1998. However, in an attempt to match perceptual task and motor task as much as possible, only one Ebbinghaus figure was presented at a time (single context versions, cf. Figure 4.1a)

4.1.1 Method

Participants Students of the University of Tübingen (and some pupils) participated in all experiments. In return for their participation, they received a payment of 13 DM per hour. Participants in all experiments had normal or corrected–to–normal vision (Snellen–equivalent of $20/25$ or better; Ferris, Kassoff, Bresnick, & Bailey, 1982). They had normal stereopsis of 60 seconds of arc or better (Stereotest–circles, Stereo Optical, Chicago). The participants of the grasping experiments (Experiments 1, 5, and 8) were all right–handed (Oldfield, 1971). Twenty six people (14 females and 12 males) participated in Experiment 1, ranging in age from 18 to 35 years (mean: 24.7 years).

Apparatus & Stimuli The apparatus of Experiment 1 is shown in Figure 4.2a. Participants sat on a stool in front of a monitor. Using a chin rest the position of the head was held constant throughout the experiment. At a distance of approximately 65 cm from the eyes, a 21 inch monitor (effective screen diagonal of 48.5 cm) was positioned. It was slightly tilted to orient its surface perpendicular to gaze direction. The monitor was used to present the comparison stimulus (an isolated circle) in the perceptual task. Also, it served as a table for the presentation of the target stimuli. For this purpose one of two boards was placed by the experimenter on top of the monitor. The context circles of the Ebbinghaus Illusion were drawn on these boards (black outlines on a white background). Aluminum discs (the targets) were placed in the middle of the context circles. On top of each disc a black circle on a white background was painted. The sides of the discs were painted black (cf. Figure 4.2b).

Attempting to generate large effects of the illusion the figural similarity between the three–dimensional central disc and the two–dimensional context circles was maximized (cf. Coren & Miller, 1974). This was achieved by minimizing shadows and having participants view the disc from above.

In all experiments concerning the Ebbinghaus Illusion, stimuli were chosen to be similar to the ones used in the original studies of Aglioti et al. (1995) and Haffenden and Goodale (1998). The large (small) context elements were 5 (12) circles, 58 mm (10 mm) in diameter, and the centers of the circles were 118 mm (60 mm) apart. In Experiment 1,

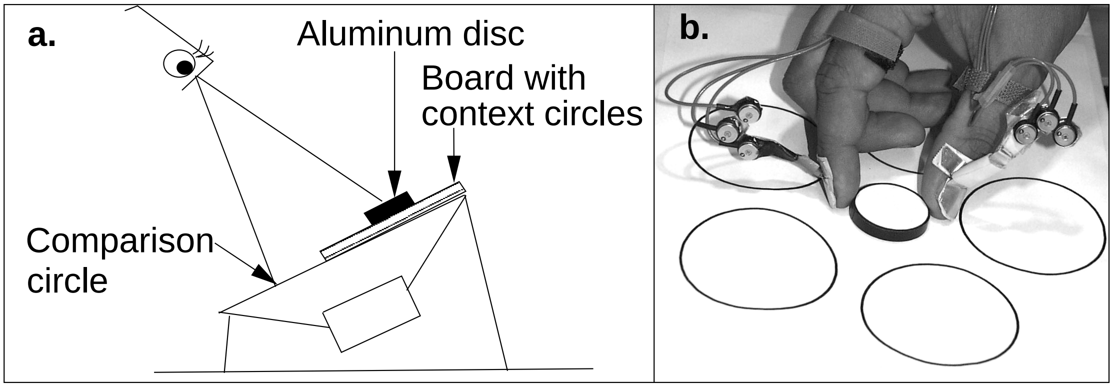

Figure 4.2: **a.** Apparatus used in Experiment 1. Participants viewed a board with either large or small context circles drawn on it. In the center of the context circles an aluminum disc was positioned. In the grasping task, participants grasped the disc. In the perceptual task, they adjusted a comparison circle displayed on the monitor to match the size of the aluminum disc. **b.** A participant grasping the aluminum disc. Note the three infrared light emitting diodes attached to thumb and index finger.

the isolated circle had a distance of 155 mm from the central disc. The central discs were 28, 31, 34 or 37 mm in diameter and 5 mm in height.

Procedure Participants wore liquid-crystal shutter glasses (Milgram, 1987) that were opaque while the stimuli for each trial were set up by the experimenter. Thereafter, the glasses became transparent and the required task was performed by the participant.

In the grasping task, participants grasped the central disc with their right hand. As soon as they started to move their hand away from the starting position the glasses became opaque again. Thus, the participants could neither see their hand nor the stimulus during grasping (open loop condition; Haffenden & Goodale, 1998; Jeannerod, 1981; Post & Welch, 1996). The participants grasped the central disc, moved it to the side, and replaced their hand in the starting position. Then the experimenter prepared the next trial. The grasp trajectory was recorded using an Optotrak^{TM} system: Three infrared light emitting diodes were attached to thumb and index finger (Figure 4.2b) allowing precise recording of orientation and position. The sampling rate was 100 Hz. For each grasp the MPA between the tips of index finger and thumb was calculated. For a detailed description of this system see Appendix D.

In the perceptual task, participants adjusted the comparison circle to match the size of the central disc. The adjustment was done by pressing the buttons of a computer mouse. After the participants finished their adjustment, the glasses became opaque again and the experimenter prepared the next trial.

The grasping task and the perceptual task were run in separate blocks, with the order of the tasks being counterbalanced across participants. Before the beginning of the grasping task, ten practice trials were performed. In the perceptual task five practice trials were performed. Subsequently, each participant performed 72 grasps and 24 adjustments. Given eight different trial types (four sizes of the central disc x two contexts), participants performed nine grasps per trial type and three adjustments per trial type.

Data analysis In all experiments a significance level of $\alpha = .05$ was used for the statistical analyses. If not stated otherwise, repeated measures ANOVAs were performed using the Greenhouse–Geisser correction if a factor had more than two levels. This corrects for possible violations of the sphericity assumption in repeated measures data (the sphericity assumption can only be violated if a factor has more than two levels). For the Greenhouse–Geisser correction, the parameter ϵ is estimated ($0 < \epsilon_{min} \leq \epsilon \leq 1$), and is used to adjust the degrees of freedom of the F–distribution. If $\epsilon = 1$ no violation of sphericity was detected and the Greenhouse–Geisser correction has no effect. If $\epsilon < 1$ the resulting test is more conservative than if no correction was performed (Greenhouse & Geisser, 1959; Vasey & Thayer, 1987; Jennings, 1987).

4.1.2 Results

Illusion effects Figure 4.3 shows the mean adjusted size of the comparison circle and the mean MPA as functions of the size of the central disc and of the illusion–inducing context. In the perceptual task, the main effects of illusion–inducing context ($F(1, 25)$ = 144, $p < .001$) and of size of central disc ($F(3, 75)$ = 2785, $\epsilon = .85$, $p < .001$) were highly significant. The interaction between the two factors was also significant ($F(3, 75)$ = 7.0, $\epsilon = .87$, $p = .001$). Similarly, in the grasping task the main effects of illusion–inducing context ($F(1, 25)$ = 15, $p = .001$) and of size of central disc ($F(3, 75)$ = 175, $\epsilon = .68$, $p < .001$) were highly significant. The interaction was not significant ($F(3, 75)$ = 0.6, $\epsilon = .75$, $p = .60$).

The slopes for perception ($s = 1.10 \pm 0.01$) and for grasping ($s = 1.12 \pm 0.06$) were similar ($t(25)$ = 0.35, $p = .73$). As reasoned in chapter 3, this finding allows a comparison of the illusion effects. For this purpose, overall illusion effects were calculated by averaging the illusion effects across all sizes of the central disc.

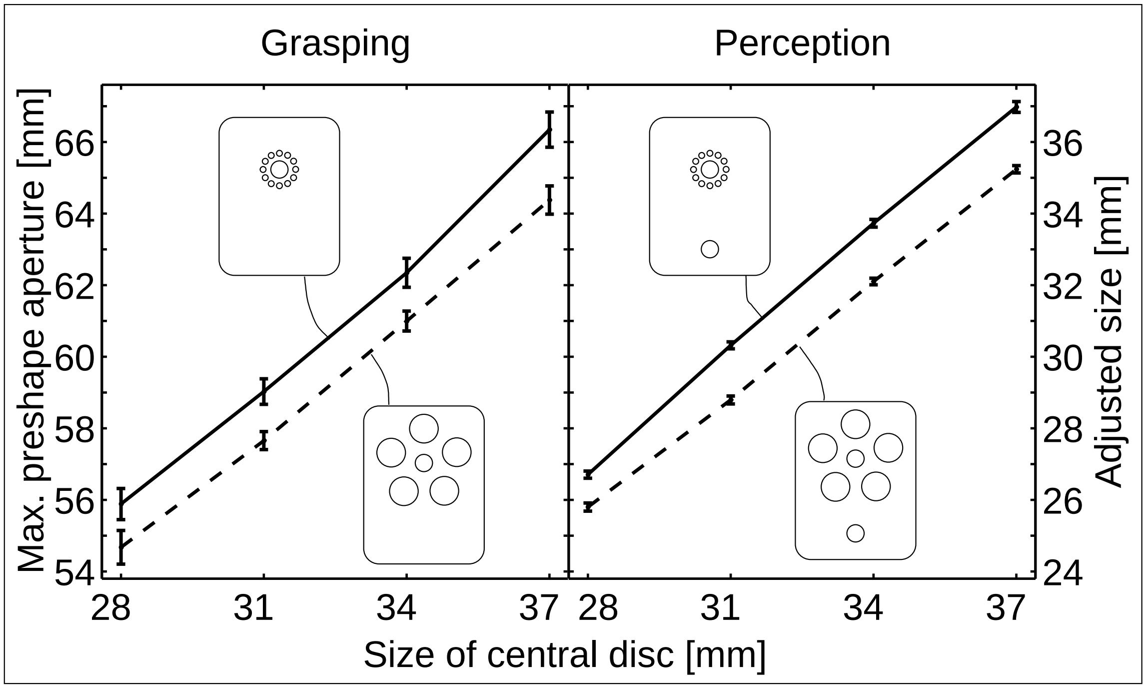

Figure 4.3: Effects of the Ebbinghaus Illusion on size perception and on maximum preshape aperture (MPA) for each diameter of the central disc in Experiment 1. Solid lines represent data for small context circles, dashed lines for large context circles. Error bars depict ±1 standard error of the mean. Data are normalized to account for absolute differences in aperture sizes between participants. See Appendix A for a description of the normalization.

Comparing motor illusion with perceptual illusion The overall illusion effects averaged across all sizes of the central disc are shown in Figure 4.4a. The overall effects of the illusion on grasping and on perception were equal ($t(25)$ = 0.07, $p = .94$). The overall illusion effects calculated for each participant individually are shown in Figure 4.5a on page 47. The individual grasping illusion was predicted by the individual perceptual illusion with a slope of $s = 1.1$. The corresponding correlation was significant ($\rho = .34$, $t(24)$ = 1.76, $p = .045$, one–tailed). The Idealized Expected Correlation (cf. description in chapter 3) was $\rho_{P,G} = \frac{\sigma_{\Delta_P}}{\sigma_{\Delta_G}} = \frac{0.62}{1.93} = .32$.

Development of the illusion over time In order to test whether the repeated presentation of the Ebbinghaus figure caused a decrement of illusion strength (for discussion of this topic see: Day, 1962; Coren & Girgus, 1972a; Schiano & Jordan, 1990; Predebon, 1998), the illusion effects were calculated separately for each trial. This was done in the framework of a multiple regression analysis: The values of each trial were corrected for

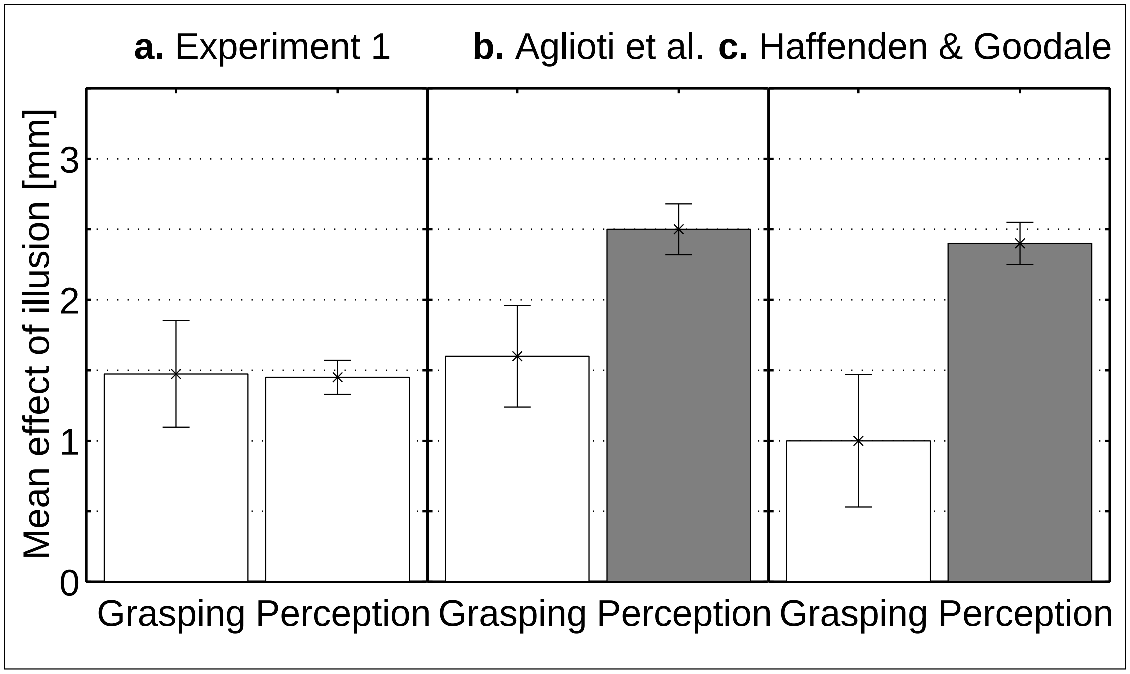

Figure 4.4: Overall effects of the Ebbinghaus Illusion on size perception and on maximum preshape aperture (MPA) in Experiment 1 and in the original studies. Conditions in which a direct comparison between two Ebbinghaus figures was required are filled. **a.** In Experiment 1, the illusion affected grasping just as much as perception. **b.** In the Aglioti et al. (1995) study, the illusion affected grasping significantly less than perception. **c.** Haffenden & Goodale (1998) replicated the findings of Aglioti et al. (1995). (A. Haffenden, personal communication, August 1998). Error bars depict ±1 standard error of the mean.

the effects of the factor participant and of the factor diameter of the central disc. The illusion effect was then calculated as the difference between the values for the large context circles and the values for the small context circles. Results are shown in Figure 4.5b. The linear regression of illusion effect as a function of trial–number showed neither in the perceptual task nor in the grasping task a decrement of the illusion effect over time:

Perception: $IE = -0.002 * TN + 1.50$ [mm]; $t(22)$ = -0.2, $p = .83$
Grasping: $IE = +0.004 * TN + 1.35$ [mm]; $t(70)$ = 0.3, $p = .76$

(IE stands for illusion effect and TN for trial–number. The t–value tests the slope of the regression).

Duration of stimulus presentation In the perceptual task, the stimulus was presented for as long as the participants needed to perform the adjustment. In the grasping task, vis-

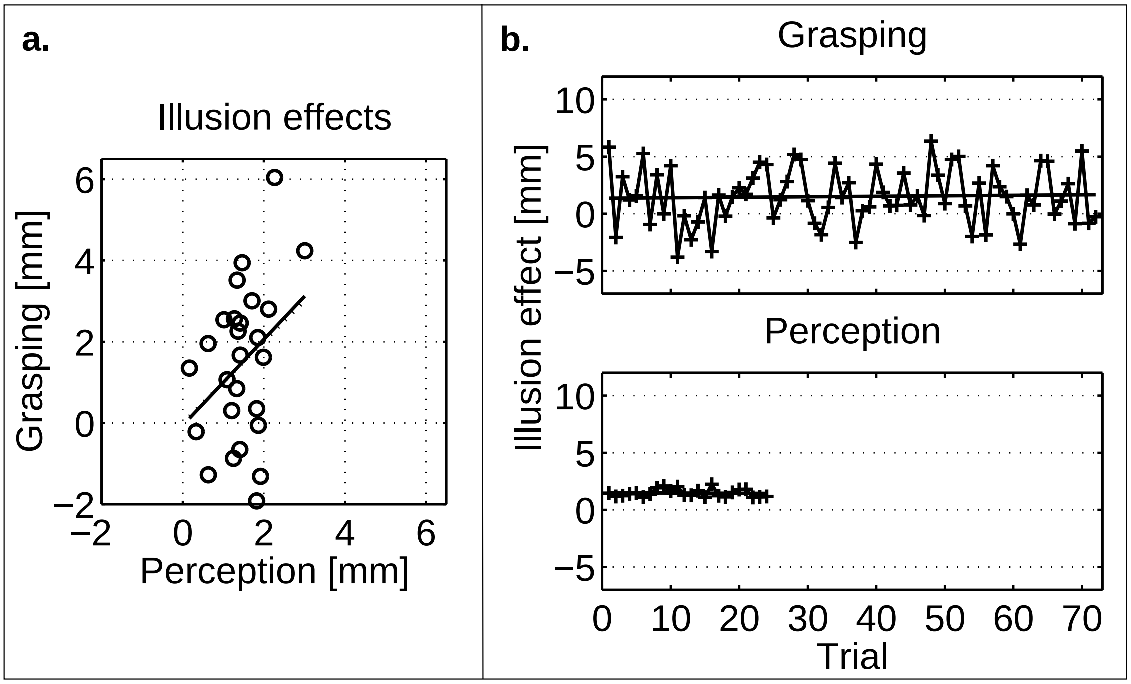

Figure 4.5: Further analyses of the results of Experiment 1. **a.** Overall illusion effects calculated separately for each participant and correlated across participants. Each data point depicts the motor illusion and the perceptual illusion of one participant. The solid line is the linear regression over all data points. The dashed line bisects the first quadrant. **b.** Illusion effects calculated separately for each trial. The solid line is the linear regression over all data points. See text for details.

ibility was suppressed by closing the glasses as soon as the participants started to move their hand. The average time until movement onset and (consequently) the average stimulus presentation time in the grasping task was 825 msec. In an ANOVA it was tested whether the onset of the movement was affected by the experimental conditions. There were no statistically reliable effects of size of central disc, of illusion–inducing context, nor of the interaction between these two factors (all $p > .33$).

4.1.3 Discussion

There were clear and highly significant effects of the Ebbinghaus Illusion on grasping as well as on perception. The magnitudes of the illusion effects were in a range typically found for the Ebbinghaus Illusion (Coren & Girgus, 1972b; Coren & Miller, 1974). Also, the grasping effect and the perceptual effect were almost perfectly equal. Finally, there was a significant across–participants correlation between perceptual illusion and motor illusion. The correlation was of about the size that was predicted by the Idealized Expected

Correlation (cf. chapter 3). These results clearly contradict the notion that the effects of the Ebbinghaus Illusion are dissociated between action and perception.

In the perceptual task of Experiment 1, the adjusted size of the comparison circle was always smaller than the physical size of the central disc (cf. Figure 4.3). This might be interpreted as indicating that the normal perceptual Ebbinghaus Illusion was not induced in this experiment, since the small context circles should lead to an overestimation. However, it is very common in illusion studies to find such a bias relative to the absolute size of the target (e.g., Coren & Girgus, 1972a; Girgus, Coren, & Agdern, 1972; Massaro & Anderson, 1971). These studies interpret such biases as constant errors being caused by differences in stimulus presentation between target and comparison. The constant error poses a problem only if one wants to compare the differential contributions of the two illusion configurations. In this case, one has to introduce a neutral condition in which the target is not influenced by the illusion. However, since this was not intended in this study, such a constant error does not pose a problem on the interpretation of the illusion effects.

The following experiments will follow two lines of investigation. First, Experiment 2 will test for one possible confound in the present experiment — the fact that presentation times were not the same in the perceptual task and in the grasping task. Second, it will be investigated why the original studies of Aglioti et al. (1995) and Haffenden and Goodale (1998) did find a difference between action and perception. A comparison shows that the grasping effects were similar in Experiment 1 and in the original studies (Figure 4.4). Only the perceptual effects were larger in the original studies. The Experiments 3 and 4 will test whether this enhancement is due to the direct comparison in the perceptual tasks of the original studies (requiring the additivity assumption, cf. Figure 4.1 on page 41).

4.2 Experiment 2: Effects of presentation time?

In the perceptual task of Experiment 1, participants had unlimited time to adjust the comparison circle. In contrast, presentation time was limited in the grasping task. As soon as the reach started, vision was suppressed by closing the shutter–glasses in order to have the grasps being performed open loop. The average presentation time in the grasping task of Experiment 1 was 825 msec. In Experiment 2 it was tested whether the perceptual effect of the illusion changes for shorter presentation times[2].

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[2] The mismatch in presentation time between perceptual task and grasping task has practical reasons. Because aluminum discs and two boards (with the context drawn on them) were used as stimuli in Experiment 1 each trial had to be set up manually by the experimenter. In order to keep the duration of the

4.2.1 Method

Eight people (5 females and 3 males) participated in Experiment 2, ranging in age from 20 to 36 years (mean: 28.3 years). Participants sat on a chair at a viewing distance of approximately 65 cm to a standard computer monitor (21 inches).

All stimuli were now presented on the monitor. That is, in contrast to Experiment 1 no real objects were presented. While in Experiment 1 the stimuli were presented on the table–like monitor and the axis between the comparison circle and the central disc was oriented along the sagittal plane of the observer, now stimuli were presented on a normal, upright monitor and the axis between the comparison circle and the central circle was horizontal. The isolated circle had a distance of 140 mm from the central circle. In all other respects, stimuli were identical to the stimuli of Experiment 1.

In the long inspection task, participants adjusted the comparison circle to match the size of the central circle. After they finished their adjustment, the stimuli disappeared from the screen. This procedure is similar to the perceptual task of Experiment 1. Each participant performed five practice trials first — and then two blocks of 24 trials each. Given eight different trial types (four sizes of the central circle x two contexts), participants performed six adjustments per trial type.

In the short inspection task the stimuli were displayed only for a duration of 800 msec. Participants had to decide whether the diameter of the comparison cirlce was larger or smaller than the diameter of the central circle (two–alternative forced choice task, 2AFC).

Each participant performed 15 practice trials first — and then six blocks of 80 trials each. Given eight different trial types, participants performed 60 judgments per trial type. The size of the comparison circle was determined via an adaptive up-down procedure: For each block and each trial type separate staircases were used with the comparison circle initially being either 5 mm larger or 5 mm smaller than the target. If the participant responded “larger” (“smaller”) the comparison circle was presented 1 mm smaller (larger) the next time this trial type was displayed. For data analysis, cumulative gaussians were fitted to the data and the point of subjective equality (PSE) was determined. The succession of the long inspection task and of the short inspection task was counterbalanced

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experiment in a reasonable range it was important to keep the number of trials per participant low. Using an adjustment procedure for the perceptual task allowed to measure the perceptual effect with only 24 trials per participant. The drawback is that in an adjustment procedure a trial takes longer than the 825 msec that were the presentation time in the grasping task. However, using a constant stimuli procedure which allows shorter presentation times would have strongly increased the number of trials needed (e.g., in the Experiment 2 there were 480 trials needed per participant to measure the perceptual effect with a constant stimuli procedure).

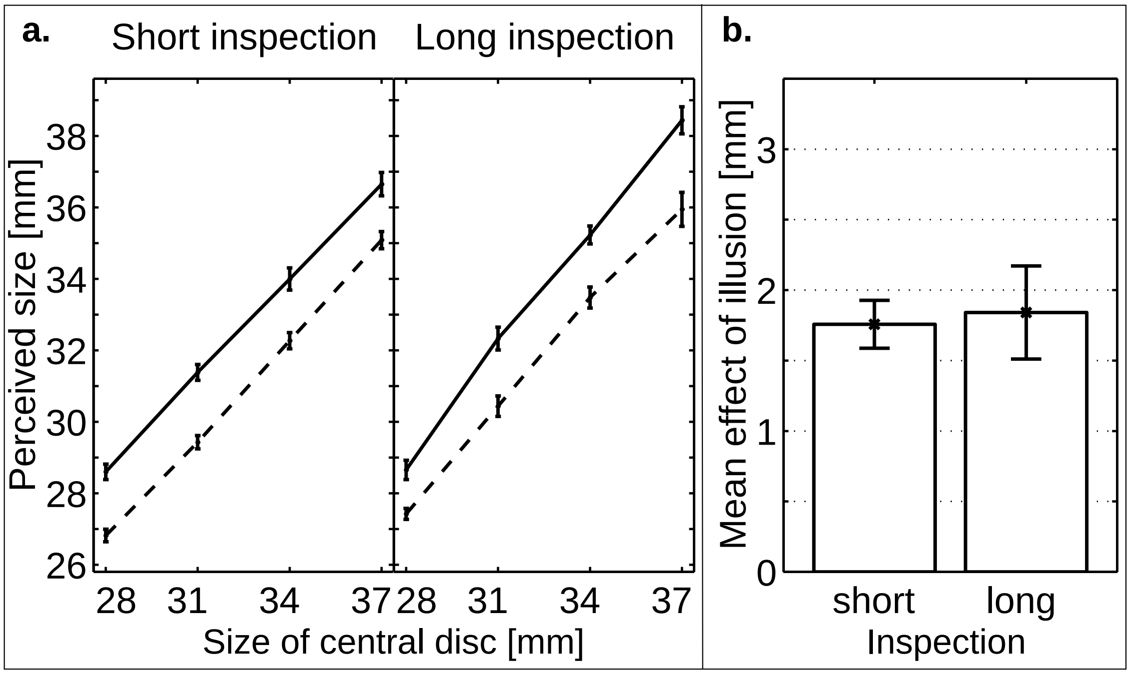


Figure 4.6: **a** Effects of the Ebbinghaus Illusion on size perception for each diameter of the central disc in Experiment 2. In the short inspection condition the mean PSEs (points of subjective equality) are shown as functions of the diameter of the central disc and of the illusion–inducing context. In the long inspection condition the mean adjusted sizes of the comparison circle are shown. Solid lines represent data for small context circles, dashed lines for large context circles. **b** Illusion effects pooled across all sizes of the central disc. Error bars depict ±1 standard error of the mean.

between participants.

4.2.2 Results and Discussion

Figure 4.6a shows the mean adjusted size of the comparison circle in the long inspection task and the mean PSEs (points of subjective equality) in the short inspection task as functions of the diameter of the central disc and of the illusion–inducing context. Figure 4.6b shows the illusion effects pooled across all sizes of the central disc.

An ANOVA for the illusion effect with the factors diameter of the central disc and task was performed. The illusion effect was highly significant ($F(1,7)$ = 65, $p < .001$). This effect depended significantly on the size of the central disc ($F(3,21)$ = 4.0, $\epsilon = .80$, $p = .03$). The effect of the size of the central disc was significantly different for the different tasks ($F(3,21)$ = 4.0, $\epsilon = .76$, $p = .04$). Figure 4.6a shows that this interaction was not very large and therefore does not seem to pose problems for the interpretation of the fact that there was no significant main effect of the task on the illusion effect ($F(1,7)$ = 0.1, $p = .77$) — as can also be seen in Figure 4.6b.

The results of Experiment 2 show that the illusion effect was almost the same for the short inspection task and for the long inspection task. This indicates that differences in presentation time between perceptual task and grasping task likely did not bias the results in Experiment 1.

4.3 Experiment 3: Test for additivity

The very good match between the perceptual effect of the Ebbinghaus Illusion and the motor effect that was found in Experiment 1 stands in contrast to the differences reported by Aglioti et al. (1995) and Haffenden and Goodale (1998). Because the geometries of the Ebbinghaus figures were almost the same between the studies, it is possible to compare the illusion effects (Figure 4.4 on page 46). The comparison shows that the grasping effects were similar in Experiment 1 and in the original studies. Only the perceptual effects were larger in the original studies. The Experiments 3 and 4 will test whether this enhancement is due to the direct comparison in the perceptual tasks of the original studies (requiring the additivity assumption, cf. Figure 4.1 on page 41).

In Experiment 3, the perceptual effects were measured for the two single–context versions (as in Experiment 1, Figure 4.1a on page 41), for a direct comparison (as in the original studies, Figure 4.1b) and for two separate comparisons (the suggestion for a better perceptual measure in the original studies, see Figure 4.1c). If the additivity assumption of the original studies holds, then the direct comparison should yield a similar effect than the sum of the effects of the two separate comparisons.

4.3.1 Method

Eighteen people (11 females and 7 males) participated in Experiment 3, ranging in age from 15 to 28 years (mean: 24.1 years). The central circles had diameters of 28, 31 and 34 mm. In the composite version, the centers of the central circles were 140 mm apart. The isolated circle had a distance of 140 mm from the central circle. Stimuli were identical to Experiment 1 in all other respects, except that they were presented on a computer monitor. The central element was now a two–dimensional circle and no longer a three–dimensional disc. This increased the figural similarity between central element and context elements, and therefore slightly increased the magnitude of the illusion (Coren &

Miller, 1974).

All three possibilities to assess the perceptual effect of the illusion were employed, as shown in the lower part of Figure 4.1 on page 41.

In the single context condition, participants adjusted the size of an isolated circle to match the size of the central circle in one Ebbinghaus figure. The effects of the large context circles and of the small context circles were added to obtain an estimate of the illusion strength.

In the direct comparison condition, participants adjusted the central circles of the two Ebbinghaus figures simultaneously. The difference between the two central circles that was needed for them to be perceived as equal in size was used as measure for the illusion strength.

In the separate comparison condition, participants viewed both Ebbinghaus figures, but adjusted the isolated circle to match the size of only one of the central circles. The illusion strength was calculated the same way as in the single context condition. Each participant performed a total of 75 adjustments.

4.3.2 Results

Figure 4.7a shows the illusion effects obtained in Experiment 3. There was a highly significant main effect of the illusion inducing context ($F(1,17)$ = 87, $p < .001$). The effect depended on the size of the central disc ($F(2,34)$ = 10, $\epsilon = .83$, $p = .001$) and on the adjustment condition ($F(2,34)$ = 6, $\epsilon = .96$, $p = .005$) — while these two factors did not interact ($F(4,68)$ = 0.5, $\epsilon = .80$, $p = .67$).

Post–hoc analyses revealed that the effects of the single–context versions and of the separate comparisons did not differ significantly (Tukey–test, $p > .10$) while the effect of the direct comparison was larger than the sum of the effects in the two separate comparisons (Tukey–test, $p < .05$) and than the sum of the effects in the single–context versions (Tukey–test, $p < .01$).

4.3.3 Discussion

The direct comparison yielded a larger perceptual effect than the sum of the effects in the separate comparisons. This failure of additivity contradicts the implicit assumption of the original studies that the perceptual effects of the two Ebbinghaus figures simply add up to yield the effect obtained by the direct comparison. Also, the results show that the illusion effect in the separate comparisons is similar to the effect in the single–context versions. Given that the motor illusions in all studies were similar to the perceptual illu-

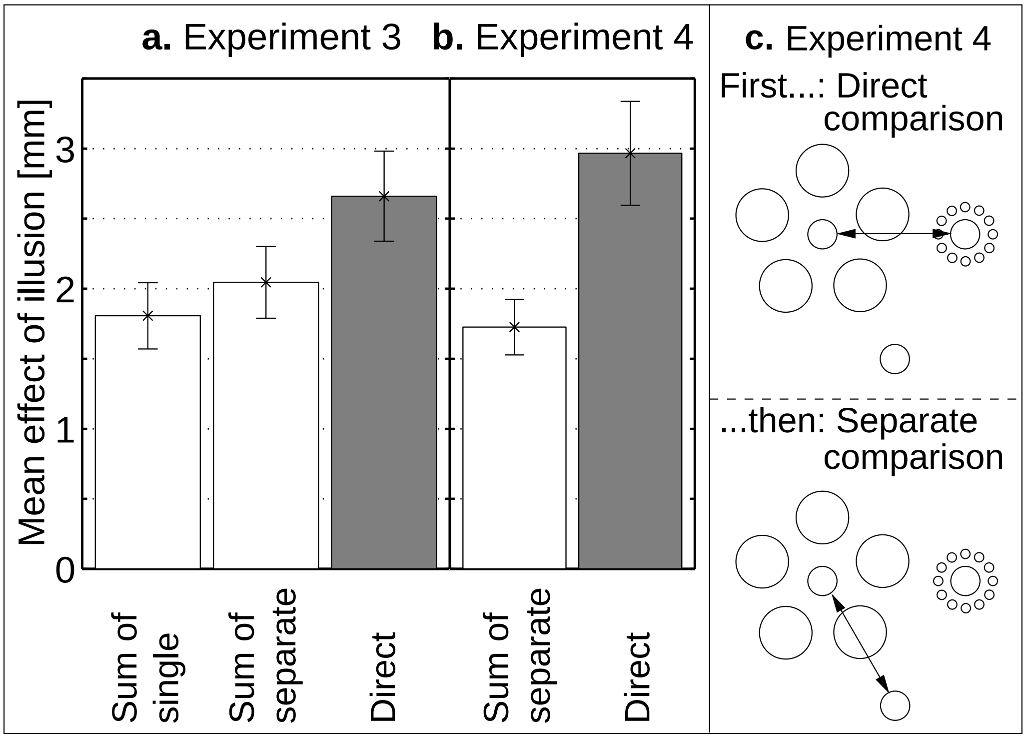


Figure 4.7: Effects of the Ebbinghaus Illusion in the Experiments 3 and 4. **a.** Experiment 3: The effect of the direct comparison was larger than the sum of the effects in the two separate comparisons and than the sum of the effects in the single–context versions. **b.** Experiment 4: Even if participants performed a direct comparison immediately before each separate comparison, the direct comparison showed a larger effect than the sum of the two separate comparisons. **c.** Typical trial of Experiment 4: Within 1 sec participants first compared the two central circles directly and then compared one of the central circles to the isolated circle. Error bars depict ±1 standard error of the mean.

sion in the single–context versions, this means that the additivity failure can account for the differences found between perception and grasping in the original studies.

These results show an interesting, non–additive effect in the Ebbinghaus Illusion: If participants directly compare two Ebbinghaus figures, they experience a larger size illusion than is predicted by the sum of the size illusions experienced in each figure separately. Interestingly, most quantitative research on the Ebbinghaus Illusion has been based on the single–context versions (e.g., Coren & Girgus, 1972b), while qualitative demonstrations of the illusion, for example in textbooks (e.g., Coren & Girgus, 1978), usually employ a direct comparison in the composite version and therefore exhibit an effect that is about 50% larger.

The additivity failure indicates that the perceptual task and the grasping task were not appropriately matched in the original studies (Aglioti et al., 1995; Haffenden & Goodale, 1998) — not allowing the conclusion that the differences between perception and grasping are due to a dissociation between perception and action.

One possible objection to this argument could be that in the original studies participants had to directly compare the two central discs immediately before grasping (this was done as a control for the perceptual effect). Could this direct comparison, in which participants were forced to attend to both central discs, induce additivity? This possibility was tested in Experiment 4.

4.4 Experiment 4: Did attention induce additivity?

In Experiment 4, the succession of the perceptual task and of the grasping task in the original studies was approximated more closely. Participants first compared the two central circles directly and then, immediately afterwards, compared one of the central circles to the isolated circle (Figure 4.7c). Both comparisons were performed within 1 sec, which is similar to the mean onset time for grasping in the Aglioti et al. (1995) study. If the first comparison induces additivity, then the effect in the direct comparison should equal the sum of the effects in the separate comparisons.

4.4.1 Method

Twelve people (9 females and 3 males) participated in Experiment 4, ranging in age from 21 to 30 years (mean: 25.7 years). The central circles had diameters of 31, 32, 33 and 34 mm. In all other respects, the stimuli and the apparatus were identical to Experiment 3. A typical trial of Experiment 4 is shown in Figure 4.7c. Participants performed the direct comparison and the separate comparison in direct succession, within 1 sec. Because this short time interval did not allow an adjustment procedure, constant stimuli and two two–alternative forced choice tasks were used. Each participant compared 462 configurations to complete the psychometric functions.

4.4.2 Results

Results are shown in Figure 4.7b. There was a highly significant main effect of the illusion inducing context ($F(1, 11)$ = 98, $p < .001$). This effect was highly significantly larger in the direct comparison than the sum of the effects in the two separate comparisons ($F(1, 11)$ = 12, $p < .005$).

4.4.3 Discussion

The results replicated Experiment 3: Again, the direct comparison yielded a larger perceptual effect than the sum of the effects in the separate comparisons. This is true despite the fact that in this experiment the separate comparisons were performed immediately after a direct comparison. This outcome provides evidence against the idea that in the original studies the direct comparison that was performed immediately before grasping could have induced additivity.

Another interesting aspect of these data is that they replicated the insensitivity of the Ebbinghaus Illusion to changes in presentation time that was found in Experiment 2. In the present experiment presentation time was limited to 1 sec. Within this time participants had to perform two “smaller” versus “larger” judgements. In contrast, participants had unlimited time to perform the adjustments required in Experiment 3. Nevertheless, the illusion effects were very similar (cf. Figure 4.7).

4.5 Discussion: Ebbinghaus Illusion

If perceptual and motor tasks are carefully matched, there are strikingly similar effects of the Ebbinghaus Illusion on perceived size and on maximum preshape aperture. In Experiment 1 the influence of the Ebbinghaus Illusion on grasping found by the original studies of Aglioti et al. (1995) and Haffenden and Goodale (1998) was replicated. The Experiments 3 and 4, however, show that the larger perceptual effect in the original studies is likely due to an additivity failure that selectively enhanced this effect.

These results are supported by the fact that since the first presentation of the results of Experiment 1 (Franz, Gegenfurtner, Bülthoff, & Fahle, 1998, see also Franz, Gegenfurtner, Bülthoff, & Fahle, 2000), there has been one more study using a similar paradigm (the single–context version in the Ebbinghaus Illusion) that reported a very similar outcome to Experiment 1. Pavani, Boscagli, Benvenuti, Rabuffetti, and Farnè (1999) found clear effects of the Ebbinghaus Illusion on perception and on grasping, the effects being almost identical between perception and grasping (cf. Table 7.1 on page 86).

These findings clearly contradict the notion that the effects of the Ebbinghaus Illusion are dissociated between action and perception. More specifically, they contradict the strong version of the Separate Representation Model because there is a motor illusion and an across–participants correlation between the perceptual illusion and the motor illusion. The results also contradict the weak Separate Representation Model because the motor illusion is of the same size as the perceptual illusion and because the across–participants correlation is not even decreased compared to the Idealized Expected Correlation. The results match the predictions of the Common Representation Model because the motor illusion and the perceptual illusion are equal and because there is an across–participants correlation between perceptual illusion and motor illusion that is of about the same size as the Idealized Expected Correlation.

As mentioned before, Haffenden and Goodale (1998) did not only replicate the study of Aglioti et al. (1995), but also employed an additional, non–standard perceptual measure. Participants estimated the size of one of the central discs using their thumb and index finger (without seeing their hand). The authors interpreted this manual estimation task as a perceptual measure. For the manual estimation they found a significantly larger influence of the illusion (4.2 ± 1 mm) than for grasping (1.0 ± 0.5 mm). However, the effect on manual estimation was also larger than on the standard perceptual measure discussed before (2.4 ± 0.2 mm, cf. Figure 4.4c on page 46 and Table 7.1 on page 86 for the illusion effects). This is even more pronounced if one corrects the standard perceptual measure for the non–additivity. Given that standard perceptual measures are much better understood (e.g., Coren & Girgus, 1972b) it seem problematic to infer a dissociation between perception and action based on the manual estimation task alone. For a further discussion of this topic see chapter 7.

The series of experiments described in this chapter identifies a mismatch between perceptual task and grasping task as the main source for the difference in perceptual illusion and motor illusion in the original studies. Given these results the question arises whether in other studies on other visual illusions similar problems arise. For this purpose, the Müller–Lyer Illusion and the Parallel–Lines Illusion were investigated (chapters 5 and 6).

Chapter 5

Müller–Lyer Illusion

Daprati and Gentilucci (1997) and Otto–de Haart, Carey, and Milne (1999) investigated the influences of the Müller–Lyer Illusion on perception and on grasping. The Müller–Lyer Illusion consists of a line with an arrow–like fin attached at each end. If the fins point inwards, the line (or shaft) is perceived as being shorter than if the fins point outwards (cf. Figure 2.8a on page 26).

Daprati and colleagues reported a clear effect of the illusion on grasping, while Haart and colleagues only found an effect on grasping if the illusion was viewed monocularly. With binocular viewing the grasping effect failed to reach significance (cf. Table 7.1 on page 86). In both studies, the grasping effect was smaller than the effect on perception (though the difference was not in both cases significant). However, both studies used non–standard perceptual measures: Either participants blindly drew a line to match the length of the shaft of the Müller–Lyer figure (Daprati & Gentilucci, 1997) or they indicated the length of the shaft using their index finger and thumb (Daprati & Gentilucci, 1997; Otto–de Haart et al., 1999). Both measures are not well established as measures for perception and therefore it seems beneficial to compare the motor illusion to a standard perceptual measure (e.g., Coren & Girgus, 1972b). Therefore, Experiment 5 was conducted. In this experiment an adjustment procedure was used as standard perceptual measure to assess the perceptual effect of the illusion (Coren & Girgus, 1972b).

5.1 Experiment 5: Grasping the illusion

In this experiment, the effects of the Müller–Lyer Illusion on grasping and on perception were assessed. As in Experiment 1, single context versions of the Müller–Lyer Illusion were used.

5.1.1 Method

Sixteen people (10 females and 6 males) participated in Experiment 5, ranging in age from 18 to 31 years (mean: 25.5 years). The apparatus was similar to Experiment 1 and is shown in Figure 5.1a. On top of the screen–surface, a black plastic bar (7 mm wide, 5 mm high and 40, 43, 46 or 49 mm long) was positioned as the target. At each end of the target bar, two black fins were displayed on the monitor. The fins were pointing either outward or inward, thus creating the Müller–Lyer figure. The outward pointing fins were 31 mm long and formed an angle of $30°$ with the main axis of the target bar. The inward pointing fins were 19 mm long and formed an angle of $150°$ to the main axis of the target bar. The fins were positioned relative to the sides of the shaft in such a way that the ends of the shaft were easily discriminable from the fins (Figure 5.1c). As in Experiment 1 the figural similarity between the three–dimensional target bar and the two–dimensional fins was maximized in order to generate large illusion effects. For this purpose, shadows were minimized and participants viewed the bar from above.

In the perceptual task, a comparison bar was displayed on the monitor. The comparison bar was parallel to the target bar at a distance of 80 mm. For each trial, the position of the comparison was randomly chosen to be left or right with a parallel displacement of ± 7 mm (Figure 5.1b). The initial length of the comparison bar differed randomly from the length of the target bar within a range of ± 10 mm. The comparison bar was 7 mm wide — as were all elements of the Müller–Lyer figure. The procedure was identical to Experiment 1.

5.1.2 Results

Illusion effects Figure 5.2a shows the mean adjusted length of the comparison bar and the mean MPA as functions of the length of the target bar and of the illusion–inducing context. In the perceptual task the main effects of illusion–inducing context ($F(1, 15)$ = 70, $p < .001$) and of length of target bar ($F(3, 45)$ = 394, $\epsilon = 0.75$, $p < .001$) were highly significant. The interaction between the two factors was not significant ($F(3, 45)$ = 0.8, $\epsilon = 0.87$, $p = .47$). Similarly, in the grasping task the main effects of illusion–inducing

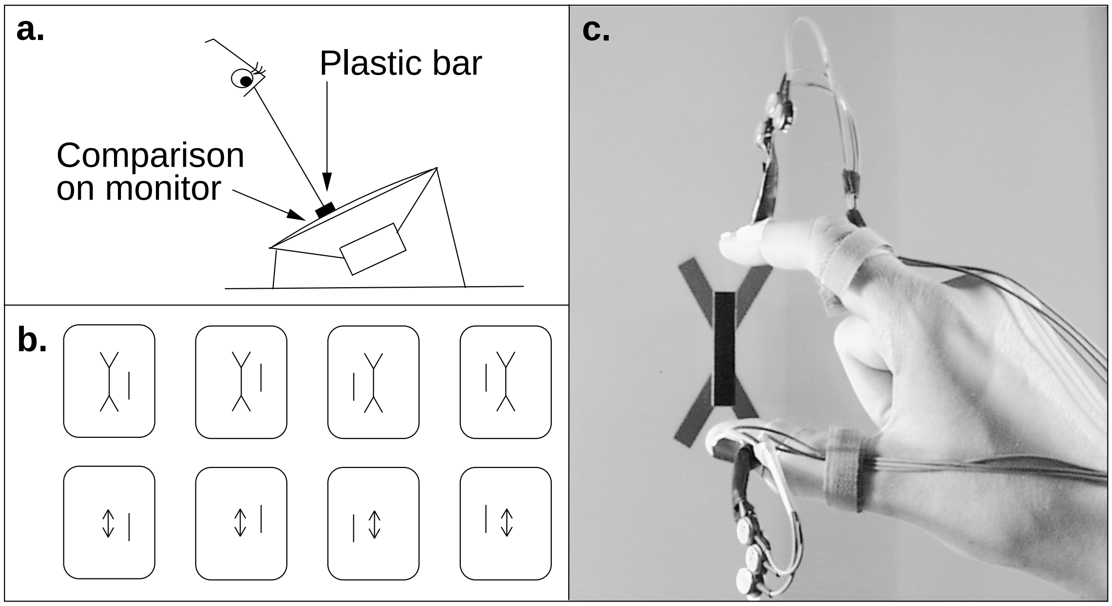


Figure 5.1: **a.** Apparatus used in Experiment 5. **b.** Stimulus conditions in the perceptual task. The comparison bar was displayed on the monitor at different positions relative to the target (left vs. right and up vs. down). **c.** A participant grasping the target bar. The fins of the Müller–Lyer figure were displayed on the monitor.

context ($F(1, 15)$ = 66, $p < .001$) and of length of target bar ($F(3, 45)$ = 136, $\epsilon = 0.59$, $p < .001$) were highly significant. The interaction was not significant ($F(3, 45)$ = 0.3, $\epsilon = 0.75$, $p = .8$).

The slopes for perception ($s = 0.88 \pm 0.03$) and for grasping ($s = 0.92 \pm 0.07$) were similar ($t(15)$ = 0.43, $p = .67$). As reasoned in chapter 3, this finding allows a comparison of the illusion effects. For this purpose, overall illusion effects were calculated by averaging the illusion effects across all sizes of the central disc.

Comparing motor illusion with perceptual illusion The overall illusion effects averaged across all lengths of the target bar are shown in Figure 5.2b. The overall effect of the illusion on grasping was significantly larger than on perception ($t(15)$ = 3.1, $p = .008$). The overall illusion effects calculated for each participant individually are shown in Figure 5.3a. The individual grasping illusion was predicted by the individual perceptual illusion with a slope of $s = 0.3$. The corresponding correlation was not significant ($\rho = .19$, $t(14)$ = 0.7, $p = .24$, one–tailed). The Idealized Expected Correlation (cf. description in chapter 3) was $\rho_{P,G} = \frac{\sigma_{\Delta_P}}{\sigma_{\Delta_G}} = \frac{0.97}{1.67} = .58$.

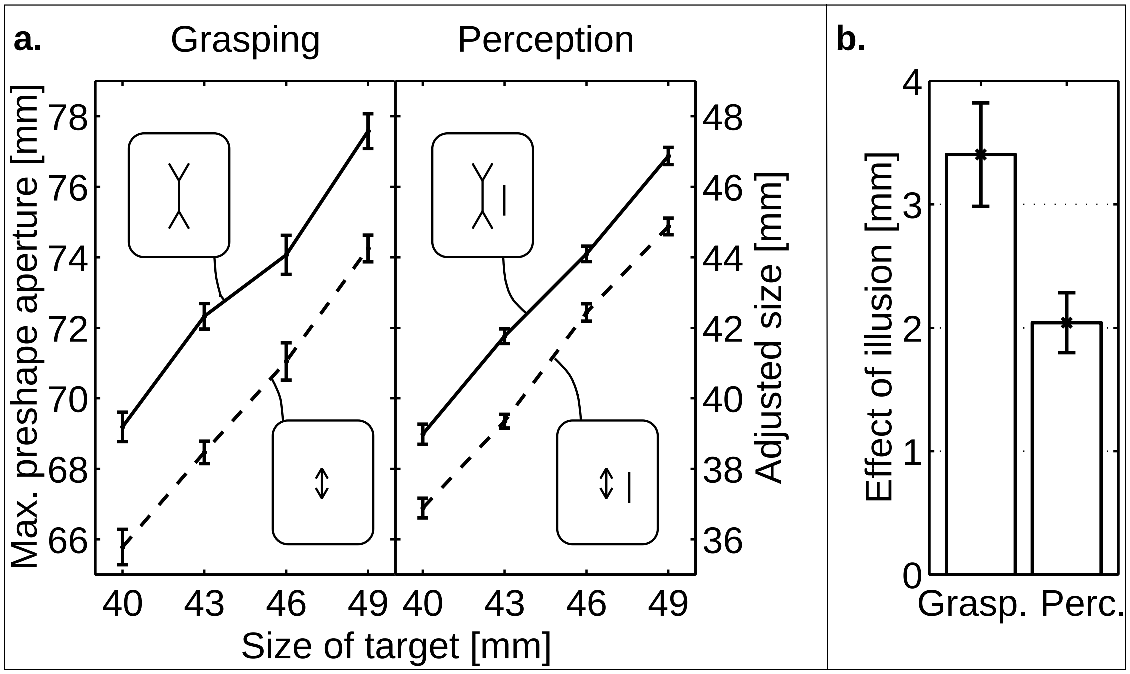


Figure 5.2: Results of the perceptual task and of the grasping task in Experiment 5. **a.** Mean adjusted length of the comparison bar and mean maximum preshape aperture (MPA) as functions of the length of the target bar and of the illusion–inducing context. Solid lines represent data for the outward pointing fins, dashed lines for the inward pointing fins. Error bars depict ±1 standard error of the mean. Data are normalized to account for absolute differences in hand sizes and aperture sizes between the participants. See Appendix A for a description of the normalization. **b.** Overall illusion effects averaged across all lengths of the target bar. Error bars depict ±1 standard error of the mean.

Development of the illusion over time In order to test whether the repeated presentation of the Müller–Lyer figure caused a decrement of illusion strength the illusion effect was calculated separately for each trial. This was done exactly the same way as in Experiment 1 (see page 45). Results are shown in Figure 5.3b. The linear regression of illusion effect as a function of trial–number showed neither in the perceptual task nor in the grasping task a decrement of the illusion effect over time:

Perception: $IE = -0.03 * TN + 2.3$ [mm]; $t(22)$ = -1.0, $p = .32$
Grasping: $IE = +0.01 * TN + 3.2$ [mm]; $t(70)$ = 0.4, $p = .73$

(IE stands for illusion effect and TN for trial–number. The t–value tests the slope of the regression).

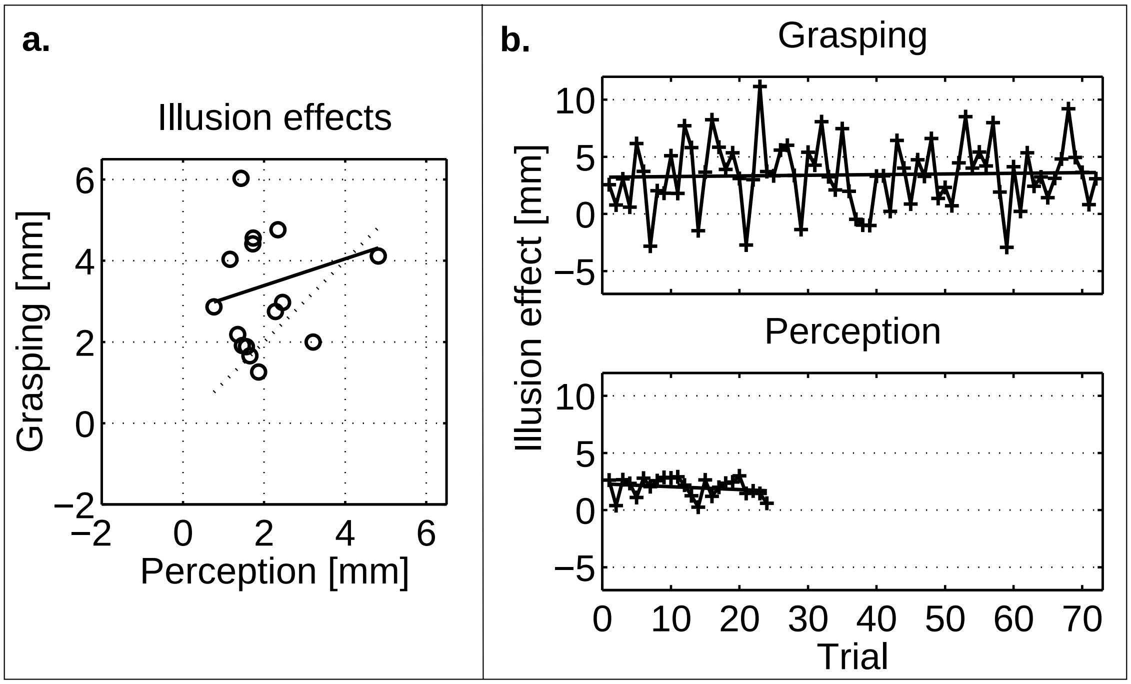


Figure 5.3: Further analyses of the results of Experiment 5. **a.** Overall illusion effects calculated separately for each participant and correlated across participants. Each data point depicts the motor illusion and the perceptual illusion of one participant. The solid line is the linear regression over all data points. The dashed line bisects the first quadrant. **b.** Illusion effects calculated separately for each trial. The solid line is the linear regression over all data points. See text for details.

Duration of stimulus presentation In the perceptual task, the stimulus was presented for as long as the participants needed to perform the adjustment. In the grasping task, visibility was suppressed by closing the glasses as soon as the participants started to move their hand. The average time until movement onset and (consequently) the average stimulus presentation time in the grasping task was 685 msec. In an ANOVA it was tested whether the onset of the movement was affected by the experimental conditions. There were no statistically reliable effects of length of target bar, of illusion–inducing context, nor of the interaction between these two factors (all $p > .15$).

5.1.3 Discussion

There was a clear and highly significant effect of the Müller–Lyer Illusion on grasping. This result is in accordance with the study of Daprati and Gentilucci (1997), who also reported an effect of the Müller–Lyer Illusion on grasping (cf. Table 7.1 on page 86). Stimuli were not identical in the two studies. For example, the target bar was much longer in the Daprati and Gentilucci study and the fins were not presented via a monitor but were drawn on a board. Also, grasping was performed open loop in this experiment, while in the Daprati and Gentilucci experiment full vision of both the hand and the stimuli was allowed during grasping. Both facts suggest that the effect of the Müller–Lyer Illusion on grasping is robust across different stimulus conditions. Only in the study of Otto–de Haart et al. (1999) and only in the binocular vision condition there was no significant effect of the Müller–Lyer on grasping (cf. Table 7.1). However, the effect was close to being significant and very similar to the effect found in the monocular viewing condition of this study. Therefore, this result is not a strong argument against an effect of the Müller–Lyer Illusion on grasping.

Interestingly, in the present experiment the motor illusion was even larger than the perceptual illusion. In contrast, Daprati and Gentilucci (1997) — using non–standard perceptual measures — reported a smaller motor illusion than perceptual illusion. The following control–experiments will investigate whether the larger perceptual effect might be due to an insufficient match between perceptual task and motor task.

A second reason for the control–experiments is that the across–participants correlation between perceptual illusion and motor illusion was quite small compared to the Idealized Expected Correlation and was not significant. While the non–significant result does not allow the conclusion that there is no correlation (to decide this question one needed a larger sample size, cf. chapter 3) the small correlation might, again, indicate an insufficient match between perceptual task and motor task.

5.2 Experiment 6: Effects of presentation time?

In the perceptual task of Experiment 5, participants had unlimited time to adjust the comparison bar. In contrast, presentation time was limited in the grasping task. As soon as the reach started, vision was suppressed by closing the shutter–glasses so that the grasps were performed open loop. In Experiment 6 it was tested whether the perceptual effect of the illusion changes for shorter presentation times.

5.2.1 Method

Six people (3 females and 3 males) participated in Experiment 6, ranging in age from 20 to 28 years (mean: 23.5 years). Participants sat on a chair at a viewing distance of approximately 65 cm to a standard computer monitor (21 inches).

All stimuli were now presented on the monitor. That is, in contrast to Experiment 5, no real objects were presented. While in Experiment 5 the stimuli were presented on the table–like monitor and were oriented parallel to the sagittal plane of the observer, now they were presented on a normal, upright monitor and were horizontal. The target bar had lengths of 43, 44, 45 and 46 mm. The comparison bar was shifted relative to the target bar along the main axis of the target bar by 160 mm. In all other respects, stimuli were identical to the stimuli of Experiment 5.

In the long inspection task, participants adjusted the comparison bar to match the size of the target bar. After they finished their adjustment, the stimuli disappeared from the screen. This procedure is similar to the perceptual task of Experiment 5. Each participant performed five practice trials, followed by two blocks of 24 trials each. Given eight different trial types (four sizes of the target bar x two contexts), participants performed six adjustments per trial type.

In the short inspection task, the stimuli were displayed only 1600 msec. Participants had to decide whether the comparison bar was longer or shorter than the target bar (two–alternative forced choice task, 2AFC). The presentation time was chosen to be roughly twice as large as the mean presentation time in the grasping task of Experiment 5, because participants had to estimate the size of two stimuli (the target bar and the comparison bar). Also, due to the distance between the stimuli (14° of visual angle) participants probably made at least one saccade from one stimulus to the other. In contrast, in the grasping task of Experiment 5 participants had to calculate only the size of one stimulus, the target. (This is different from Experiment 2: In this experiment the short presentation time was chosen to be about the same as the presentation time in the grasping task of Experiment 1).

Each participant performed 15 practice trials, followed by six blocks of 80 trials each. Given eight different trial types, participants performed 60 judgments per trial type. The size of the comparison bar was determined via an adaptive up-down procedure: For each block and each trial type separate staircases were used with the comparison bar initially being either 5 mm larger or 5 mm smaller than the target. If the participant responded “larger” (“smaller”), the comparison was presented 1 mm smaller (larger) the next time this trial type was displayed. For data analysis, cumulative gaussians were fitted to the data and the point of subjective equality (PSE) was determined. The succession of long inspection task and short inspection task was counterbalanced between participants.

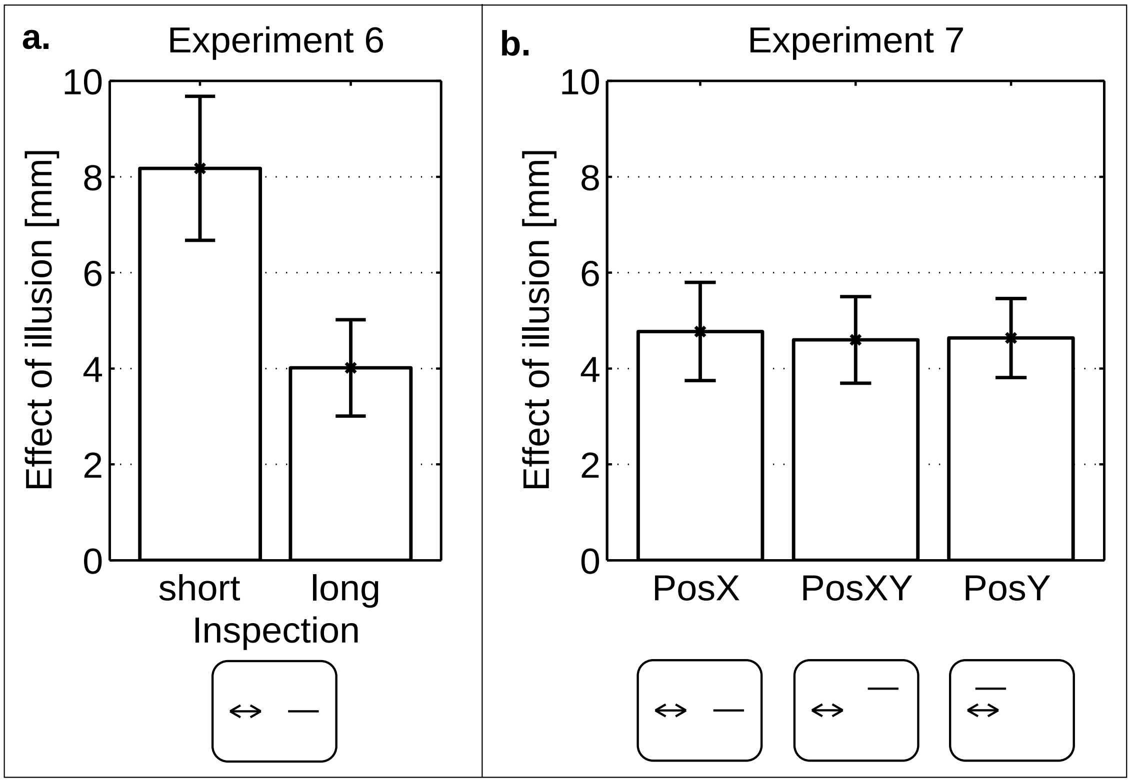


Figure 5.4: Overall illusion effects averaged across all lengths of the target bar for Experiment 6 (**a**) and Experiment 7 (**b**). Error bars depict ±1 standard error of the mean.

5.2.2 Results and Discussion

Figure 5.4a shows the mean illusion effects of the long inspection task and of the short inspection task. There was a highly significant main effect of the illusion ($F(1,5)$ = 27, $p = .003$). The illusion effect was larger for the short inspection task than for the long inspection task ($F(1,5)$ = 21, $p = .006$). The different sizes of the target bar had no differential effect on the size of the illusion ($F(3,15)$ = 2.2, $\epsilon = .50$, $p = .18$). Also, the interaction between target size and task was not significant ($F(3,15)$ = 1.1, $\epsilon = .63$, $p = .37$).

Results show that in the Müller–Lyer Illusion, short presentation times lead to a larger illusion than longer presentation times. Because presentation times were shorter in the motor task of Experiment 5 this fact could account for the larger motor illusion in this experiment.

5.3 Experiment 7: Effects of comparison position?

In this experiment one more possible source of differences between the perceptual task and the motor task of Experiment 5 was tested. It was hypothesized that in the perceptual task of Experiment 5 the comparison bar might have been so close to the target bar that the illusion influenced not only the target but also the comparison. Because in this case the comparison would no longer be neutral, this could have changed the perceptual effect measured. If this were the case then varying the position of the comparison would yield different perceptual measures for the illusion.

5.3.1 Method

Eight people (4 females and 4 males) participated in Experiment 7, ranging in age from 16 to 30 years (mean: 23.0 years). Procedure and stimuli were similar to the long inspection task of Experiment 6 and to the perceptual task of Experiment 5. The only difference was that the comparison was now presented at three different locations. For easier description imagine an x–axis parallel to the main axis of the target bar, and a y–axis perpendicular to this. In the PosX–condition the comparison was shifted along the x–axis by 160 mm. In the PosY–condition the comparison was shifted along the y–axis by ±80 mm and along the x–axis by ±8 mm, with the signs of the shifts being determined randomly from trial to trial. Finally, in the PosXY–condition the comparison was shifted along the x–axis by 160 mm and along the y–axis by ±80 mm (see Figure 5.4b for examples for each condition). Note that the PosY–condition corresponds to the stimulus arrangement of Experiment 5 and that the PosX–condition corresponds to the stimulus arrangement of Experiment 6.

Each participant performed five practice trials followed by six identical blocks of 24 trials each. Given 24 different trial types (four sizes of the target bar x two contexts x three positions of the comparison), participants performed six adjustments per trial type.

5.3.2 Results and Discussion

Figure 5.4b shows the mean illusion effects measured at the different positions of the comparison bar. While the main effect of the illusion inducing context was highly significant ($F(1, 7)$ = 29, $p = .001$), there was no difference of the illusion effects between the different positions of the comparison bar ($F(2, 14)$ = 0.07, $\epsilon = .61$, $p = .84$), no difference in illusion effects for the different sizes of the target bar ($F(3, 21)$ = 2.7, $\epsilon = .61$,

$p = .11$) and no significant interaction between the last two factors ($F(6, 42)$ = 1.6, $\epsilon = .34, p = .24$).

These results indicate that the position of the comparison bar does not seem to be critical for the measurement of the perceptual effect in Experiment 5.

5.4 Discussion: Müller–Lyer Illusion

There were clear effects of the Müller–Lyer Illusion on grasping. This result fits well to the results reported by Daprati and Gentilucci (1997), who also found a clear effect of the Müller–Lyer Illusion on grasping. Also it suggests that the results of Otto–de Haart et al. (1999) who found for the Müller–Lyer Illusion a non–significant influence with binocular viewing ($p = .08$), but a significant effect with monocular viewing might be attributed to a lack of statistical power (cf. Table 7.1 on page 86). Taken together, these results rule out the possibility that grasping is not affected by the Müller–Lyer Illusion and therefore vote against the strong version of the Separate Representation Model.

Different to the studies of Daprati and Gentilucci (1997) and of Otto–de Haart et al. (1999) standard perceptual measures were used in Experiment 5 to assess the perceptual effect of the illusion (Coren & Girgus, 1972b). While those studies reported a large difference between the motor illusion and the perceptual illusion with a much larger perceptual illusion (cf. Table 7.1 on page 86), this was not found with standard perceptual measures: In Experiment 5 the difference between the perceptual illusion and the motor illusion was smaller. However, now the grasping effect was even somewhat larger than the perceptual effect.

This larger motor illusion is neither predicted by the weak Separate Representation Model nor by the Common Representation Model. It might indicate that some additional effect biased either the perceptual task or the motor task. Such an additional effect could also explain the fact that the across–participants correlation between perceptual illusion and motor illusion ($\rho = .19$) was small compared to the Idealized Expected Correlation ($\rho_{P,G} = .58$).

The perceptual control experiments revealed one possible cause for such a bias: The shorter presentation time in the motor task. Experiment 6 showed that a shorter presentation time can lead to an increase in the perceptual effect of the illusion. This could explain the difference in illusion effects between perception and grasping.

A second possible reason for the increased motor illusion is a fundamental confound in the Müller–Lyer Illusion: The overall size of the fin–out figure (that enlarges the perceived size of the target bar) is larger than the size of the fin–in figure. Maybe participants were influenced in grasping by this overall size and this caused an additional increase in the measured illusion. It was attempted to minimized this problem by clearly separating the target bar and the fins (see Method section of Experiment 5). Nevertheless, this problem is always present in the standard version of the Müller–Lyer Illusion.

Note, that this problem is not present in the Ebbinghaus Illusion. The Ebbinghaus figure with large context circles has a larger overall size than the figure with small context circles, but decreases the perceived size of the central disc. If participants were affected in grasping by the overall size of the figure, this should attenuate the measured grasping effect of the Ebbinghaus Illusion. However, Experiment 1 did not provide evidence for a decreased grasping effect in the Ebbinghaus Illusion, but showed a very good match between the grasping effect and the perceptual effect of the Ebbinghaus Illusion.

The following experiments attempted to minimize the confound of overall size and perceptual illusion that is present in the Müller–Lyer Illusion. For this purpose another variant of the Müller–Lyer Illusion was employed: the Parallel–Lines Illusion.

Chapter 6

Parallel–Lines Illusion

The Parallel–Lines Illusion might be the most simple of all visual distortions: A long line causes a shorter, parallel line to be perceived longer, and vice versa (assimilation effect, cf. Figure 2.8e on page 26). With a large distance between the two lines, this effect can also be reversed. In this case the long line causes a shorter, parallel line to be perceived as being even shorter (contrast effect, cf. Jordan & Schiano, 1986).

It has been argued (Pressey, 1983, as cited in Jordan & Schiano, 1986) that the Parallel–Lines Illusion may serve as a prototype for more complex visual illusions like the Müller–Lyer Illusion. In the context of the grasping experiments of this study the Parallel–Lines Illusion has the advantage that there are no fins that might distort grasping. In order to obtain a strong illusion two context lines were presented with one target bar in between (see Figure 6.1c). For the Parallel–Lines Illusion, the same set of experiments was performed that were performed for the Müller–Lyer Illusion.

6.1 Experiment 8: Grasping the illusion

In this experiment, the effects of the Parallel–Lines Illusion on grasping and on perception were compared. The experiment is similar to Experiment 5, with the difference that the Parallel–Lines Illusion was used.

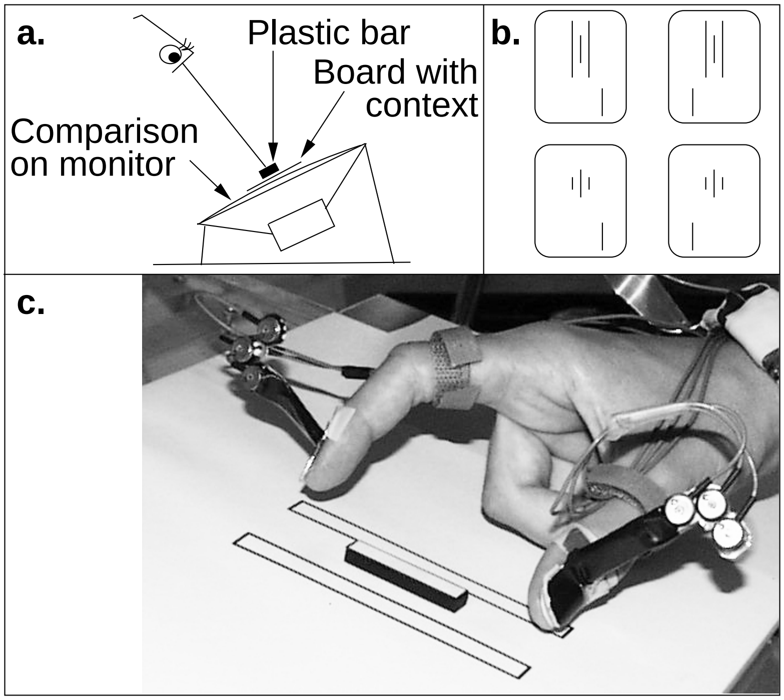


Figure 6.1: **a.** The apparatus of Experiment 8. **b.** Stimulus conditions in the perceptual task of Experiment 8. The comparison bar was displayed on the monitor either left of right of the target. **c.** A participant grasping the target bar. The illusion context was drawn on a board.

6.1.1 Method

Twenty six people (15 females and 11 males) participated in Experiment 8, ranging in age from 17 to 36 years (mean: 24.7 years). The apparatus of Experiment 8 is shown in Figure 6.1. Stimuli, apparatus and procedure were identical to Experiment 5 except for the following: Instead of adding fins to the target bars, the target bars were now accompanied by two parallel lines that had a distance of 11 mm to the mid line of the target bar and were either 100 mm long (this is the enlarging version of the illusion) or 22 mm long (this is the shrinking version of the illusion). As in Experiment 5, all elements of the Parallel–Lines figure were 7 mm wide. The target bars were 7 mm wide, 5 mm high and 40, 43, 46 or 49 mm long. Because in the Parallel–Lines Illusion the parallel lines do not touch the target bar it was no longer necessary to adapt the illusion–inducing context to each length of the target bar (as was needed in the Müller–Lyer Illusion in Experiment 5). Therefore, instead of presenting the illusion–inducing context on the monitor, two boards were used (as in Experiment 1) on which the long and the short parallel lines were drawn. The boards were placed underneath the target bars (see Figure 6.1a,c).

As one final difference to Experiment 5 a group factor was added for exploratory purposes: Ten of the participants viewed the whole stimulus configuration as 1 mm thick outlines, while the other sixteen participants saw the stimuli configuration filled black.

6.1.2 Results

Outlines versus filled stimuli For both dependent variables, the adjusted length of the comparison bar and MPA, there was no difference between the filled stimuli and the stimuli that were drawn only as outlines. This is reflected by the fact that ANOVAs for both dependent variables (Within–Subjects Factors: length of target bar and illusion inducing context; Between–Subjects Factor: outlines) did not show any significant main effect or interaction of the factor outlines (all $p > .12$). Also, adding or removing the factor outlines only minutely changed the results of the ANOVAs. Therefore, the two groups were pooled.

Illusion effects Figure 6.2a shows the mean adjusted length of the comparison bar and the mean MPA as functions of the length of the target bar and of the illusion–inducing context. In the perceptual task the main effects of length of target bar ($F(3,75)$ = 377, $\epsilon = 0.61$, $p < .001$) and of illusion–inducing context ($F(1,25)$ = 82, $p < .001$) were highly significant. The interaction between the two factors was also highly significant ($F(3,75)$ = 5.5, $\epsilon = 0.83$, $p = .004$). Similarly, in the grasping task the main effects of length of target bar ($F(3,75)$ = 135, $\epsilon = 0.89$, $p < .001$) and of illusion–inducing context ($F(1,25)$ = 16, $p < .001$) were highly significant. There was no interaction between these two factors ($F(3,75)$ = 0.2, $\epsilon = 0.96$, $p = .87$).

The slopes for perception ($s = 0.91 \pm 0.04$) and for grasping ($s = 0.88 \pm 0.05$) were similar ($t(25)$ = 0.57, $p = .57$). As reasoned in chapter 3, this finding allows a comparison of the illusion effects. For this purpose, overall illusion effects were calculated by averaging the illusion effects across all sizes of the central disc.

Comparing motor illusion with perceptual illusion Overall illusion effects averaged across all lengths of the target bar are shown in Figure 6.2b. The overall effect of the illusion on grasping was significantly smaller than on perception ($t(25)$ = 4.2, $p < .001$). Overall illusion effects calculated for each participant separately and correlated across participants are shown in Figure 6.3a. The individual grasping illusion was predicted by the individual perceptual illusion with a slope of $s = 0.7$. The corresponding correlation was highly significant ($\rho = .61$, $t(24)$ = 3.8, $p < .001$, one-tailed). The Idealized Expected Correlation (cf. description in chapter 3) was $\rho_{P,G} = \frac{\sigma_{\Delta_P}}{\sigma_{\Delta_G}} = \frac{1.32}{1.60} = .82$.

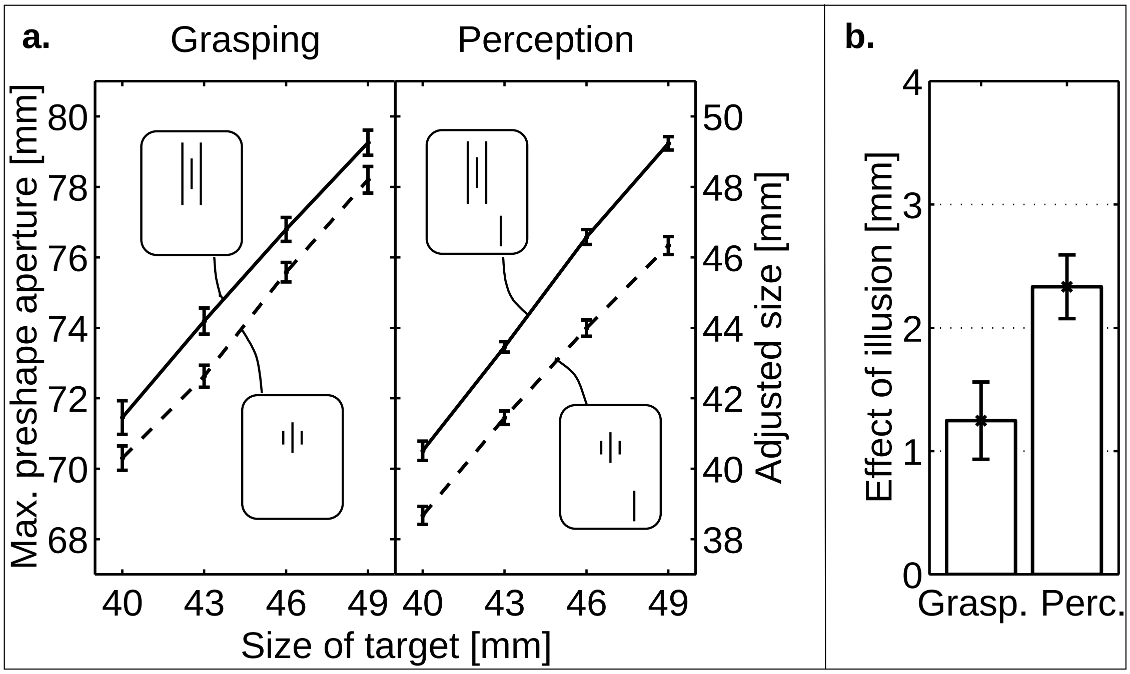


Figure 6.2: Results of the perceptual task and of the grasping task in Experiment 8. **a.** Mean adjusted length of the comparison bar and mean maximum preshape aperture (MPA) as functions of the length of the target bar and of the illusion–inducing context. Solid lines represent data for the long context lines, dashed lines for the short context lines. Error bars depict ±1 standard error of the mean. Data are normalized to account for absolute differences in hand sizes and aperture sizes between the participants. See Appendix A for a description of the normalization. **b.** Overall illusion effects averaged across all length of the target bar. Error bars depict ±1 standard error of the mean.

Development of the illusion over time In order to test whether the repeated presentation of the Parallel–Lines figure causes a decrement of illusion strength the illusion effect were calculated separately for each trial. This was done in exactly the same way as in Experiment 5 and in Experiment 1 (see page 45). Results are shown in Figure 6.3b. The linear regression of illusion effect as a function of trial–number showed in the perceptual task a small, just about significant increase of the illusion over time. In the grasping task, no change of the illusion effect over time was found:

Perception: $IE = 0.04 * TN + 1.9$ [mm]; $t(22)$ = 2.1, $p = .048$
Grasping: $IE = 0.01 * TN + 0.7$ [mm]; $t(70)$ = 1.1, $p = .28$

(IE stands for illusion effect and TN for trial–number. The t–value tests the slope of the regression).

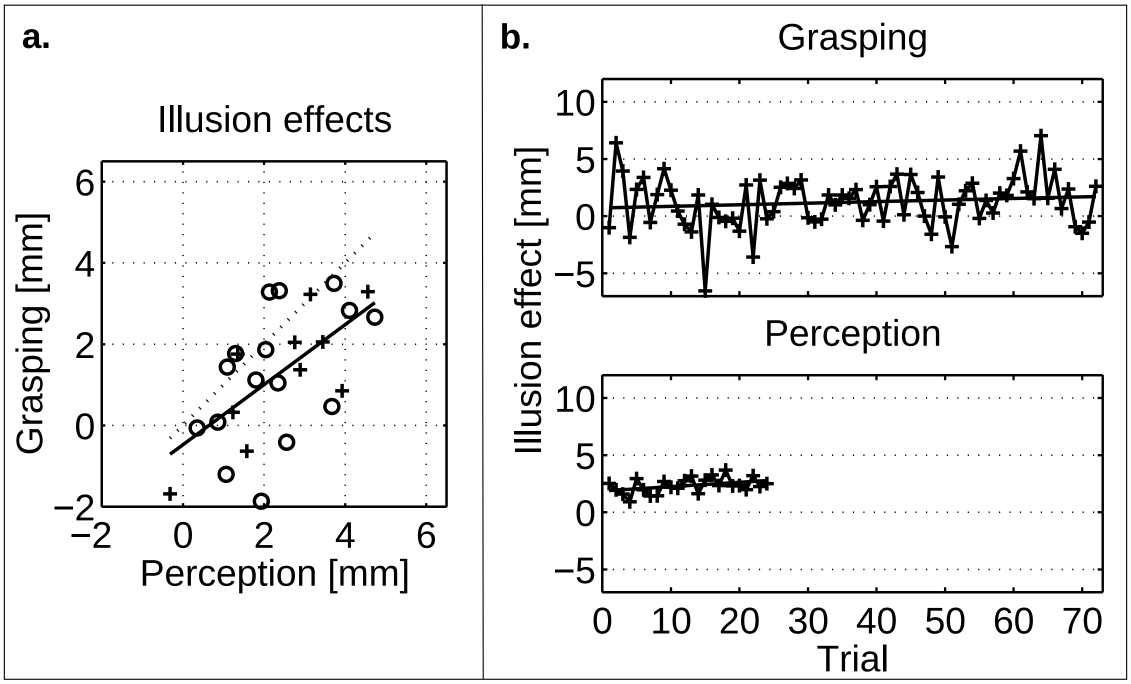


Figure 6.3: Further analyses of the results of Experiment 8. **a.** Overall illusion effects calculated separately for each participant and correlated across participants. Each data point depicts the motor illusion and the perceptual illusion of one participant. Illusion effects of participants that saw outlines are shown as crosses, while data for those who saw filled bars are shown as circles. The solid line is the linear regression over all data points. The dashed line bisects the first quadrant. **b.** Illusion effects calculated separately for each trial. The solid line is the linear regression over all data points. See text for details.

Duration of stimulus presentation As in Experiment 1 and in Experiment 5 the stimulus was presented in the perceptual task as long as the participants needed to perform the adjustment while in the grasping task visibility was suppressed by closing the glasses as soon as the participant started to move the hand. The average duration of stimulus presentation in the grasping task was 739 msec. Interestingly, participants started to grasp faster when the short parallel lines were presented (726 msec) than when the long parallel lines were presented (752 msec). This main effect of illusion–inducing context was significant ($F(1, 25)$ = 7.7, $p = .01$), while there were no statistically reliable effects of length of target bar, nor of the interaction between these two factors (all $p > .89$).

6.1.3 Discussion

As in the Müller–Lyer Illusion, clear and highly significant effects of the Parallel–Lines Illusion on grasping were found. The motor illusion as well as the perceptual illusion stayed exactly the same irrespective of whether the stimuli were presented as outlines or filled — indicating that results are consistent for different ways of stimulus presentation.

In contrast to the results in the Müller–Lyer Illusion, the perceptual illusion was larger than the motor illusion. This outcome is consistent with the assumption that in the Müller–Lyer Illusion the fins might have exerted an additional effect on the motor system. Also, in contrast to the Müller–Lyer Illusion there is a strong and highly significant across–participants correlation between perceptual illusion and motor illusion — suggesting that the same signal is responsible for the illusion effects in perception and in grasping.

In an attempt to find possible reasons for the (again) different sizes of the perceptual illusion and of the motor illusion the same control experiments were performed as for the Müller–Lyer Illusion.

6.2 Experiment 9: Effects of presentation time?

As in Experiment 6, it was tested perceptually whether the different presentation times in the perceptual task and in the grasping task can cause different strengths of the Parallel–Lines Illusion.

6.2.1 Method

Eight people (3 females and 5 males) participated in Experiment 9, ranging in age from 21 to 26 years (mean: 23.3 years). Stimuli, apparatus and procedure were almost identical to Experiment 6. The sole difference was that the Parallel–Lines Illusion was used instead of the Müller–Lyer Illusion.

6.2.2 Results and Discussion

Figure 6.4a shows the mean illusion effects of the long inspection task and of the short inspection task. There was a highly significant main effect of the factor illusion ($F(1,7)$ = 25, $p = .002$). The illusion effect was almost the same for the short inspection task and for the long inspection task ($F(1,7)$ = 0.1, $p = .77$). The different sizes of the target bar had no differential effect on the size of the illusion ($F(3,21)$ = 0.4, $\epsilon = .76$, $p = .71$). Also,

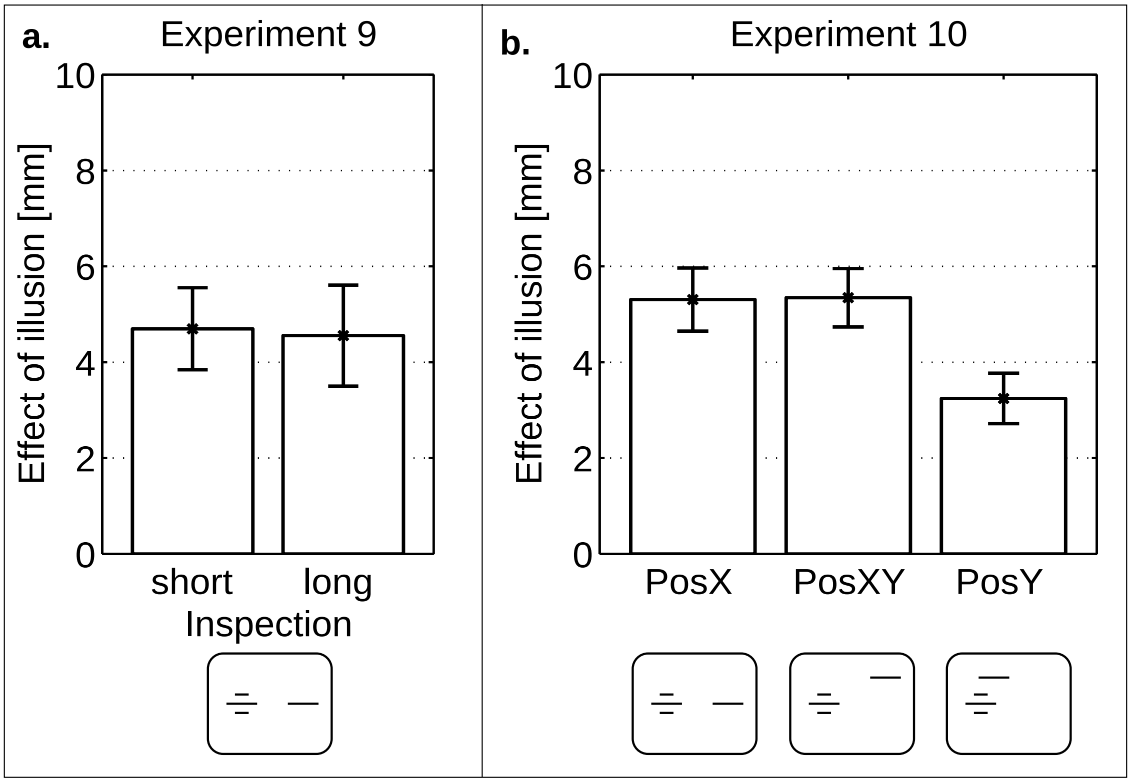


Figure 6.4: Overall illusion effects averaged across all lengths of the target bar for Experiment 9 (**a**) and Experiment 10 (**b**). Error bars depict ±1 standard error of the mean.

the interaction between target size and task was not significant ($F(3, 21)$ = 0.3, $\epsilon = .73$, $p = .74$).

The presentation time does not seem to have an influence on illusion strength in the Parallel–Lines Illusion. This is different from the Müller–Lyer Illusion and might indicate that the influence of short presentation times on the Müller–Lyer Illusion is caused by a decrement in the ability to separate the fins from the target with short presentation times in the Müller–Lyer Illusion. For the purposes of the comparison of motor illusion and perceptual illusion in the Parallel–Lines Illusion this result means that presentation time likely does not bias the results in one of the two measures.

6.3 Experiment 10: Effects of comparison position?

As in Experiment 7, the possibility that the comparison bar might have been influenced by the illusion inducing context of the Parallel–Lines Illusion was tested. If this were the case, then varying the position of the comparison would yield different perceptual measures for the illusion.

6.3.1 Method

Six people (3 females and 3 males) participated in Experiment 10, ranging in age from 17 to 25 years (mean: 22.3 years). Stimuli, apparatus and procedure were almost identical to Experiment 7. The sole difference was that the Parallel–Lines Illusion was used instead of the Müller–Lyer Illusion.

6.3.2 Results

Figure 6.4b shows the mean illusion effects measured at different positions of the comparison bar. The main effect of the illusion inducing context was highly significant ($F(1,5)$ = 70, $p < .001$) and the position of the comparison bar had a highly significant influence on the illusion effect ($F(2,10)$ = 18.3, $\epsilon = .82$, $p = .001$). Illusion effects were similar for the different sizes of the target bar ($F(3,15)$ = 3.9, $\epsilon = .57$, $p = .07$) and the interaction between the last two factors was not significant ($F(6,30)$ = 0.1, $\epsilon = .41$, $p = .95$).

Post–hoc analyses showed that there was no difference between the illusion effects in the PosX and PosXY conditions (Tukey–test, $p > .10$). However, there were highly significant differences between the illusion effects in the PosX and PosXY conditions one one side and the illusion effect in the PosY condition on the other side (Tukey–test, all $p < .01$).

6.3.3 Discussion

The position of the comparison bar had a strong influence on the measured strength of the Parallel–Lines Illusion. This suggests that the illusion–inducing context not only influences the target but also the comparison. In other words, spatial separation does not seem to be sufficient in the Parallel–Lines Illusion to keep the comparison uninfluenced. This, however, is a prerequisite to accurately measure the size distortion of the target.

Jordan and Schiano (1986) described an effect that could account for these results. They found that the Parallel–Lines Illusion switches from assimilation (the target is perceived as being longer if the context is longer) to contrast (the target is perceived as being shorter if the context is longer) with large spatial separation between target and context.

Applying this finding to the comparison bar could account for the data found in the present experiment. For example, consider the case in which the context lines were long and the comparison had a large distance to the Parallel–Lines figure. In this configuration, one expects the target to be perceived as longer (assimilation effect, short distance) and the comparison to be perceived as shorter (contrast effect, long distance). If participants now match target and comparison, they have to change the length of the comparison by a larger amount than if the comparison were unaffected by the context elements. This leads to a larger value of the measured illusion.

This effect interferes with any comparison of perceptual illusion and motor illusion. For a valid comparison, the perceptual task should only measure an illusory change induced in one stimulus because only one stimulus can be grasped. The other stimulus, the comparison bar, should be uninfluenced by the illusion.

In other words, grasping is inherently a “unipolar” measure of size information, because only the size of one stimulus needs to be computed to guide grasping. In contrast, the perceptual measures that were used in all of the experiments reported here sofar were “bipolar” measures because two sizes had to be computed — the size of the target and the size of the comparison. This procedure does not lead to any problem as long as the comparison can be assumed to be unaffected by the illusion. In the Parallel–Lines Illusion, however, this assumption is not valid.

A solution to this problem would be to find a unipolar perceptual measure that requires only to compute the size of one stimulus, the target. For this purpose participants were trained in Experiment 11 to estimate the length of stimuli in millimeters and then asked to estimate the length of the target in the Parallel–Lines Illusion.

6.4 Experiment 11: Using a unipolar perceptual measure

In order to obtain a unipolar perceptual measure of the Parallel–Lines Illusion, Experiment 10 was replicated, and extended by adding a magnitude estimation method. For the magnitude estimation, participants were first trained to estimate the length of bars in millimeters and subsequently had to estimate the length of the target in the Parallel–Lines Illusion (cf. Coren & Girgus, 1972b for a similar estimation method in which, however, no training was performed. See also Vishton, Rea, Cutting, & Nunez, 1999).

6.4.1 Method

Eight people (4 females and 4 males) participated in Experiment 11, ranging in age from 16 to 30 years (mean: 24.4 years). The experiment consisted of two tasks. The adjustment task was almost identical to Experiment 10. However, the number of blocks was reduced from six to four. Given 24 different trial types (four sizes of the target bar x two contexts x three positions of the comparison), participants performed four adjustments per trial type. Also, to be as comparable as possible to Experiment 8, the target bar had lengths of 40, 43, 46 and 49 mm (instead of 43, 44, 45 and 46 mm).

In the magnitude estimation task, participants were first trained to give absolute estimates of the length of a single bar. The bar had lengths between 33 mm and 56 mm (in steps of 1 mm). Participants viewed the bar without any context elements on the monitor and set a number (by pressing the buttons of a computer mouse) that should reflect the length of the bar in mm. After the participants had set the number, a feedback was provided that gave the true length of the bar and scores depending on the performance of the participant. Participants did this training for 48 trials and were instructed to be as precise as possible. After the training, they performed the experimental condition. Exactly the same stimuli as in the adjustment task were presented for 48 trials and the participants were requested to estimate their length. No feedback was given in the experimental condition. Given eight different trial types (four sizes of the target bar x two contexts), participants performed six estimates per trial type. After the experimental condition, participants performed the training again for 24 trials to control for changes in response during the experimental condition.

6.4.2 Results

Figure 6.5 shows the mean adjusted lengths of the comparison bar and the mean estimated lengths as functions of the length of the target bar and of the illusion–inducing context. All dependent measures showed linear relationships to physical size. Most importantly, magnitude estimation showed a similar relationship as the other dependent measures — indicating that participants reacted to physical size differences in the magnitude estimation condition in the same manner as they did in the other conditions. This fact allows to compare the illusion effects between the different dependent measures.

The main effect of the illusion inducing context was highly significant ($F(1,7)$ = 77, $p < .001$) and the different ways to assess the illusion effects (different positions of the comparison bar and the magnitude estimation task) had a highly significant influence on the illusion effect ($F(3,21)$ = 11.6, $\epsilon = .92$, $p < .001$). There was no difference of the illusion effects for the different sizes of the target bar ($F(3,21)$ = 0.4, $\epsilon = .79$, $p = .72$) and the interaction between the last two factors was not significant ($F(9,63)$ = 2.3, $\epsilon = .31$, $p = .11$).

Overall effects, averaged across all lengths of the target bar, are shown in Figure 6.6.

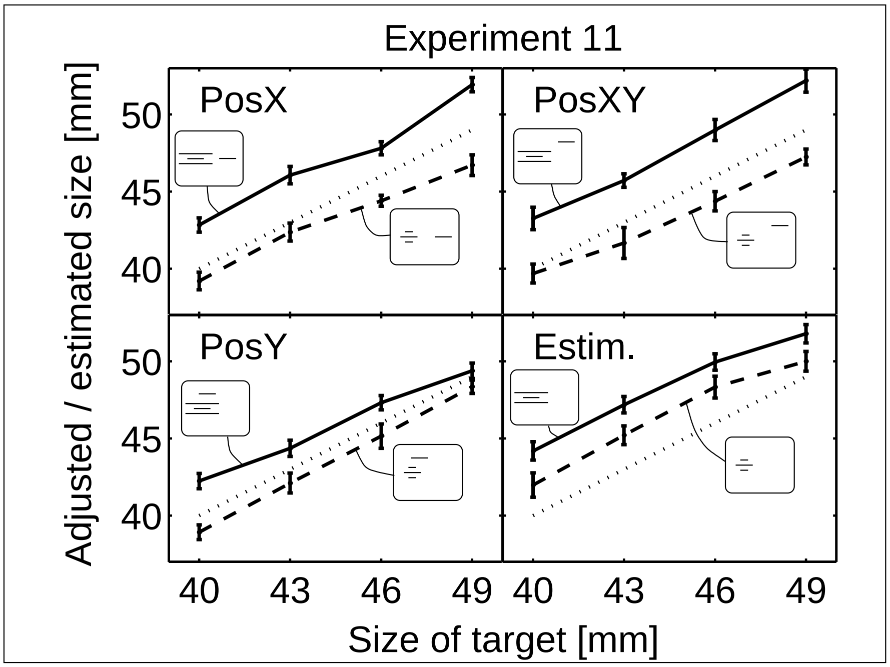


Figure 6.5: Results of Experiment 11. Mean adjusted length of the comparison bar for the different positions of the comparison bar in the adjustment task and mean estimated size in the estimation task. Error bars depict ±1 standard error of the mean.

Post–hoc analyses showed that there was no difference between the illusion effects in the PosX and PosXY conditions and between the illusion effects in the PosY condition and the magnitude estimation task (Tukey–test, all $p > .10$). However, there were highly significant differences between the illusion effects in the PosX and PosXY conditions on one hand and the illusion effects in the PosY condition and in the magnitude estimation task on the other hand (Tukey–test, all $p < .01$).

6.4.3 Discussion

Several conclusions can be drawn from the results of Experiment 11. First, the results of Experiment 10 were replicated in the adjustment tasks, showing that different illusion strengths are obtained if the position of the comparison bar is varied. Second, magnitude estimation could be introduced as a linear, unipolar measure. Third, magnitude estimation gave a smaller illusion effect than the adjustment task in the conditions in which the distance between target and comparison was large. This is exactly what is expected according to the contrast interpretation: With large distances between the illusion context and the comparison a contrast effect changes the perceived size of the comparison

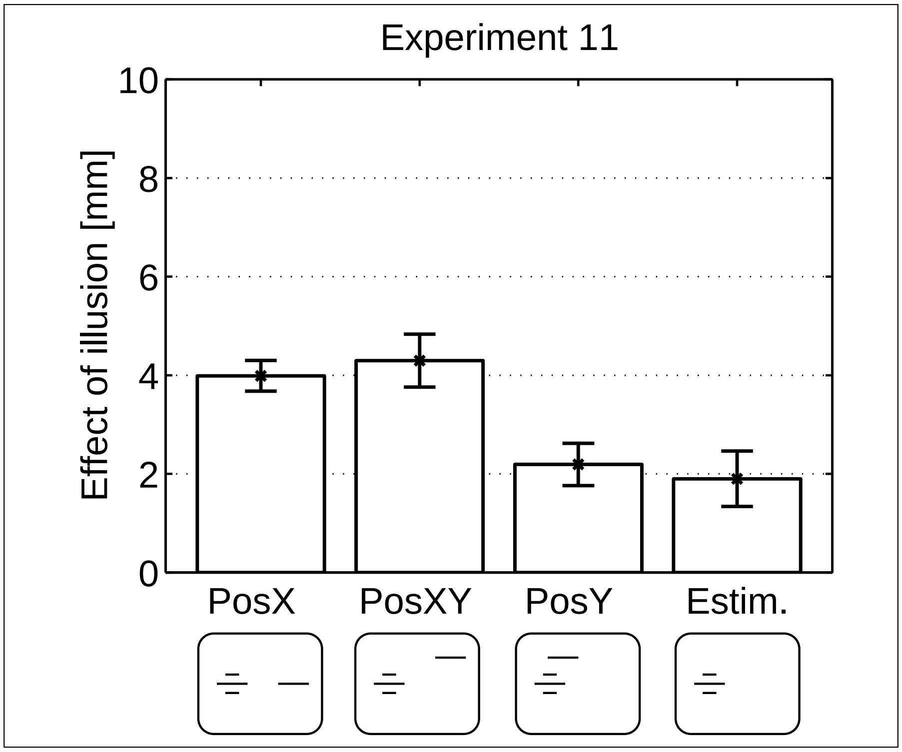


Figure 6.6: Overall illusion effects averaged across all length of the target bar for the different positions of the comparison bar in the adjustment task and for the estimation task of Experiment 11. Error bars depict ±1 standard error of the mean.

and this enlarges the measured illusion. Because this effect is not possible in magnitude estimation, the measured illusion is smaller.

In the light of this outcome it is interesting to discuss an explanation for the relatively small illusion effect in the PosY condition which is alternative to the contrast interpretation discussed sofar. The explanation assumes that it is somehow easier to compare the comparison bar to the target bar in the PosY condition. The reasons could be that the comparison bar and the target bar are very close together and that participants are, for example, able to mentally "move" the comparsion bar to the target bar. Such a strategy could make the comparison easier and therefore reduce the measured illusion. This explanation is different from the explanations discussed sofar because it does not assume that the comparison bar is affected by the illusion, but that the comparison is more veridical in the PosY condition. There are two problems with this explanation. First, the same strategy should also be possible in the Müller–Lyer Illusion. Experiment 7 showed that this is not the case: The illusion effect in the Müller–Lyer Illusion was not decreased for the PosY condition. Second, the magnitude estimation in the present experiment showed exactly the same (small) illusion effect as the PosY condition. This, however, cannot be explained by the strategy, because there is no comparison bar involved in this task.

What do the results mean with respect to the interpretation of the difference between the grasping illusion and the perceptual illusion observed in Experiment 8? The perceptual task of Experiment 8 was similar to the POSXY–condition of the present experiment. The magnitude estimation as the more appropriate unipolar measure showed an illusion effect that was about half the size of the effect in the POSXY–condition. This suggests that the perceptual illusion measured in Experiment 8 was over–estimated, due to effects of the illusion context onto the comparison. Correcting for this bias, one expects a perceptual illusion of roughly the same size as in grasping.

6.5 Discussion: Parallel–Lines Illusion

There were clear effects of the Parallel–Lines Illusion on grasping. This extents the results found for the Ebbinghaus Illusion and the Müller–Lyer Illusion and indicates that grasping clearly is affected by visual illusions. Again, the result clearly votes against the strong Separate Representation Model.

The Parallel–Lines Illusion is the only illusion in the present study which consistently showed a smaller grasping effect than perceptual effect. This could be counted as evidence for the weak Separate Representation Model which predicts a smaller motor illusion than perceptual illusion. However, there was also a strong and highly significant across–participants correlation between perceptual illusion and motor illusion. That is, a participant showing a large motor illusion also tended to show a large perceptual illusion. This suggests a common source of the perceptual illusion and of the motor illusion (see the discussion in chapter 3).

Investigating the reasons for the smaller motor illusion showed that (a) presentation time was not critical (different to the Müller–Lyer Illusion) and (b) the measured perceptual effect varied in a wide range if the position of the comparison bar relative to the target bar was changed (this is also different to the Müller–Lyer Illusion). Here the problem arises, which perceptual effect should be used for the comparison between motor illusion and perceptual illusion. Grasping does not involve a comparison bar (it is unipolar) and therefore the ambiguity in the perceptual effect cannot easily be resolved.

In Experiment 11 size estimation was used as a unipolar perceptual measure that also does not involve a comparison bar. Therefore, it seems to be more comparable to grasping than the other perceptual measures. Results showed that the perceptual effect is also smaller for this unipolar measure. This suggests that the perceptual effect measured in the grasping experiment (Experiment 8) should be corrected and therefore the smaller motor illusion can be reconciled with the notion that the effects of the Parallel–Lines Illusion are similar for grasping and for perception.

Chapter 7

General Discussion

There were clear and highly significant effects of the Ebbinghaus Illusion, of the Müller–Lyer Illusion, and of the Parallel–Lines Illusion on grasping. In the Ebbinghaus Illusion, the grasping effect matched the perceptual effect very well. In the Müller–Lyer Illusion, the grasping effect was larger than the perceptual effect, while in the Parallel–Lines Illusion it was smaller. In the Ebbinghaus Illusion, there was a significant across–participants correlation between the motor illusion and the perceptual illusion of about the size of the Idealized Expected Correlation. In the Müller–Lyer Illusion, the across–participants correlation was small and non–significant, and in the Parallel–Lines Illusion it was large and highly significant.

In the Müller–Lyer Illusion, there are two possible reasons for the stronger motor illusion. First, the presentation time was shorter in the motor task. Experiment 6 showed that shortening presentation time can increase illusion strength. Second, the illusion effect is confounded with the overall size of the Müller–Lyer figure. This may have selectively influenced grasping and hence increased the motor illusion (Note, that this confound is not present in the Ebbinghaus Illusion, see section 5.4).

To minimize this confound, the Parallel–Lines Illusion was investigated since it has a larger separation between the target and the illusion–inducing context than the Müller–Lyer Illusion. In the Parallel–Lines Illusion, the motor illusion was smaller than the perceptual illusion. However, there was also a strong and highly significant across–participants correlation between the perceptual illusion and the motor illusion. That is, a participant showing a large perceptual illusion also tended to show a large motor illusion — suggesting that both illusions have the same origin.

Investigating the reasons for the (in this case) smaller motor illusion, showed that the measured perceptual effect depended strongly on placement of the comparison bar relative to the target bar. Since grasping does not involve a comparison bar (this feature was called unipolar) the question arises which position of the comparison bar should be used to compare the perceptual illusion with the motor illusion. Using size estimation as a unipolar perceptual measure showed that the perceptual effect is also smaller for this unipolar measure. This fact suggests that the perceptual effect measured in the grasping experiment (Experiment 8) should be corrected and therefore can reconcile the smaller motor illusion with the hypothesis that the effects of the Parallel–Lines Illusion are similar for grasping and for perception.

In conclusion, the evidence presented here argues against the strong Separate Representation Model because there clearly are effects of the Ebbinghaus Illusion, the Müller–Lyer Illusion, and the Parallel–Lines Illusion on grasping. The experiments provide no convincing evidence for the weak Separate Representation Model because the motor effects were not consistently smaller than the perceptual effects but were equal in the Ebbinghaus Illusion and larger in the Müller–Lyer Illusion. The Parallel–Lines Illusion is the only illusion in which a smaller motor effect was found. In this illusion, however, there was a strong across–participants correlation between perceptual effect and motor effect — suggesting that the illusion effects have the same origin.

Finally, there is relatively good (however not perfect) agreement of the data with the predictions of the Common Representation Model. For the Ebbinghaus Illusion, this agreement is very good: The perceptual illusion and the motor illusion match well and the across–participants correlation of perceptual illusion and motor illusion is of about the size of the Idealized Expected Correlation. For the Müller–Lyer Illusion and the Parallel–Lines Illusion, this agreement is not as good. However, there are plausible reasons for the differences that likely lie in an incomplete match between the perceptual tasks and in the motor tasks.

The present study demonstrates, how difficult it is to adequately match the perceptual task and the grasping task (cf. Post & Welch, 1996; Smeets & Brenner, 1995). This problem might lead to the pessimistic view that an adequate comparison of the tasks, and therefore a discrimination between the weak Separate Representation Model and the Common Representation Model, is not possible. However, this endeavor can give insights about subtleties of the cognitive system — as, for example, the influence of the Parallel–Lines Illusion on the comparison bar. Also, it is clear that point hypotheses — such as predicted by the strong Separate Representation Model and the Common Representation Model— are to be valued more highly than hypotheses that only predict differences —

such as predicted by the weak Separate Representation Model (Meehl, 1967; Popper, 1980). In the following section the findings of this study will be related to the results of previous studies.

7.1 Comparison with previous studies

Table 7.1 summarizes the results of studies that were performed on the influences of visual illusions on grasping using MPA as dependent variable. It seems clear from these data that visual illusions do influence grasping, as most of the studies found significant effects of visual illusions on grasping. The remaining studies found effects that were almost significant (Otto–de Haart et al., 1999; Haffenden & Goodale, 1998) — or used a small perceptual illusion and a small sample size (Brenner & Smeets, 1996). It is noteworthy that with respect to the Ebbinghaus Illusion there is an unusual agreement: All four studies, performed in three different laboratories, used almost the same geometry for their stimuli. And all four studies found very similar sizes for the motor illusion! Taken together the evidence clearly votes against the strong version of the Separate Representation Model which assumes that there is no influence of visual illusions on grasping.

What about the relationship between perceptual effects and grasping effects? In Table 7.1 a distinction is made between standard and non–standard perceptual measures. Standard perceptual measures means measures that are typically used to investigate visual illusions. Participants either chose one object out of a series of objects to match the size of the target or adjusted the size of a comparison stimulus (see for example Coren & Girgus, 1972b for an investigation of these measures). The non–standard measures are quite different and will be discussed later.

The studies of Aglioti et al. (1995) and of Haffenden and Goodale (1998) used the composite version of the Ebbinghaus Illusion (indicated in the last column of Table 7.1). The experiments described in chapter 4 showed that this can lead to an enlarged perceptual effect. The studies that avoided this problem found a very good match of perceptual and motor effects in the Ebbinghaus Illusion (Experiment 1 and Pavani et al., 1999).

Brenner and Smeets (1996) also used a composite version and the Aglioti paradigm to investigate the Ponzo Illusion (Figure 2.8g on page 26). It is likely that the same problem of an enlarged perceptual effect as in the Aglioti et al. study arises for this illusion (In fact, I conducted control experiments similar to Experiment 3. These experiments showed that a failure of additivity can also occur in the Ponzo Illusion and in the Müller–Lyer Illusion).

Table 7.1: Effects of visual illusions on perception and on grasping.

Illusion and study	N	Grasping	Perception (standard)	Perception (non–standard)	Comp.–version[d]
Ebbinghaus Illusion:					
Aglioti et al., ’95	14	1.6 ± 0.4[f,g] *	2.5 ± 0.2 *		yes
Haffenden & Goodale, ’98	18	1.0 ± 0.5[f,h] ns.	2.4 ± 0.2 *	4.2 ± 1.0[a,f,h] *	yes
Pavani et al., ’99	18	1.0 *	0.7 *		no
Experiment 1, this study	26	1.5 ± 0.38 *	1.5 ± 0.12 *		no
Ponzo Illusion:					
Brenner & Smeets, ’96	8	0.3 ($p = .18$)	0.8[i] *		yes
Müller–Lyer Illusion:					
Daprati & Gentilucci, ’97	8	1.0 *		3.7[b] * 2.4[c] *	no
Haart et al., ’99, binoc.[e]	14	1.7 ($p = .08$)		9.0[b] *	yes
Haart et al., ’99, monoc.[e]	14	2.1 *		12.6[b] *	yes
Experiment 5, this study	16	3.4 ± 0.42 *	2.0 ± 0.24 *		no
Parallel–Lines Illusion:					
Experiment 8, this study	26	1.2 ± 0.32 *	2.3 ± 0.26 *		no

Note. All Illusion effects are in millimeters and are the differences between an enlarging version of the illusion and a shrinking version. The grasping effects are based on maximum preshape aperture. N is the number of participants. If available standard errors of the mean are presented. One study (Marotta et al., 1998) did not report sizes of the effects and is not included.

In the non–standard perceptual measures participants indicated target size by[a] opening index finger and thumb without seeing hand and stimulus, or [b] with full vision of hand and stimulus, or [c] by drawing a line of the length of the target without seeing hand and paper, but seeing the stimulus. [d] This column indicates whether the composite version of the illusion was used. [e] binoc. = binocular viewing; monoc. = monocular viewing. [f] Effects are calculated from only 50% of the trials (for which calculations are comparable to the other studies, see Appendix C). [g] values are taken from Fig. 5, p. 683. [h] values: A. Haffenden, personal communication, August 1998. [i] the value is significantly different from zero, E. Brenner, personal communication, January, 2000.

*$p < .05$.

Therefore, it is difficult to interpret the difference between the perceptual illusion and the motor illusion in the study of Brenner and Smeets. Also, the focus of this study was not on MPA but on measuring the force that was applied to lift the objects. This measure was clearly affected by the illusion indicating an influence of the visual illusion on the motor system.

Three of the studies listed in Table 7.1 used different, non–standard perceptual measures to assess the perceptual effects of the illusion. Haffenden and Goodale (1998) used a manual estimation task. Participants estimated target size by opening index finger and thumb without seeing their hand or the stimulus during performance of the task. Daprati and Gentilucci (1997) and Otto–de Haart et al. (1999) also used a manual estimation task, but their participants had full vision of stimulus and hand during the task. Finally, Daprati and Gentilucci used a second task in which participants drew a line of the length of the target without seeing their hand or the paper.

All these tasks have potential benefits. The manual estimation tasks are, for example, very similar to the grasping task (e.g., Haffenden & Goodale, 1998 matched the haptic feedback in the manual estimation task and in the grasping task by having participants grasp the targets after each manual estimation). Also, all tasks are unipolar measures because participants act on only one object at a time — avoiding the problems with ambiguous perceptual measures that were described for the Parallel–Lines Illusion. However, there are also serious problems related to these measures:

First, it is not clear whether these measures can be interpreted as perceptual measures. To the contrary, one might very well argue that the motor system is tapped with these tasks (in fact, Vishton et al., 1999 used a similar task and interpreted it as motor task; see below for a description of this study). This is even more problematic if no visual feedback of the hand is allowed. In this case participants have to rely strongly on feedback of the motor system. Before these measures can be interpreted as perceptual, they should be compared to standard perceptual measures. For example, they should yield effects of a similar size as the standard perceptual measures. Also, they should correlate across participants with standard perceptual measures. Furthermore, the slope of the function relating these measures to physical size of the object should be known in order to validly compare them to grasping as well as to standard perceptual measures (this is the same situation as was described for the comparison of grasping with standard perceptual measures in chapter 3).

Second, Table 7.1 shows that the non–standard perceptual measures yield diverging results. The manual estimations tasks (indicated by a and b) in particular tend to show very large illusion effects. In the Haffenden and Goodale (1998) study, the difference between the effect in the manual estimation task and the effect in the standard perceptual measure is of about the same size as the difference between grasping and the standard perceptual measure. This is even more true if one takes into account that in this study the standard perceptual measure likely are an overestimate because of the use of the composite version of the illusion in the Aglioti paradigm (as argued in the experiments on the Ebbinghaus Illusion, chapter 4). The same is true for the Daprati and Gentilucci (1997) study. The drawing task (indicated by c) differs from the grasping task by about the same amount as from the manual estimation task (indicated by b). This is also reflected by the fact that there was only one significant difference in the post–hoc comparisons of this study: The fin–in configuration of the Müller–Lyer figure showed a larger illusion effect in the manual estimation task than in both the grasping task and the drawing task. The grasping illusion and the illusion in the drawing task were not significantly different. In conclusion, the non–standard perceptual measures do not seem to be understood well enough and show too inconsistent results to argue in favor of a dissociation between perception and action based on these measures alone.

As a final issue, two recently published studies will be discussed that come to similar conclusions as the present study, however used different approaches and are therefore not listed in Table 7.1. Vishton et al. (1999) investigated the Horizontal–Vertical Illusion (Figure 2.8d on page 26). Participants did not grasp three–dimensional objects but reached for two–dimensional objects that were printed on paper. They were instructed to perform this movement as if they were grasping the drawn objects. The dependent measure was the opening of the fingers at the moment when the paper was touched (and not MPA). It is not clear that this is a valid measure for grasping. One potential problem is that participants did not get any haptic feedback. For example, Opitz, Gegenfurtner, and Bülthoff (1996) reported that reach movements change qualitatively if no haptic feedback is provided. Participants start to perform stereotyped movements that are quite different from normal grasp movements. Nevertheless, it is interesting to compare the results of this study to the results presented here. In their first experiment, Vishton et al. compared the effect of the Horizontal–Vertical Illusion on the (mimicked) grasping with the effect on perception — and found a smaller effect on grasping than on perception. However, they argued that in the perceptual task a relative judgment was required because participants compared the horizontal line with the vertical line — both being part of the Horizontal–Vertical Illusion figure (this is the same problem as with the composite version in the Aglioti paradigm). They argued that, contrary to the perceptual task, participants operated on only one of the two lines in the grasping task and therefore an absolute judgment of size was required (in the present study this was called a unipolar measure). In further experiments, they introduced absolute (or unipolar) measures of perception, one of which was a task similar to the magnitude estimation task of Experiment 11. Using these measures, the differences between the (mimicked) grasping and perception vanished. This is highly congruent with the results presented here.

Van Donkelaar (1999) investigated whether pointing movements are affected by the Ebbinghaus Illusion. The study is based on Fitts' law, the fact that pointing movements to smaller targets take longer than to larger targets (Fitts, 1954). According to the perception versus action hypothesis the illusory change in size caused by the Ebbinghaus Illusion should not affect the pointing movement. Yet, van Donkelaar found such an effect: If participants pointed to the central circle of the Ebbinghaus Illusion, the movement times were affected just as if a physical change of the size had happened. This is one more piece of evidence showing that the Ebbinghaus Illusion affects the motor system.

7.2 Consequences for the perception versus action hypothesis

The perception versus action hypothesis is an attempt to integrate evidence from lesion studies on monkeys, neuropsychological studies, and psychophysical studies (cf. chapter 2). Goodale and Milner (1992, Milner & Goodale, 1995) proposed that the two systems of the primate brain, the dorsal stream and the ventral stream, are used selectively for perception and action. They suggested that the function of the dorsal stream is to guide the manipulation of objects, while the function of the ventral stream is to perform computations that are necessary for object recognition and conscious perception. They argued that these computations have to fulfill totally different requirements. Computations for the guidance of actions have to be fast, they only need a short term memory because the position of the object can change quickly and they have to code the position of the object relative to the effector (egocentric coding). In contrast, computations for the purposes of object recognition do not need to be as fast. Also, to allow object constancy a long term memory is needed. Finally, it is not as important to code the objects relative to an effector but the object should be coded relative to other objects (allocentric coding).

The original finding of Aglioti et al. (1995) was interpreted as suggesting that there exists hardly any influence of visual illusions on grasping: "Size–contrast illusions deceive the eye but not the hand" (title of the study). The study fitted well with the perception versus action hypothesis, because it not only showed a dissociation between perception and action, but also a dissociation fitting the functional border that the hypothesis draws.

The action system is assumed to work in egocentric coordinates and to represent a grasp object relative to the hand — quite independent of other objects. Because visual illusions such as the Ebbinghaus Illusion are created by special arrangements of objects, the theory predicts that the motor system should hardly be deceived by the illusion — and this is what the study of Aglioti et al. found.

The results of the present study suggest that this strong claim should be questioned. Of course, this challenges the perception versus action hypothesis — especially its functional statements (e.g., its statements about the character of the coding in the two systems). Nevertheless, the findings of this study alone do not and cannot disprove the hypothesis. The idea of two distinct systems for perception and action could be held up if visual illusions are relative early phenomena created before the two systems separate. Future research might reveal whether this is a feasible assumption. However, there is evidence suggesting that visual illusions (and especially the Ebbinghaus Illusion) are partially dependent on higher cognitive functions (e.g., Coren & Enns, 1993; Deni & Brigner, 1997; Zanuttini, Zavagno, & Agostini, 1996).

In the light of the other psychophysical studies that were discussed in chapter 2 there is even more reason for doubt. Most of the studies that have been counted as evidence for the perception versus action hypothesis were seriously criticized. The criticism was always similar, namely that a difference caused by an incomplete match of perceptual task and motor task had been attributed to a dissociation between action and perception.

It needs to be stressed that psychophysical differences between perception and action in the healthy visual system are a necessary condition for the perception versus action hypothesis in its current form. The reason for this is that Milner and Goodale assume the two streams to create different representations *because of* different output requirements for motor acts and visual perception. Therefore, the perception versus action hypothesis clearly predicts differences in the output characteristics of the two systems.

Future research might examine the possibility of finding other experimental paradigms that clearly provide psychophysical evidence for the perception versus action hypothesis. The present study suggests some directions for research on visual illusions and grasping. Specifically, it shows that more emphasis should be put on the perceptual task and on the question of whether perceptual task and motor task are appropriately matched. Also, it shows the need to discriminate between unipolar and bipolar measures. Perceptual measures that rely on a comparison between two stimuli (the target and the comparison stimulus) were called bipolar, because two sizes have to be computed to perform the task. In bipolar measures both the target stimulus and the comparison stimulus can be affected by the illusion configuration. This can lead to ambiguous measures of the perceptual illusion. Therefore, size estimation as a unipolar perceptual measure was investigated because only one size (the size of the target) has to be computed. It could be that such unipolar perceptual measures prove to be more adequate for a comparison with grasping since grasping is per se unipolar.

Appendix A

Maximum preshape aperture

A.1 Individual profiles

Figure A.1 shows an example for the time course of the aperture between index finger and thumb in grasping. Shown are all grasps that were performed by one participant in two conditions of Experiment 1. In one condition the participant grasped a large disc (a) and in the other the participant grasped a small disc (b). In both conditions the discs were surrounded by large context circles. Clearly visible is the MPA which is reached between 1 and 2 sec after stimulus onset. The second large peak in the curves reflects the release of the disc and the flat region between the two peaks reflects holding the disc. The difference in size between the two discs (9 mm) clearly is reflected in the MPA. Some of the curves show more than one peak for the MPA. In these cases, always the first peak was used to determine the MPA. The plots demonstrate that the grasping data are quite variable, although they are qualitatively consistent. This issue will be discussed in the following sections.

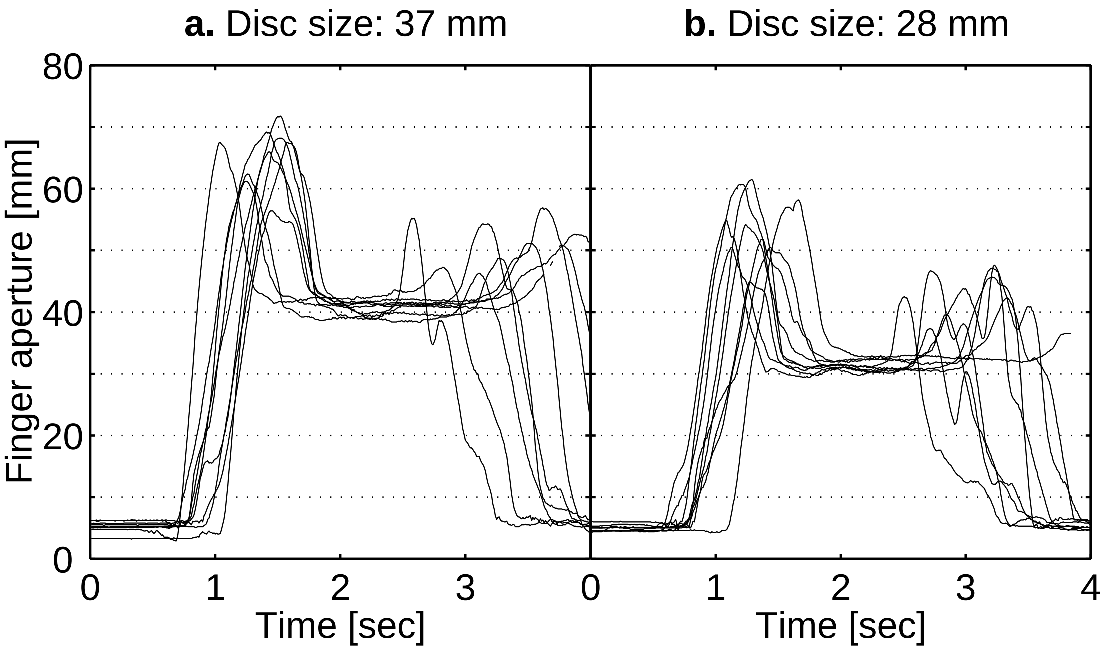


Figure A.1: The aperture between index finger and thumb as a function of time for a participant of Experiment 1. Shown are all nine grasps to a disc that was 37 mm in diameter (**a**) and the nine grasps to a disc that was 28 mm in diameter (**b**). Both discs were surrounded by large context circles.

A.2 Variability between participants and normalization

A large amount of variability in the grasping data is caused by differences between participants. Some participants always open their fingers relatively wide, while others do not. This might be due to individual habit as well as, for example, to different hand sizes. The upper panel of Figure A.2 shows the average MPA for each condition and each participant of Experiment 1. Each data point is the average of nine grasps performed by one participant in the corresponding condition. Each combination of color and line style codes a different participant. Clearly, there is (on average) a linear relationship between disc size and MPA (cf. Jeannerod, 1981, 1984). However, the intercepts of the curves are largely different indicating the variability between participants.

The middle panel of Figure A.2 shows normalized data. The data of each participant

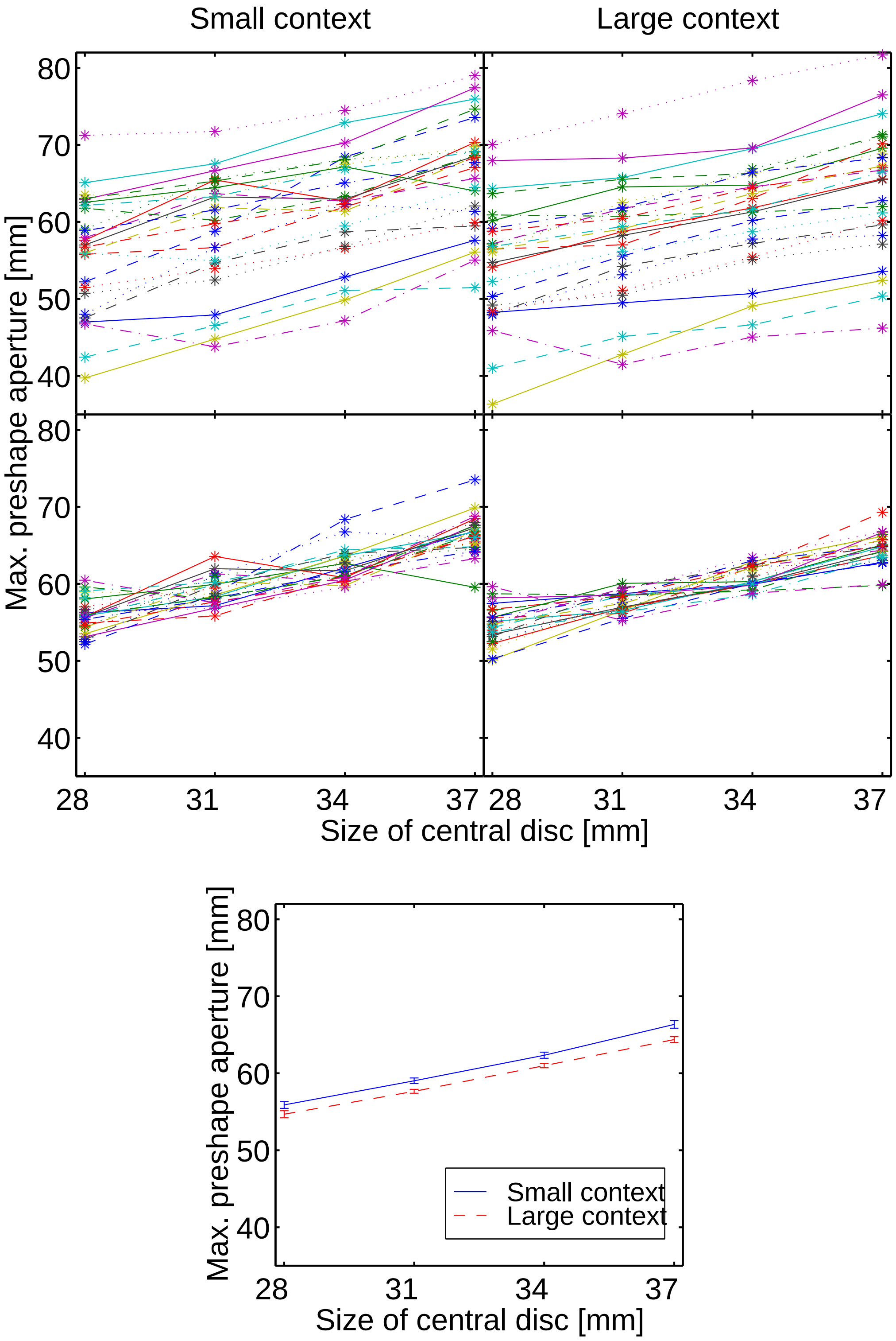


Figure A.2: Individual data of Experiment 1. The upper panel shows for each participant the mean maximum preshape aperture (MPA) as a function of disc size and of the context elements (large versus small context circles of the Ebbinghaus Illusion). For each participant a different combination of color and line style is used. Each data point is the average of nine different grasps. The middle panel shows the normalized data. The lower panel shows the normalized data averaged across all participants. For further details see the text.

are normalized by subtracting the participant's mean (averaged across all conditions) and adding the grand mean of all participants:

$$n_{ij.} = x_{ij.} - x_{i..} + x_{...}$$

With:

$n_{ij.}$	the normalized value of participant i in condition j.
$x_{ij.}$	the mean response of participant i in condition j, averaged across all trials the participant performed in this condition.
$x_{i..}$	the mean response of participant i, averaged across all trials and all conditions.
$x_{...}$	the grand mean, averaged across all trials, all participants and all conditions.

The normalization procedure removes variability that is caused by constant differences in response between participants (see Loftus & Mason, 1994, for an extensive discussion of the normalization). The lower panel of Figure A.2 shows the mean values and the standard errors that were calculated from the normalized data. These are exactly the same data as were shown in Figure 4.3 on page 45. The curves could also be achieved by simply averaging the data of the upper panel — or by averaging the data of each single trial. Only the standard errors would be larger because they still would reflect the differences between participants.

It is possible to give one single estimate for the standard errors by assuming that the expected values (the "true" values) of the standard errors are equal in all eight conditions. The estimate is calculated by averaging the corresponding variances (this is valid because of the balanced design with an equal number of measurements and of participants in each condition). The estimated standard error of each data point in the normalized data is 0.39 mm. The corresponding standard deviation is 2.01 mm. The estimated standard error of the *not* normalized data is 1.49 mm, the corresponding standard deviation is 7.54 mm. The values demonstrate the large contribution of differences between participants to the overall variance.

This example of the normalization can give an understanding of the variability in the data and of the different sources for this variability. The statistical analyses performed in the present study accounted for this fact by using ANOVAs that incorporated the participants as a random factor (as is common practice to deal with this problem). The ANOVA removes the between participants variability in a very similar way as the normalization.

Appendix B

Common Representation Model

B.1 Comparing illusion effects

In this section two relationships between the perceptual illusion and the motor illusion will be derived from the explicit version of the Common Representation Model, the equations 3.1 and 3.2 of chapter 3.

Figure 3.1 on page 34 shows the explicit version of the Common Representation Model. The model is fully linear, an assumption that is justified by the fact that both the perceptual measure and the MPA are linearly related to object size. It is assumed that an internal estimate (I) of object size (S) is affected by the illusion:

$$I(S,k) = b_{SI} * S + a_{SI}(k)$$

(where $k = 1, 2$ stands for two versions of the illusion that are going to be compared). Note that the internal estimate is a linear function of object size and that for both versions of the illusion the same slopes b_{SI} are assumed. In the experiments of this study the slopes for the different illusion conditions were similar enough to work with this assumption. No further assumptions are needed about the intercepts $a_{SI}(k)$ and the slope b_{SI} — except for the trivial assumption that the slope is unequal zero: $b_{SI} \neq 0$.

The linear functions that relate the internal estimate to the perceptual measure (P) and to grasping (G) are assumed to be unaffected by the illusion:

$$\begin{aligned} P(I) &= b_{IP} * I + a_{IP} \\ G(I) &= b_{IG} * I + a_{IG} \end{aligned}$$

Again, it is set: $b_{IP} \neq 0$ and $b_{IG} \neq 0$. Simple calculations yield the differences between the two illusion versions:

$$\begin{aligned} \Delta_P &= P(I(S,2)) - P(I(S,1)) = b_{IP} * (a_{SI}(2) - a_{SI}(1)) \\ \Delta_G &= G(I(S,2)) - G(I(S,1)) = b_{IG} * (a_{SI}(2) - a_{SI}(1)) \end{aligned}$$

Note that Δ_P and Δ_G are independent of S. Combining the two equations yields:

$$\frac{\Delta_G}{b_{IG}} = \frac{\Delta_P}{b_{IP}}$$

Multiplying this equation with $\frac{1}{b_{SI}}$ gives an equivalent of equation 3.1 of chapter 3:

$$\frac{\Delta_G}{b_G} = \frac{\Delta_P}{b_P}$$

(with: $b_G = b_{SI} * b_{IG}$; this is the slope with which MPA depends on physical size and: $b_P = b_{SI} * b_{IP}$; this is the slope with which the perceptual measure depends on physical size). Finally, if b_P and b_G are equal, this simplifies to the equation 3.2 of chapter 3:

$$\Delta_G = \Delta_P$$

For assessment of this model note that the model is an attempt to use as few assumptions as possible. For example, it could have been assumed that b_{SI} (the slope with which the internal size estimate depends on physical size) equals unity: $b_{SI} = 1$. This would simplify the model while the predictions would be exactly the same. However, it was attempted to be as general as possible and therefore as many parameters were left unspecified as possible.

B.2 Prediction for the Aglioti paradigm

It is easy to show that the Aglioti paradigm as described in section 2.5.3 and in Appendix C is valid in the framework of the Common Representation Model. In the Aglioti paradigm two discs of different size (S_1 and S_2) are chosen to be perceived as being of equal size in the two illusion conditions:

$$P(I(S_2, 2)) = P(I(S_1, 1))$$

Using the equations of the last section this is equivalent to:

$$\begin{aligned} b_{IP} * (b_{SI} * S_2 + a_{SI}(2)) + a_{IP} &= b_{IP} * (b_{SI} * S_1 + a_{SI}(1)) + a_{IP} \\ b_{SI} * S_2 + a_{SI}(2) &= b_{SI} * S_1 + a_{SI}(1) \end{aligned}$$

If the two discs are grasped the predictions of the model for the grasping measure are:

$$\begin{aligned} G(I(S_2, 2)) &= b_{IG} * (b_{SI} * S_2 + a_{SI}(2)) + a_{IG} \\ G(I(S_1, 1)) &= b_{IG} * (b_{SI} * S_1 + a_{SI}(1)) + a_{IG} \end{aligned}$$

Combining these two equations with the previous equation yields:

$$G(I(S_2, 2)) = G(I(S_1, 1))$$

This is the prediction of the Aglioti paradigm for the case that there exists a common representation of object size for grasping and for perception: If the two discs in the two illusion conditions are perceived as being equal in size, they are also grasped equally. Note that this prediction does not depend on the slopes with which the perceptual measure and the grasping measure depend on physical size. It is valid even if the slopes are different.

B.3 Idealized Expected Correlation

The Common Representation Model allows an idealized prediction of the across-participants correlation between the motor illusion and the perceptual illusion. To obtain this prediction it is assumed that the perceptual measure of the illusion (Δ_P) is noise–free. That is, it is assumed that all variation in the random variable Δ_P reflects differences in the internal size estimates across participants and that there is no noise added in the transformation from internal size estimate to the perceptual measure. This is a strongly idealized assumption. However, it helps estimating the statistical power of studies because it yields a larger expected value for the across-participants correlation (the Idealized Expected Correlation) than if the noise in the perceptual system was taken into account. If it turns out that the power is not even sufficient to detect the Idealized Expected Correlation then one cannot expect to detect any actual correlation.

A second assumption is related to the noise in the motor system. In order to account for the larger variation in grasping than in the perceptual measures, additional noise in the transformation from internal size estimate to grasping is assumed. Based on equation 3.2 on page 35 it is set:

$$\Delta_G = \Delta_P + N$$

with Δ_P and Δ_G being random variables describing the perceptual effect and the grasping effect of the illusion for each participant individually. N reflects the added motor noise which is assumed to be uncorrelated to the perceptual effect: $Cov(\Delta_P, N) = 0$. The covariance of Δ_P and Δ_G calculates to:

$$\begin{aligned}
Cov(\Delta_P, \Delta_G) &= E(\Delta_P * \Delta_G) - E(\Delta_P) * E(\Delta_G) \\
&= E(\Delta_P * (\Delta_P + N)) - E(\Delta_P) * E(\Delta_P + N) \\
&= E(\Delta_P^2) - E^2(\Delta_P) + E(\Delta_P * N) - E(\Delta_P) * E(N) \\
&= \sigma_{\Delta_P}^2 + Cov(\Delta_P, N) \\
&= \sigma_{\Delta_P}^2
\end{aligned}$$

Using this relationship the Idealized Expected Correlation can be calculated:

$$\rho_{P,G} = \frac{Cov(\Delta_P, \Delta_G)}{\sigma_{\Delta_P} * \sigma_{\Delta_G}} = \frac{\sigma_{\Delta_P}^2}{\sigma_{\Delta_P} * \sigma_{\Delta_G}} = \frac{\sigma_{\Delta_P}}{\sigma_{\Delta_G}}$$

This is the equation 3.3 which was used in chapter 3 on page 35.

Appendix C

Aglioti Paradigm

The studies of Aglioti et al. (1995), Haffenden and Goodale (1998) and of Marotta et al. (1998) used a slightly different approach than the present study and than the other studies shown in Table 7.1 on page 86. This approach does not use direct estimates of the illusion effects and therefore some recalculations are needed to obtain values for the illusion effects that can be compared to the other studies. In this appendix the rationale of this paradigm will be described (see also section 2.5.3 for a description of the paradigm). After this, the procedure that was used to implement this paradigm will be described and it will be shown how estimates for the illusion effects can be derived from this paradigm (the values that were used in Table 7.1).

C.1 Procedure: Titrating the illusion

Consider two versions of a visual illusion, an enlarging version and a shrinking version and a pair of targets that are perceived as being equal in size if one target is exposed to the enlarging version while the other is exposed to the shrinking version. The Aglioti paradigm predicts that if grasping is affected by the illusion just as much as perception then there should be no difference in grasping between these two targets. This is the central hypothesis being tested in the Aglioti paradigm (Appendix B.2 shows that this prediction is valid in the framework of the Common Representation Model).

Note that for the Aglioti paradigm it is not necessary to use explicit estimates of the illusion effects (and, in fact, Haffenden & Goodale, 1998 and Marotta et al., 1998 did not

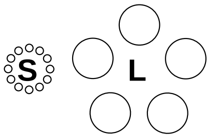
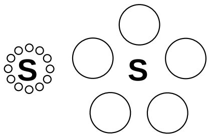
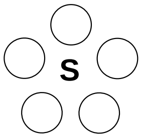
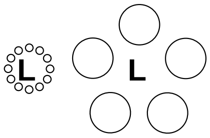
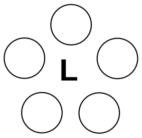
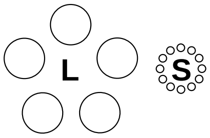
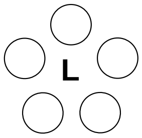
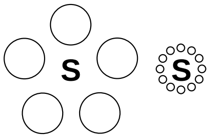
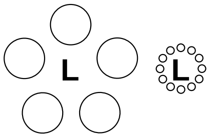
Condition	Stimulus	Perceived as...	Grasped	Trials
a		equal		18
b		different		9
c		different		9
d		equal		18
e		different		9
f		different		9

Figure C.1: The Aglioti paradigm as implemented in the study of Aglioti et al. (1995). Shown are all conditions (i.e., trial types) and required responses for one half of the participants. These participants were instructed to grasp the left disc if they perceive the discs as being equal in size and the right disc if they perceived them as being different in size. The other half of the participants grasped the right disc if they perceive the discs as being equal in size. The "Stimulus" column shows the stimulus that was presented to the participants. The small and the large central discs of the Ebbinghaus figures are not shown, but indicated by the letters S and L. The "Grasped" column shows which choice had to be performed by the participant. For example, in the a–condition, the participants perceived the two discs as being equal in size and consequently grasped the left disc (the small disc). The last column indicates the number of repetitions that were performed in each condition.

report illusion effects for grasping). Nevertheless, estimates of the illusion effects can be calculated from the actual implementation of the Aglioti paradigm.

In the actual implementation of the Aglioti paradigm a pair of discs was selected in a pre–test for each participant. The discs were chosen such that if the small disc was surrounded by small context circles and the large disc was surrounded by large context circles, the participant reported to perceive them as being equal in size. After the pre–test participants were faced with the different experimental conditions that are shown in Figure C.1. In each trial the participants first judged whether they perceived the discs as being equal in size. If they perceived them as being equal they were instructed to grasp the disc on one side of the display. If they perceived them as being different they grasped the disc on the other side. This instruction was counterbalanced between participants such that half of them grasped right if they perceived the discs as being equal and the other half grasped left (Figure C.1 shows the conditions for one participant grasping left if perceiving the discs as being equal in size).

The crucial question in the Aglioti paradigm was, whether there would be a difference in MPA in the conditions in which participants perceived the discs as being equal in size (that is, between the condition a and the condition d of Figure C.1). In this case, the Common Representation Model could be rejected.

In the present study it was argued that this conclusion is not valid because the illusion effects are larger if participants operate on both discs simultaneously (as in the perceptual task) than if they operate on them successively (as in the grasping task). Therefore differences between the tasks cannot be attributed solely to a dissociation between perception and grasping. This issue is discussed in chapter 4 and shall not be reiterated here. Despite this caveat, it is still desirable to obtain information about the illusion effects because this information allows a comparison across studies.

C.2 Estimating illusion effects

Inspecting Figure C.1 shows that the easiest way to obtain an estimate of the illusion effects on grasping in the Aglioti paradigm is to calculate:

$$IE = \frac{(f - c) + (e - b)}{2} \tag{C.1}$$

That is, for each disc the illusion effect is calculated as the difference between the MPA if the disc was surrounded by small context circles and the MPA if the disc was surrounded by large context circles. Then the two illusion effects are averaged. This is the same type of calculation that was used in the other studies. The only drawback is that only 50% of the trials are used to obtain this estimate. However, there seems to be no straightforward way to include the other 50% of the trials (i.e., the conditions a and d of Figure C.1). The problem is, that in these conditions change of object size and change of illusion condition are confounded. Even if one wanted to correct for the change of object size by using the conditions b, c, e and f, one still faces the problem, that grasping in these conditions was performed at the other side of the display.

In short, the illusion effects presented in Table 7.1 on page 86 are calculated as shown in equation C.1. While Aglioti et al. explicitly reported these values (Aglioti et al., 1995, p. 683, Figure 5), I asked A. Haffenden to calculate the corresponding values for her study (A. Haffenden, personal communication, August 1998).

Appendix D

Apparatus

In the present study the grasp trajectories were recorded using an Optotrak 3020 system (Northern Digital). The system uses infrared light emitting diodes (infrared LEDs). These ”markers” are filmed with three high speed video cameras. The cameras are mounted in a 1.1 m rigid frame (Figure D.1). The left and the right cameras are turned inwards such that the fields of view of all three cameras cross at a distance of 1.33 m. This is the minimal distance at which the system can operate because each marker must be visible to each camera. The largest possible distance is larger than 6 m.

Each marker emits light at a certain rate. The markers are synchronized such that at any time only one marker emits light. This enables the system to unambiguously identify each marker (even if it had been invisible for a certain time). The maximum sampling rate is 3500 markers per second. This means, that one single marker could be tracked with a rate of 3500 Hz, two markers with 1750 Hz, etc.. In the experiments of the present study, six markers were used at a rate of 100 Hz.

Each camera obtains a slightly different picture of the markers. This effect (equivalent to the stereopsis in humans) is used to calculate the positions of the markers. Theoretically, only two cameras would suffice for this calculation. By using three cameras in the Optotrak 3020 the accuracy of the system is increased. The marker positions are transformed to a coordinate system that is defined relative to the cameras. The data of each camera are processed in a separate transputer and an additional transputer is dedicated to the integration of the data.

In the experimental setup of the present study, the Optotrak system was connected via a SCSI Bus to an ONYX Reality Engine I (Silicon Graphics). Control of the exper-

Figure D.1: The Optotrak 3020 system that was used to record the grasp trajectories. Clearly visible are the three infrared video cameras. The system is attached to a concrete wall which inhibits vibrations of the cameras.

imental procedure and analysis of the raw data were performed on the ONYX using the programming languages C/C++ and the graphics library OpenGL. Further data analysis was carried out using shell–scripts, Matlab, UNIX–STAT which is a package of statistical analysis programs (Perlman, 1980; Perlman & Horan, 1986), and MrF which is an ANOVA program written by Prof. Jeff Miller, University of Otago, Dunedin, New Zealand.

D.1 Accuracy and calibration

The Optotrak 3020 system is pre–calibrated. The manufacturer (Northern Digital) specifies an accuracy of 0.1 mm in the plane perpendicular to the camera axis of the central camera and of 0.15 mm parallel to the camera axis of the central camera (i.e., in depth). These values apply to one marker at a distance of 2.5 m from the cameras. During the experiments the distances between the cameras and the experimental setup were between 2 m and 2.5 m. Extensive tests in our laboratory showed that the Optotrak system conforms to the specifications of the manufacturer and that there is, for example, no bias regarding warming of the system due to long operation.

During the experiments, three markers on a flag–like holder were attached with adhesive tape to index finger and thumb of the participants (Figure D.2a). For each participant

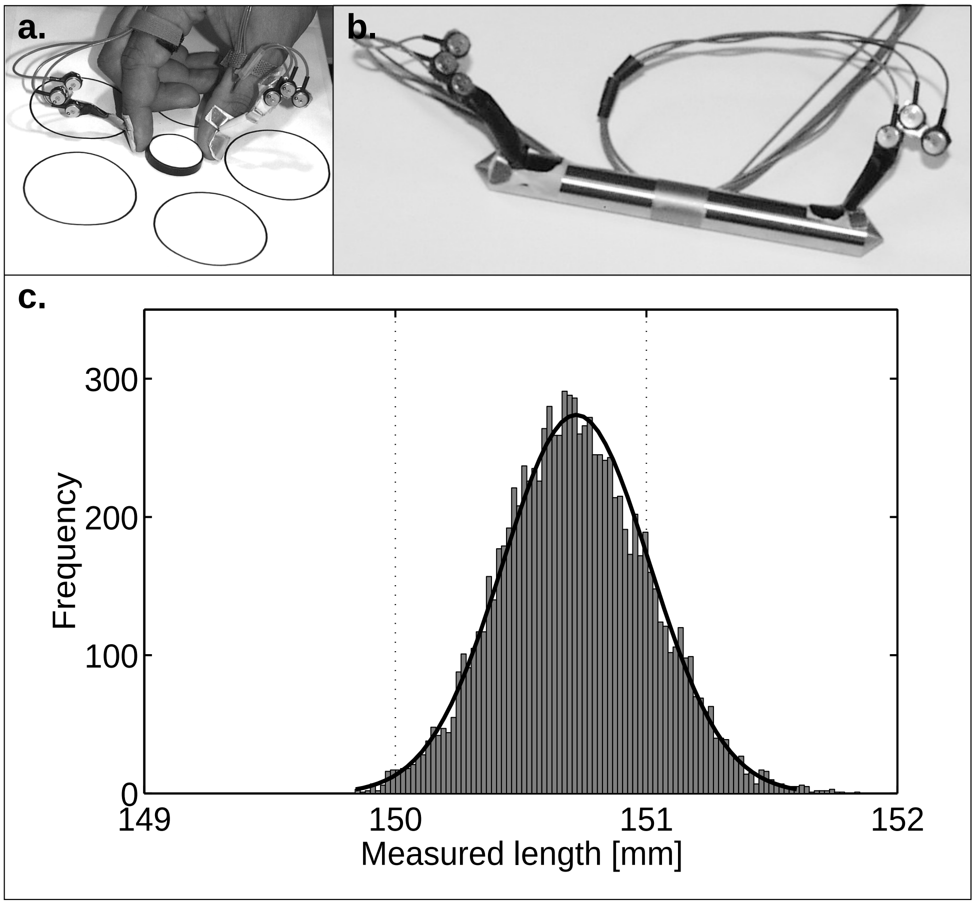


Figure D.2: **a.** During the experiments, three infrared light emitting diodes (the markers) were attached on a flag–like holder to index finger and thumb of the participants. **b.** The accuracy of the system was tested by attaching the flag–like holders to a metal rod instead of index finger and thumb. The same calibration procedure as for the participants was used. It was tested how accurate and how reliable the distance between the points of the rod was tracked by the Optotrak system. **c.** Results of the test. The histogram shows 10000 data points measured while the rod with the markers was moved 175 times from the starting position to the goal position of the grasps that were performed by the participants during the experiments. Consequently, the data are measured at different speeds, positions, and at different angles relative to the cameras. The curve is a fitted normal distribution. See text for details.

the position of the finger tips relative to these markers was determined and expressed in an (orthogonal) coordinate system that was defined relative to the three markers. Using this coordinates it was possible to calculate the trajectories of the finger tips from the trajectories of the markers.

The accuracy of this method was tested with a metal rod of 150 ± 0.04 mm length (Figure D.2b). The rod ended in two points. The points mimicked the finger tips of the participants and it was tested how accurate and how reliable the system determined the constant distance between the two points. 175 reaching movements were performed with the metal rod. The movements started at the same position where the participants started their grasping and ended in the position where the grasping object was placed during the experiments. The movements were performed at a range of different speeds in an attempt to cover the whole range of possible reaching movements that could be produced by the participants. A histogram of all measured distances during this test (10000 data points) is shown in Figure D.2c. The mean measured distance was 150.72 mm, with a standard deviation of 0.29 mm. These values have two aspects. First, the mean measured distance was close to the true length of the rod (the error was 0.72 mm). This error might have been caused by an imprecise measurement of the six marker positions relative to the two points of the rod. The error seems tolerable, because there is always an uncertainty in determination of the finger tips which is, for example, due to the elasticity of the skin.

The more important question is how reliable the distance measurements were. Here, the system performed very well. The standard deviation (0.29 mm) was very close to the value specified by the manufacturer for one single marker — despite the fact that the measurements were performed at very different speeds, at different positions and at different angles relative to the cameras. This variability is small compared to the variability within and between participants. For example, in Appendix A it was shown that the estimated standard deviation for each condition of Experiment 1 was 7.54 mm. After normalization (i.e., after removing the variability that was due to constant differences in responses between participants), the standard deviation was 2.01 mm. The values are based on nine different grasps that were performed by each participant in each condition.

How should these values be compared to the variability caused by the Optotrak? Assume each participant had grasped with exactly the same MPA in each of the nine grasps and that there were no differences between participants in the MPA. In this case, all variability were caused by the Optotrak. Assume, the Optotrak measured the MPA with a standard deviation of 0.29 mm (as suggested by the test described above). The resulting standard deviation for each condition would be $\frac{0.29}{\sqrt{9}}$ mm $\simeq 0.01$ mm. This variability is small compared to the empirically measured variability.

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