

# Comparison of length judgments and the Müller-Lyer illusion in monkeys and humans

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**Abstract** Visuo-spatial magnitude judgements are abstract in that they are detached from the specific sensory parameters on which they are based. Nevertheless, the visual system is actively reconstructing and interpreting the outside world, which sometimes causes reproducible geometric illusions. Here, we investigated the visual length perception of rhesus macaques, an Old World monkey species, in a delayed match-to-sample task and compared the non-human primates' performance to the length judgment of human participants under identical conditions. The quantitative analysis of the length discrimination shows that humans and macaques both show a distance and size effect in judging length and have almost identical length judgment characteristics as determined by the widths of the discrimination functions and the Weber fractions. Moreover, both monkeys and humans were subject to the geometric Müller-Lyer illusion caused by inward or outward pointing 'arrows' at the ends of a line, resulting in over- or underestimation of length, respectively. The strength of the illusion effects (i.e., the magnitude of length misjudgement for stimuli with inward and outward pointing arrows at the end of the lines) was in the range between 1.17 and 1.57° of visual angle for both monkeys and the human participants, and thus very similar between the two primate species. Our results suggest that the visuo-spatial mechanisms underlying simple horizontal line-length perceptions in the human and macaque monkey are qualitatively and quantitatively similar, offering the possibility to investigate the neural correlates of geometric illusions in the monkey and to translate the findings to the human visual system.

**Keywords** Rhesus monkey · Human · Magnitude judgment · Optical illusion · Geometry

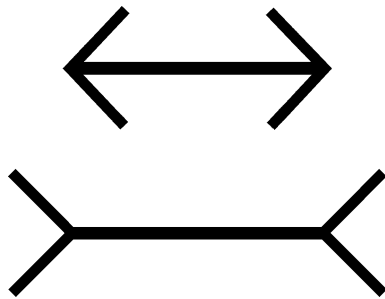
## Introduction

Optical illusions are unequivocal evidence that the brain is not a passive mirror of the outside world. Rather, the visual system of humans and animals is actively engaged in organising information (Nieder 2002). Sometimes these active reconstruction processes lead to the percept of non-existent features, such as the illusory contours forming a Kanizsa triangle (Kanizsa 1979), or percepts that systematically deviate from the physical reality, as in the case of geometric illusions. It is nowadays appreciated that the systematic investigation of illusions provides important clues to the neural architecture and its constraints, which in turn nourishes physiological studies in awake, behaving animals, and primates in particular. Investigations of different types of illusions, such as luminance illusions that arise from lateral inhibition and excitation, the encoding of illusory contours in macaque area V2, multistable percepts represented along the visual pathway, or visual after-effects have helped to distil biological principles of information processing in the brain (for a review, see Eagleman 2001).

Among the best-known geometric illusions is the Müller-Lyer illusion (Müller-Lyer 1889/1981). It leads to a misjudgement of length, due to the presence of 'arrows' with a particular angle placed at each end of a line (see Fig. 1). If the arrows point outward, the line is perceived shorter than it really is, whereas it is judged longer than it physically is when the arrows are pointing inward.

We determined lengths judgments and the Müller-Lyer illusion in macaques and human adults. The perceptual capabilities of monkeys are of special interest because of

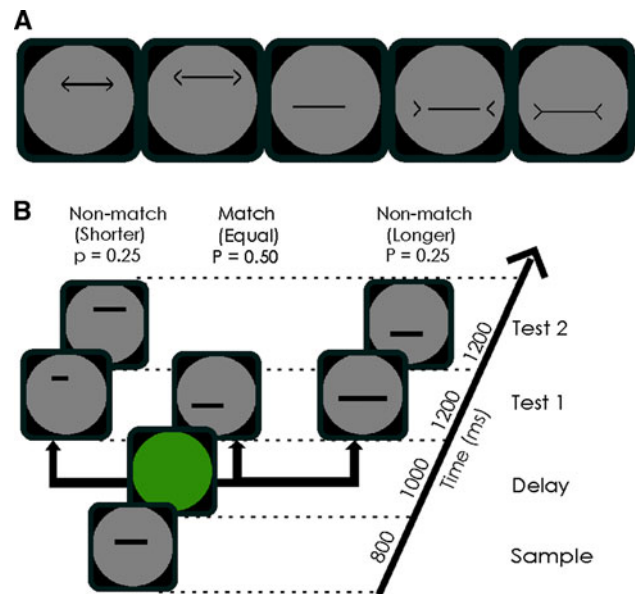
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**Fig. 1** The Müller-Lyer illusion. The perception of the length of a line is distorted by the presence of *outward* or *inward pointing* arrow heads at the ends of the line. The *upper line* is perceived as being shorter than the *bottom line*, although the two lines are equal in length

the relative similarity of primate brains and the suitability of non-human primates to study the neuronal mechanisms of perception (Tudusciuc and Nieder 2007). Some primate species have already been shown to be susceptible to geometric illusions. For example, the Ponzo illusion was shown in rhesus macaques (Bayne and Davis 1983; Fujita 1997) and chimpanzees (Fujita 1997), baboons are deceived by the Zöllner illusion (Benhar and Samuel 1982) and the corridor illusion (Barbet and Fagot 2002), and rhesus macaques, mangabeys and capuchin monkeys experience the vertical–horizontal illusion (Dominguez 1954). Recently, Suganuma and co-workers (Suganuma et al. 2007) reported that capuchin monkeys were susceptible to the Müller-Lyer illusion. They trained the monkeys to assign lines of different lengths to one of two groups (the “short” group and the “long” group) and found that the capuchin monkeys classified the inward pointing arrows Müller-Lyer figures more often in the “long” group, and the outward pointing arrows Müller-Lyer figures more often in the “short” group. This showed that the animals perceived the Müller-Lyer illusion, but prevented a quantitative determination of the size of the illusion in the monkeys. Moreover, it is not known whether length representations and geometric illusions in humans and non-human primates are quantitatively similar.

Here, we first characterise in detail the length judgments of rhesus macaques trained to perform a line-length discrimination task and compare the monkeys’ capabilities to those of human adults in the identical task. We then quantitatively compare the judgment deviations of rhesus macaques to Müller-Lyer figures to the humans’ percepts. The results indicate that both length judgments and geometric illusions are qualitatively and quantitatively similar in non-human and human primates. Since we can tackle the representation of visual length information at the level of single neurons in monkeys, this finding bears implications for length (mis)judgement in the human primate.



**Fig. 2** Stimuli and behavioural protocol. **a** Example of the five types of figures used for each length as sample stimuli: Müller-Lyer figures with *outward pointing arrows*; control stimuli with *outward pointing arrows*; *simple lines*; control stimuli with *inward pointing arrows*; Müller-Lyer figures with *inward pointing arrows*. The delayed match-to-sample protocol (**b**) consisted of a sample phase, followed by a delay of 1,000 ms, depicted in *green*, and then by a test stimulus. In 50% of the trials, this test stimulus was a match, showing a line of equal length to the sample stimulus (the example in the middle column). In this case, the monkey had to release the bar in order to get a reward. In the other 50% of the trials, the first test stimulus was a *non-match*, consisting of a line either shorter (*left-hand* example) or longer (*right-hand* example) than the sample line. The participants had to make the decision to release or hold the lever during the first test stimulus phase (Test 1 in the display)

## Materials and methods

### Subjects

Two male rhesus monkeys (*Macaca mulatta*), weighing 5.3 kg (monkey M) and 12.0 kg, (monkey W) were tested in a delayed match-to-sample protocol for their ability to discriminate the lengths of lines (Fig. 2a). They were implanted with a head bolt to immobilise the head during the sessions to allow for eye movement measurement. All surgeries were performed under sterile conditions while the animals were under general anaesthesia. The animals received postoperative antibiotics and analgesics. They were housed in social groups of 4 (monkey W) and 6 monkeys (monkey M). All procedures were in accordance with the guidelines for animal experimentation approved by the Regierungspräsidium Tübingen, Germany. In addition, 10 human participants (3 males) were tested in the identical delayed match-to-sample protocol and with identical stimuli for their ability to discriminate the lengths of lines

(Fig. 2b). The human participants were naïve to the task and had a mean age of 25.9 years at the time of testing (range 22–30).

### Setup

The monkeys were seated inside a chamber and faced a 15" flat screen monitor (with a resolution of 1,024 by 768 pixels and a refresh rate of 75 Hz) at a distance of 57 cm. Stimulus presentation and performance monitoring was accomplished using the NIMH Cortex program. To maintain a stable visual field, the monkeys had to keep their gaze on the central fixation spot on the screen during sample presentation and the memory delay (monitored with an infrared eye tracking system, Iscan, Cambridge, MA).

The human participants were seated in a chair in a dark room. The stimuli were presented on a 15" monitor placed in front of the participants at a distance of 57 cm. The two-computer Cortex platform was used for stimulus presentation and recording of behavioural responses. All participants were instructed to fixate the centrally presented fixation spot. To test whether an eye movement monitoring system (as was used for collecting data from the monkeys) would influence the performance on the task, the eye movements of three of the ten human participants were controlled with the identical eye tracking system as used for the monkeys.

### Stimuli

Line-length stimuli consisted of one horizontal black line displayed at random locations within a grey background circle (9° of visual angle in diameter, centred on the screen, RGB values of [128,128,128]). The lengths of the lines were seven consecutive multiples of 0.6° of visual angle, from 1.8 (shortest line) to 5.4 (longest line) degrees of visual angle. Both monkeys and human participants were tested with different displays for each trial, and the displays were generated randomly each day, by assigning random positions for the lines in the display. In each trial, sample and test displays never showed the identical images, but various positions and thicknesses of the lines, to ensure that only the length was relevant for solving the task. One-fifth (20%) of the stimuli were simple line stimuli; the rest of the stimuli (80%) had inward (50%) or outward (50%) pointing arrows at the ends of the line, either connected to the shaft (50%) or at a constant distance (equal to the length of the arrow) to the shaft (50%). Thus, there were five types of stimuli, each presented in 20% of the trials in a session (Fig. 2a):

- Simple line stimuli, of angular lengths 1.8°, 2.4°, 3.0°, 3.6°, 4.2°, 4.8°, and 5.4°, and a thickness of 0.1° of visual angle.
- Müller-Lyer figure with inward pointing arrows. The shafts had the same lengths and thickness as the simple stimuli. The arrows had a fixed length of 0.6° of visual angle, were 0.06° of visual angle thick, and were symmetrically oriented at 135° from the shaft.
- Müller-Lyer figure with outward pointing arrows. The shafts had the same lengths and thickness as the simple stimuli. The arrows had a fixed length of 0.6° of visual angle, were 0.06° of visual angle thick, and were symmetrically oriented at 45° from the shaft.
- Control figure with inward pointing arrows. The shafts had the same lengths and thickness as the simple stimuli. The arrows had a fixed length of 0.6° of visual angle, were 0.06° of visual angle thick, and were symmetrically oriented at 135° from the shaft, starting at a gap of 0.6° of visual angle.
- Control figure with outward pointing arrows. The shaft, arrows and gap were identical to the control figures with inward pointing arrows, but the angle between the arrow ends and the shaft was 45°.

### Behavioural task

We trained rhesus monkeys in a delayed match-to-sample (DMS) task (Tudusciuc and Nieder 2007) to discriminate lines of different lengths randomly alternating within each session (Fig. 2b). A trial started when the monkey grabbed a lever and achieved fixation of a fixation spot that appeared in the middle of the screen. While maintaining fixation, monkeys viewed a sample stimulus (800 ms) followed by a delay (1,000 ms) and a test stimulus (1,200 ms). The sample stimulus line could have arrow ends, inward (inML) or outward (outML) pointing, which could also be presented shifted away from the shaft (in shift and out shift). The test stimuli always consisted of ordinary lines, without arrows. To receive a reward, the animals had to release a lever if the test line had the same length as the sample stimulus. The monkey had to maintain the lever if the first test was showing a different length. After the reward (or the wrong response), the monkey had again to grab the lever to start another trial. Each session consisted of simple lines, inML, outML, in shift and out shift trials, in random order, with equal probability (20% each) (Fig. 2a). The stimuli were generated anew for each recording session, using a custom made MatLab program (The MathWorks, Natick, MA) designed to randomly assign the position of the length stimuli in the displays.

For the human participants, the protocol was identical with the only difference that the participants, instead of grabbing a lever to start a trial, had to press the left mouse button of a PC and indicated their answer by releasing the button. For a correct response, the monkeys received a few drops of fluid reward. For incorrect

responses, both monkeys and human participants received negative feedback consisting in 300-ms presentation of a red screen.

#### Data analysis

The stimuli were generated anew for each session, using a custom made MatLab program (The MathWorks, Natick, MA) that randomly assigned the positions of the lines in the display for each stimulus. The stimuli were randomly selected from a pool of one hundred different stimuli generated for each length in each session. They were presented to the participants in the delayed match-to-sample protocol by means of a two-computer Cortex system, in random order and with equal probability for each session. The performance data from each participant was analysed by a custom made MatLab program (The MathWorks, Natick, MA), and the general performance compared to the chance level performance of 0.5 by means of a binomial test. For each response distribution and each participant, we determined the best gaussian fit using the Origin statistical package (OriginLab, Northampton, MA). We then computed and plotted the half-bandwidths ( $\sigma$ ) for each of these curves.

Weber's law states that the smallest noticeable difference in magnitude is proportional to the starting value of that quantity. Thus, in the case of length discrimination, the just noticeable difference between two lengths should be proportional to their lengths. Since the just noticeable difference is a statistical measure, we have calculated the just noticeable differences (jnd's) for each of the tested lengths and each participant at the 50% correct level (that is, the average difference that was needed between two lines in order for the participant to perform at a 50% correct rate in discriminating them from each other). We therefore derived the jnd's for each curve obtained through gaussian fitting, as previously described, by noting the lengths on the left and on the right of the sample length where the participant has correctly performed in 50% of the trials.

We then quantitatively assessed the illusory effects to the five types of stimuli by performing a Friedman test across all five distributions of gaussian fits centres. The centre of each gaussian fit gave a measure of the deviation of the perceived length from the actual stimulus (point of subjective equality) for the respective type of stimulus (ordinary lines, Müller-Lyer figures, and control stimuli). We compared the distribution of the deviations for each of the 2 types of Müller-Lyer stimuli and for each of the 2 types of control stimuli to the distribution of the deviations obtained for simple lines with paired samples *t* tests. All statistical tests were performed at  $\alpha = 0.05$ .

## Results

### General performance

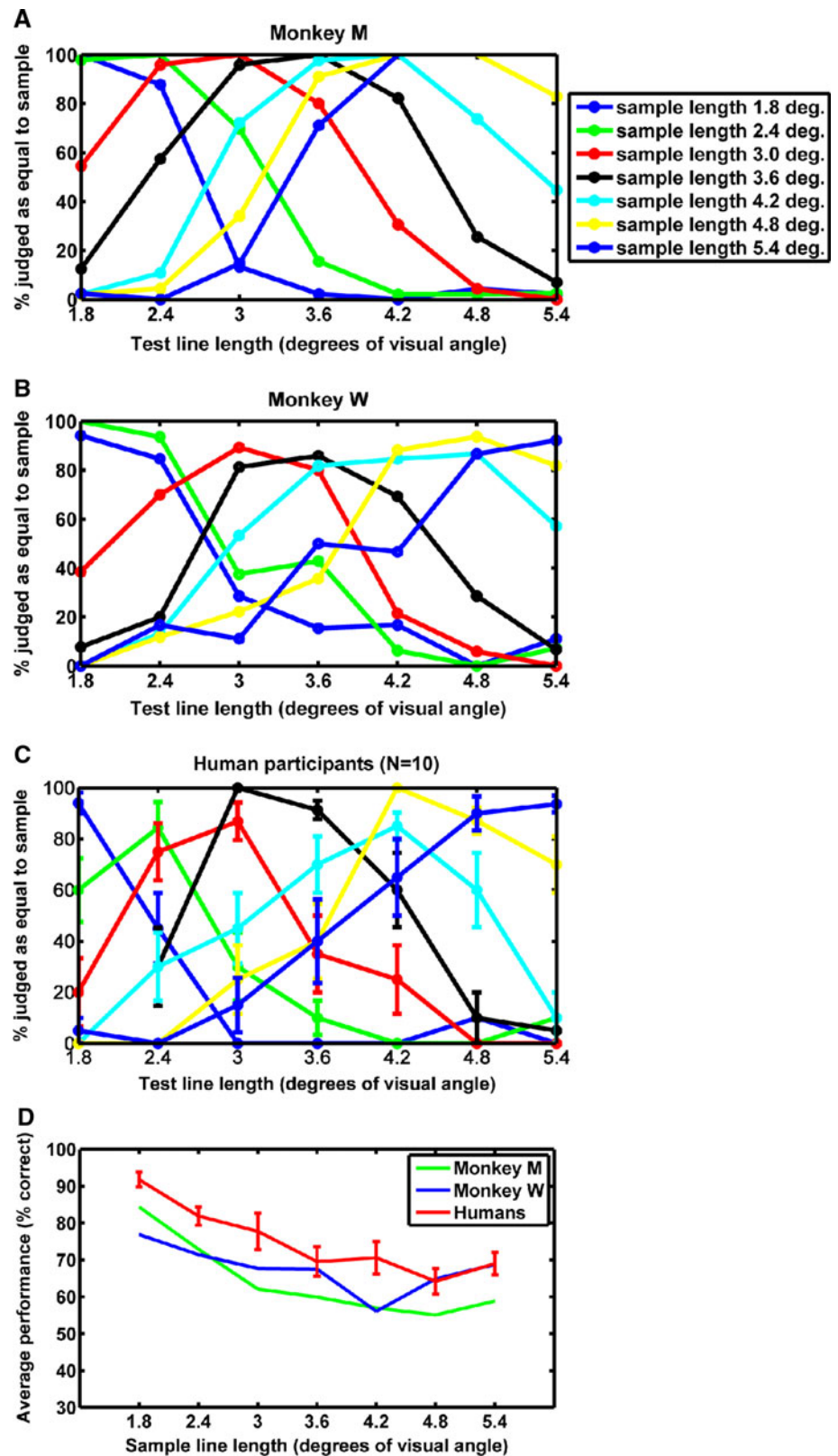
#### Monkeys

Monkey M had an average performance of 75% correct discrimination for the length stimuli, significantly above chance level of 50% ( $P < 0.01$ , binomial test). Monkey W also performed well above chance level at 77% correct discriminations ( $P < 0.01$ , binomial test). The overall performance of monkey M and monkey W on line-length discrimination is plotted in Fig. 3a, b, respectively. The functions in Fig. 3a, b show the probability the monkeys judged the line length in the first test display as being equal to the sample line length. The black curve in Fig. 3a, for example, represents all trials in which the sample stimulus was a line with a length of  $3.6^\circ$  of visual angle, presented to monkey M. The length of the first test stimulus is represented on the *x*-axis. The black dot on this curve that corresponds to  $3.6^\circ$  of visual angle on the *x*-axis represents the match trials (comparing  $3.6^\circ$  to  $3.6^\circ$  lengths). The monkey judged correctly in 100% of these trials. To the left and right of this central point are data points corresponding to non-match trials. When the non-match length of  $3.0^\circ$  of visual angle appeared in the first test display, the monkey released the lever to indicate a match in 96% of the trials, thus making errors (note that for non-match trials, this graph displays the percentage of incorrect trials, whereas for match trials it displays the percentage of correct trials). For more dissimilar lengths, however ( $1.8$  and  $2.4^\circ$ ), monkey M had a lower rate of errors, namely he judged  $3.6^\circ$  to be equal to  $2.4^\circ$  in only 50% of the trials, and made only 17% errors when discriminating a line of  $3.6^\circ$  in length from a line measuring  $1.8^\circ$ .

#### Human participants

On the line-length discrimination task, the human participants could reliably distinguish between the 7 lengths used, as shown in Fig. 3c. The ten participants had an overall average performance of 76.5% correct discrimination of the lengths, which is better than the 50% chance level ( $P < 0.01$ , binomial test) and almost identical to the monkeys' performance. Similarly to the monkeys, the performance of the human participants was governed by the *distance* and the *size effects*, i.e., discrimination of the line lengths improved with increased absolute difference between the lengths of the two lines, and worsened at constant length ratio with increased absolute lengths. This size effect mirrored by a progressive widening of the discrimination functions with line lengths is expected based on Weber's law.

**Fig. 3** Performance on the simple line-length discrimination task. Behavioural functions for monkey M (a), monkey W (b) and the average for 10 human participants (c) on the line-length discrimination task. The colour-coded functions indicate the probability that a participant judged displays in the test period as having equal length to the *sample line*. The seven different test lengths used are represented on the *x*-axis. The lengths presented during the sample period are coded by different colours (see legend). The centre data point of each function, corresponding to a match between the sample stimulus (indicated by the colour) and the test stimulus (indicated on the *x*-axis) represents the percentage of correct responses in the match trials (where the first test display showed the same length information as that presented during the sample period). The data points to the *left* and the *right* of the centre indicate performance in the non-match trials (i.e., where the first test display showed a shorter or longer line); thus, for the non-match trials, the percentage of errors for the respective non-match length is plotted. The functions illustrate the distance effect, i.e., it is more difficult for the monkey to discriminate close lengths (3.6 versus 3.0 and versus 4.2, in this example) than line lengths that are remote from each other (3.6 versus 1.8 or versus 5.4). **d** Average performance of the humans and monkeys as a function of line lengths

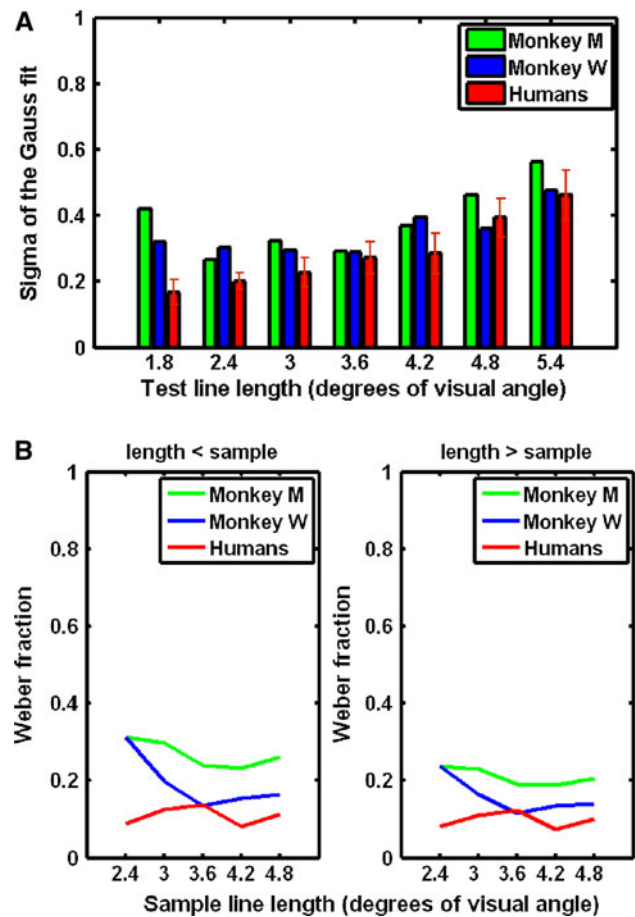


## Comparison of length discrimination in monkeys and humans

The pattern of errors all participants made shows that, on average, they had more difficulty in comparing lines of similar lengths (with a difference of  $0.6$  or  $1.2^\circ$  of visual angle between them) than in comparing lines with a larger difference in length ( $3.6$  or  $3.0^\circ$  of visual angle), consistent with the *distance effect*. For example, the participants made more errors when comparing a line of  $3.6^\circ$  to lines of  $3.0$  to  $4.2^\circ$  than when comparing the same length to lines of  $1.8$  or  $5.4^\circ$ , as shown in Fig. 3 by the mid-grey-level curve in each panel. Both monkeys and the humans present inverted V-shaped curves. The performance of the participants also revealed a *size effect*, since they made fewer errors when comparing a line of  $1.8^\circ$  to a line of  $2.4^\circ$  of visual angle than when they had to compare lines of  $5.4^\circ$  to lines of  $4.8^\circ$  of visual angle, even though the absolute length difference was constant at  $0.6^\circ$ . Because of the size effect, a drop in correct performance with increasing line lengths was detected (Fig. 3d). Interestingly, overall performance for the human participants and the monkey subjects was very similar and showed the identical monotonically decreasing functions.

To determine quantitatively whether the precision of the humans was comparable to the precision of the monkeys on the line-length discrimination task, we plotted the  $\sigma$  (half-bandwidth) of the gaussian fit to the performance curve for each individual sample length. Thus, we compared the error rates of each monkey in discriminating each length to the error rates of the humans. We found that the standard deviations were comparable for the humans and monkeys. The performance functions systematically widened with an increase in line lengths, as evidenced by progressively larger values for sigma (Fig. 4a). This was not true for the smallest tested line length of  $1.8^\circ$  of visual angle, probably a reflection of a performance end effect (the shortest line in our stimulus set was always compared to a longer line, while the longest one was always compared to a shorter line, thus artificially improving the performance on discriminating the end stimuli). We therefore excluded the performances on the smallest and largest line lengths from further analysis of the Weber fraction (see Fig. 4b). Moreover, for all participants there was a slight shift of the performance curves towards the left, reflecting a systematic underestimation of the sample lines. The shift is consistent across participants and may be due to the memory decay over the 1,000 ms delay period.

A key property of the behavioural performance for magnitudes is that it obeys the Weber-Fechner law. In other words, the just noticeable difference (jnd) represents a constant fraction of the stimulus magnitude. We tested the distribution of the 50% jnd's for each monkey and for the

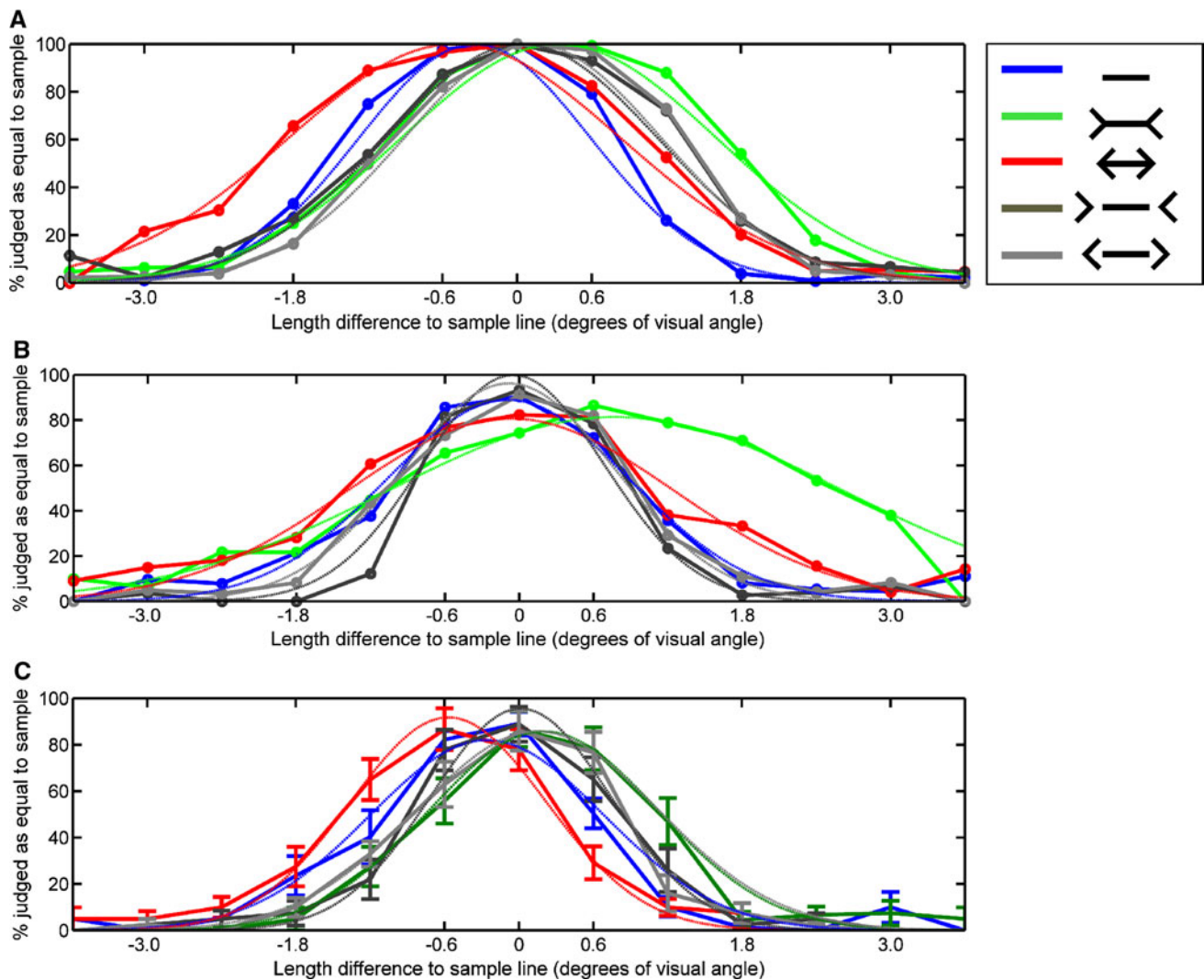


**Fig. 4** Length discrimination of plain bars in monkeys and in humans. The *bar diagram* in (a) shows the half-bandwidths ( $\sigma$ ) for the gaussian fits to the behavioural data for each length (on the *x*-axis). The plot in (b) shows a comparison of the computed Weber fractions for each monkey versus the 10 human participants, pooled together, as a function of the sample length (on the *x*-axis)

humans and plotted the results in Fig. 4b, both leftwards of the sample length (left-hand panel) and rightward of the sample length (right-hand panel). Our results strongly suggest that, for both monkeys and humans, the ratios between the jnd's and the stimulus length were constant across the range of tested quantities.

### Illusory effects in Müller-Lyer figures

To investigate whether human and non-human primates are similarly subject to geometric illusions, we determined the pattern of errors the participants made in assessing the length of the Müller-Lyer stimuli and compared it to the performance on simple lines. Fig. 5 depicts the performance of our participants to the simple line, the two Müller-Lyer lines, and the two controls separately (the five types of stimuli used are colour-coded), as a function of the difference between the length of the test line and the length of the sample line. An ideal subject, responding with 100%



**Fig. 5** Behavioural performance on the illusory figures. Behavioural curves are shown for monkey M (a), for monkey W (b), and for the 10 human participants (c). The *solid curves* represent the percentage of trials in which the participants judged the first test stimulus to be equal in length to the sample stimulus as a function of the difference between the test stimulus length and the sample length, in degrees of visual angle. *Dotted lines* show gaussian fits to the behavioural data. The *blue curve* in each panel represents the discrimination performance of the

simple lines. The *green curve* stands for trials in which the Müller-Lyer figure with *inward pointing arrows* was presented as a sample line, and the *red curve* represents the performance on trials in which the Müller-Lyer figure with *outward pointing arrows* was presented during the sample phase. The two *grey curves* stand for the two control stimuli we used: the arrows were shifted away from the shaft of the figure, by a distance equal to the total horizontal length of the arrow itself. *Error bars* in (c) represent standard error of the mean ( $N = 10$  participants)

accuracy, would produce an inverted V-shaped performance curve, centred on the zero on the  $x$ -axis, that is a 100% value for match trials (the trials in which the distance between the sample length and the test length is zero), and zero per cent for all other trials. The peak of the curve indicates the point of subjective equality, which for the ideal performer was equal to the objective point of equality (zero on the  $x$ -axis). The blue curves in Fig. 5 represent the performance of the participants on the simple line stimuli, and the green and red curves represent the performance on the Müller-Lyer stimuli (inward pointing arrows and outward pointing arrows, respectively). For instance, in panel

a (performance of monkey M), the blue curve peaks at 0 on the  $x$ -axis, meaning that the monkey, on average, judged the test lines that were equal to the sample lines as such in most cases (100%). The test lines that were  $0.6^\circ$  shorter than the sample lines were erroneously judged to be equal to the sample in 99% of the cases, and the lines that were  $0.6^\circ$  longer than the sample lines were judged to be equal to these in 78% of the trials.

The curves in Fig. 5a show that monkey M overestimated the inward pointing arrow Müller-Lyer figures and strongly underestimated the ones with outward pointing arrows. Similarly, Monkey W (Fig. 5b) strongly overestimated

the inward pointing arrow Müller-Lyer figures and slightly underestimated the outward pointing arrow Müller-Lyer figures. For the human participants, in Fig. 5c, the ordinary lines curve, depicted in blue, peaked at zero, while the outward pointing Müller-Lyer figures curve peaked at  $-0.6^\circ$  and was shifted to the left relative to the ordinary lines curve. This indicates that the human participants judged, on average, that the test stimuli that were  $0.6^\circ$  shorter than the sample stimulus (which in this case was always a Müller-Lyer figure with outward pointing arrows) were in fact equal to the sample length. In other words, the humans underestimated the length of the outward pointing Müller-Lyer figures by  $0.6^\circ$  of visual angle. The inward pointing Müller-Lyer figures curve, depicted in green, although peaking at zero, is also shifted relative to the simple lines curve, this time to the right, indicating that the human participants overestimated the Müller-Lyer stimuli with inward pointing arrows. In both monkeys (Fig. 5a, b) and humans (Fig. 5c) the performance curves for the control stimuli appear slightly shifted to the right relative to the ordinary lines curve. These results indicate that the humans, as well as the monkeys, were susceptible to the Müller-Lyer illusion. The observed shift of  $0.6^\circ$  of visual angle is related to the fact that our stimuli were binned in increments of  $0.6^\circ$  of visual angle. They do not, however, reflect the actual difference between actual and perceived length. To quantitatively assess the illusion effect on our participants we determined the strength of the illusion by computing the points of subjective equality for each type of stimulus and each participant separately.

We defined the centre of the best gaussian fit for each curve in Fig. 5 as the point of subjective equality for each of the corresponding stimulus types. For the human participants, we thus obtained the distribution of the centre of the gaussian fit for each of the participants on each of the five types of sample stimuli, and for the monkeys for each participant and session. The goodness-of-fit values ( $r^2$ ) for all fits were in the range of 0.93–0.99 and highly significant. We then used the distributions of the centres of these gaussian curves (averaged over the ten participants for the humans and over all the working sessions for the monkeys) as a measure of the point of subjective equality (PSE) for the given stimulus type.

We first determined that there were significant differences between the five types of stimuli (Friedman test across all five stimulus types,  $P < 0.05$ ). The distribution of the subjective deviations from the actual lengths (the calculated points of subjective equality, or PSE's) for the inward pointing arrows Müller-Lyer figures was significantly different from the distribution of the deviations perceived for the simple line stimuli (paired  $t$  test,  $P < 0.05$ , monkey M:  $t$  value = 14.15,  $df = 14$ , monkey W:  $t$  value = 4.32,  $df = 7$ , human participants:  $t$  value = 4.48 and  $df = 9$ ), both

for the monkey data and for the human data, indicating that humans and monkeys are susceptible to the Müller-Lyer illusion. The same was true for the distribution of the deviations for the outward pointing arrows Müller-Lyer figures, which were as well significantly different than the deviations distribution determined for the ordinary line stimuli, thus confirming the susceptibility to the illusion for both monkey and humans. The same comparison to the performance for the simple lines was carried out for the control stimuli, namely our Müller-Lyer figures with the arrows shifted away from the shafts. Again, the deviations for the control stimuli were each significantly different from those for the simple line stimuli, both for the monkeys and for the humans (paired  $t$  test,  $P < 0.05$ , monkey M:  $t$  value =  $-2.22$ ,  $df = 14$ , monkey W:  $t$  value =  $-2.37$ ,  $df = 7$ , human participants:  $t$  value =  $-3.29$ ,  $df = 9$ ).

#### Direct comparison of the illusion strength in monkeys and humans

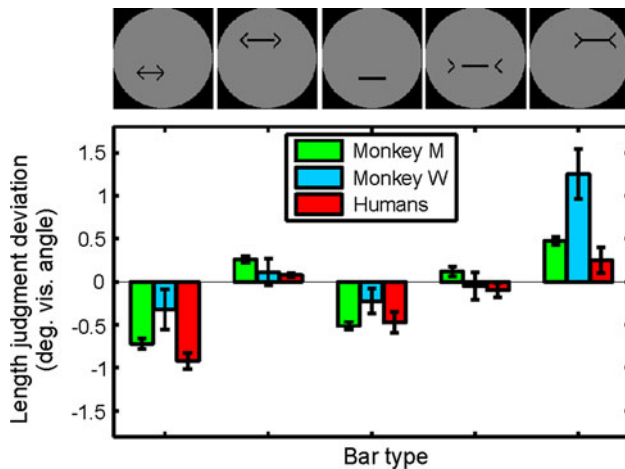
Finally, we directly compared the illusion strength for the monkeys to the illusion strength for the humans by computing the difference between the PSE's and the actual line length (judgment deviation) for each stimulus type and each participant group. The results plotted in Fig. 6 depict the judgment deviation (always as distance zero on the plots in Fig. 5) as a function of the stimulus type. The judgment deviation further confirmed that the monkeys, as well as the humans, were susceptible to the Müller-Lyer illusion, that all participants underestimated the inward pointing arrow Müller-Lyer figures and overestimated the outward pointing arrow Müller-Lyer figures, relative to the ordinary lines.

We measured the strength of the classical Müller-Lyer illusion as the difference between the judgment deviations for the two types of Müller-Lyer figures. This difference was  $1.17^\circ$  of visual angle for monkey M,  $1.57^\circ$  for monkey W, and  $1.19^\circ$  of visual angle for the humans. Furthermore, the judgment deviations for monkeys and humans on the control stimuli are all close to zero, and thus the control stimuli were neither overestimated nor underestimated by the participants, demonstrating the robustness of our results on the illusory strength measured for the Müller-Lyer figures. The ordinary lines were systematically underestimated by our participants, both the monkeys and the humans, while the control stimuli were easier to discriminate and typically had judgment deviations close to zero.

## Discussion

We have trained two monkeys on a delayed match-to-sample task with line-length and Müller-Lyer stimuli. The quantitative analysis of the length discrimination





**Fig. 6** Points of subjective equality for the illusory figures. The relative centres of the gaussian fitted curves, computed as the difference between the computed gauss centre and the gauss centre of the ideal performance curve (where the participant would make no mistakes in judging the length of the lines) are plotted as a function of the type of stimulus presented during the sample phase. The units are degrees of visual angle. These relative centres of the gaussian fits represent the magnitudes of the deviations from the actual lengths or the distance between the points of subjective equality (PSE) of our participants and the points of objective equality as predicted by a 100% correct performance. The *error bars* represent standard error of the mean ( $N = 15$  sessions for monkey M,  $N = 8$  sessions for monkey W,  $N = 10$  participants for the humans)

shows that humans and macaques have almost identical length judgments. Moreover, both monkeys and humans exhibited systematic judgment deviations from the actual length for Müller-Lyer figures. Our results indicate that human and non-human primates are similarly subject to the geometric Müller-Lyer illusion, both qualitatively and quantitatively.

Our data provides the first evidence that monkeys are as proficient as humans at discriminating and comparing length information. The behavioural filter functions in Fig. 3 show that the performance of the monkeys on the delayed match-to-length task is qualitatively similar to the performance of normal humans. Furthermore, when discriminating length on illusion inducing stimuli, the two species show similar half-width ( $\sigma$ ) of the gaussian fits and similar jnd's, demonstrating a quantitative resemblance of the length discrimination systems in monkeys and humans. But non-human primates and mammals are not the only animals susceptible to the Müller-Lyer illusion. Birds, although possessing very different brain organisations, are also subject to geometric distortions. Whereas differences in perception of the Müller-Lyer illusion between pigeons and humans have been reported (Nakamura et al. 2006), a recent study in an African Grey parrot (Pepperberg et al. 2008) reported that this bird and humans process the illusion in analogous ways.

## Characteristics of the Müller-Lyer illusion in primates

Our results reveal that the illusion is still present when the two lines to be compared are not simultaneously visually available. In our delayed match-to-sample protocol, the participants had to compare a Müller-Lyer figure to a simple line, presented after a 1,000 ms delay. Thus, they had to match the length of a simple line to the length of the Müller-Lyer figure retrieved from short-term memory. Our data clearly show that the humans, as well as the animals, were susceptible to the Müller-Lyer illusion and that the strength of the illusion effects was very similar for humans and monkeys.

The Müller-Lyer illusion has been previously tested in the capuchin monkey (Suganuma et al. 2007), using a short/long-line classification task. The monkeys were presented with two lines of equal length, simultaneously presented on the screen, one with inward pointing arrows and the other with outward pointing arrows, of which the one with inward pointing arrows was always the rewarded one. Thus, the results cannot exclude a bias towards the inward pointing arrows line, which was always the rewarded stimulus, and poses an additional difficulty in interpreting the data since the experiment design did not specifically control for the animal's discrimination of the figure as a whole versus the length of the line. The Müller-Lyer illusion is difficult to test in animals, due to the fact that one cannot explicitly instruct the participants to attend to the shaft of the figure and not to the whole. In our experimental design, we set careful controls for ensuring that the monkeys performed a length discrimination task. To avoid this problem, we trained the monkeys to discriminate line-length stimuli prior to exposing them to the Müller-Lyer figures. In addition, we constantly provided reinforcement (positive, through liquid rewards, and negative, through lack of reward and brief presentation of a red screen) throughout the sessions. Thus, our monkeys were motivated to attend to the shaft (length of the line) in all five variants of the sample stimuli, and to match this length to the length of the test stimulus. Importantly, our test stimuli were always simple lines, thus making it more parsimonious for the monkeys to attend to the length of the line, than to evaluate the figure as a whole. Lastly, if the monkeys had indeed attended to the whole figure instead of only the shafts, then the performance curves should be shifted even stronger in the control stimulus conditions, in which the whole figures are even larger. Nevertheless, our results show that the participants, both monkeys and humans, made fewer errors in judging the length of the controlled stimuli than they made when evaluating the length of the shafts of the Müller-Lyer stimuli.

A previous account of the comparison of the geometrical illusory figures perception in humans and non-human

primates argued in favour of a species difference, assessing that rhesus monkeys perceive the Ponzo illusion only within a converging lines context, but that they show no illusion when this context is replaced by dots, a modification that induces an even stronger illusion in humans (Fujita 1997). The author argues that fundamental visual information processing could be greatly different in humans and in rhesus monkeys. Our results are refuting this hypothesis, showing highly similar patterns of illusory perception in the Müller-Lyer figure between the rhesus monkey and the human participants. The contradiction could reside in the fact that, in his study, Fujita had different stimuli, of different lengths, and different experimental conditions for the humans versus monkeys. Furthermore, the monkeys in his study were tested with six a priori set lengths, while the humans were tested with a titration of the bar lengths, making a direct comparison of the strengths of the illusion difficult to interpret.

The Müller-Lyer illusion is of course not the only prominent approach to study length judgments and deception of length judgements. The classical horizontal-vertical illusion (Fick 1852; Oppel 1855) has also been used excessively to investigate geometric distortions and may have specific advantages. For our concerns, however, the Müller-Lyer illusion seemed more appropriate, given that we could work with monkeys already trained to discriminate horizontal line lengths. Most important, we also have neuronal data for simple line representations (Tudusciuc and Nieder 2009) that can now be compared with corresponding Müller-Lyer stimuli. To exclude putative working memory effects during the delay phase, more direct testing techniques, such as having the participants to adjust the length of stimuli (Hamburger et al. 2007) might be helpful in future studies.

#### Putative neuronal basis of the Müller-Lyer illusion

Our results bring clear evidence that the visual system of the macaque monkey is similarly prone to geometrical-optical illusions as the visual system of humans, thus confirming the use of electrophysiological techniques in the monkey visual system for the translation of the results to infer the mechanisms involved in human vision as well. Further work will be needed to clarify the neuronal bases of illusory perception and putative top-down influences at the single cell level. The neuropsychological data of one patient with hemispatial neglect supports the hypothesis that geometric illusions are generated through preattentive processes at early visual processing stages (Ro and Rafal 1996). Functional imaging studies in humans, on the other hand, suggest that the Müller-Lyer illusion may be influenced by top-down modulations from the anterior cingulate (Qiu et al. 2008) and posterior parietal (Weidner and Fink

2007) cortices. In an fMRI study, Weidner and Fink (2007) found the neural processes associated with the perception of the Müller-Lyer illusion to be located bilaterally in the lateral occipital cortex as well as the right superior parietal cortex and right intraparietal sulcus (IPS). Interestingly, the IPS is a well-known key node for representing continuous-spatial magnitudes (Fias et al. 2003; Pinel et al. 2004; Hubbard et al. 2005; Castelli et al. 2006) and discrete-numerical quantity, such as set size and number (Piazza et al. 2007). Single neurons in the macaque IPS (Tudusciuc and Nieder 2007) and lateral prefrontal cortex (Tudusciuc and Nieder 2009) have been shown to represent specific line lengths and numerosities. Moreover, neurons in the prefrontal cortex even encode the proportional lengths between two lines (Vallentin and Nieder 2008). The way is now paved for an investigation of the single neuron correlates of the illusory percept and the nature of the top-down control on the generation of the illusion by analysing single cell activity in response to simple lines when compared to the Müller-Lyer figures in the monkey posterior parietal cortex, using the same task described in this paper.

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#### References

- Barbet I, Fagot J (2002) Control of the corridor illusion in baboons (*Papio papio*) by gradient and linear-perspective depth cues. *Perception* 36:391–402
- Bayne KAL, Davis RT (1983) Susceptibility of rhesus monkeys (*Macaca mulatta*) to the Ponzo illusion. *Bull Psychom Soc* 21:476–478
- Benhar E, Samuel D (1982) Visual illusions in the baboon (*Papio anubis*). *Anim Learn Behav* 10:115–118
- Castelli F, Glaser DE, Butterworth B (2006) Discrete and analogue quantity processing in the parietal lobe: a functional MRI study. *Proc Natl Acad Sci USA* 103:4693–4698
- Dominguez KE (1954) A study of visual illusions in the monkey. *J Genetic Psychol* 85:105–127
- Eagleman DM (2001) Visual illusions and neurobiology. *Nat Rev Neurosci* 2:920–926
- Fias W, Lammertyn J, Reynvoet B, Dupont P, Orban GA (2003) Parietal representation of symbolic and nonsymbolic magnitude. *J Cogn Neurosci* 15:47–57
- Fick A (1852) Erörterung eines physiologisch-optischen Phänomens. *Zeitschrift für rationelle Medizin* 2:83–94
- Fujita K (1997) Perception of the Ponzo illusion by rhesus monkeys, chimpanzees, and humans: similarity and difference in the three primate species. *Percept Psychophys* 59:284–292
- Hamburger K, Hansen T, Gegenfurtner KR (2007) Geometric-optical illusions at isoluminance. *Vis Res* 47:3276–3285
- Hubbard EM, Piazza M, Pinel P, Dehaene S (2005) Interactions between number and space in parietal cortex. *Nat Rev Neurosci* 6:435–448
- Kanizsa G (1979) *Organization in vision*. Praeger, New York
- Müller-Lyer FC (1889/1981) “*Optische Urtheilstäuschungen*” *Archiv für Anatomie und Physiologie, Physiologische Abteilung* 2

- (Supplement) 263–270, Translation by Day RH, Knuth H, 1981 “The contributions of F.C. Müller-Lyer” *Perception*, 10:126–14
- Nakamura N, Fujita K, Ushitani T, Miyatani H (2006) Perception of the standard and the reversed Müller-Lyer figures in pigeons (*Columba livia*) and humans (*Homo sapiens*). *J Comp Psychol* 120:252–261
- Nieder A (2002) Seeing more than meets the eye: processing of illusory contours in animals. *J Comp Physiol A* 188:249–260
- Oppel JJ (1855) Über geometrisch-optische Täuschungen. Jahresbericht des physikalischen Vereins zu Frankfurt am Main, 37–47
- Pepperberg IM, Vicinay J, Cavanagh P (2008) Processing of the Müller-Lyer illusion by a Grey parrot (*Psittacus erithacus*). *Perception* 37:765–781
- Piazza M, Pinel P, Le Bihan D, Dehaene S (2007) A magnitude code common to numerosities and number symbols in human intraparietal cortex. *Neuron* 53:293–305
- Pinel P, Piazza M, Le Bihan D, Dehaene S (2004) Distributed and overlapping cerebral representations of number, size, and luminance during comparative judgments. *Neuron* 41:983–993
- Qiu J, Li H, Zhang Q, Liu Q, Zhang F (2008) The Muller-Lyer illusion seen by the brain: an event-related brain potentials study. *Biol Psychol* 77:150–158
- Ro T, Rafal RD (1996) Perception of geometric illusions in hemispatial neglect. *Neuropsychologia* 34:973–978
- Suganuma E, Pessoa VF, Monge-Fuentes V, Castro BM, Tavares MCH (2007) Perception of the Müller-Lyer illusion in capuchin monkeys (*Cebus apella*). *Behav Brain Res* 182:67–72
- Tudusciuc O, Nieder A (2007) Neuronal population coding of continuous and discrete quantity in the primate posterior parietal cortex. *Proc Natl Acad Sci USA* 104:14513–14518
- Tudusciuc O, Nieder A (2009) Contributions of primate prefrontal and posterior parietal cortices to length and numerosity representation. *J Neurophysiol* 101:2984–2994
- Vallentin D, Nieder A (2008) Behavioral and prefrontal representation of spatial proportions in the monkey. *Curr Biol* 18:1420–1425
- Weidner R, Fink GR (2007) The neural mechanisms underlying the Müller-Lyer illusion and its interaction with visuospatial judgments. *Cereb Cortex* 17:878–884