

Saccades and the Müller-Lyer illusion: implications for the two-visual-systems hypothesis

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Abstract

Background and aim: The cortical visual system is divided anatomically into the dorsal and ventral stream. Goodale and Milner in 1992 proposed that this division was functional: the dorsal stream processes ‘vision-for-action’ whereas the ventral stream processes ‘vision-for-perception’. This model of vision is known as the ‘two-visual-systems hypothesis’ (TVSH). Pictorial illusions, such as the Müller-Lyer (ML) illusion, have been used by advocates of the TVSH to demonstrate dissociation between vision-for-action and vision-for-perception in healthy subjects. However, this literature is controversial, and not least in experiments investigating the magnitude of the illusion effect on saccades. This review aims to synthesise and critically evaluate evidence from saccade experiments on the effect of the ML illusion, in order to determine whether it provides support for the TVSH.

Methods: Literature searches were performed using the Web of Science, Google Scholar and PubMed. Text books were referred to for additional information. Data were extracted from relevant papers and collated using Microsoft Excel. Statistical analysis was performed using SPSS.

Results: Analysis revealed that saccades are affected by the ML illusion. The magnitude of the illusion effect on saccades is comparable to its effect on perception. Reflexive saccades are affected by the illusion, yet they receive little input from the ventral stream. This is inconsistent with the TVSH as it demonstrates that a dorsally controlled action is affected by a perceptual illusion.

Conclusion: Evidence from experiments on the effect of the ML illusion on saccades provides no general support for the TVSH.

Key words: Brentano illusion, Müller-Lyer illusion, Saccades, Two-visual-systems hypothesis

Introduction

Orthoptics is, in part, about seeing, how it is accomplished and the purposes for which it takes place. While functioning eyes are certainly necessary in order to see, they are not sufficient. Thus classically orthoptics has been concerned both with the eyes and with the functioning of the whole visual pathway, including central visual processing structures.

The cortical visual system can be divided anatomically into dorsal and ventral streams¹ which project from V1 to the posterior parietal cortex (PPC) and to the inferotemporal cortex (ITC) respectively. Goodale and Milner² proposed a functional counterpart to this anatomical arrangement. According to their ‘two visual systems hypothesis’ (TVSH), the dorsal and ventral streams receive the same visual input but process it in different ways to achieve different visual outputs: the dorsal stream processes ‘vision-for-action’ whereas the ventral stream processes ‘vision-for-perception’.

According to the TVSH, the dorsal processing of vision-for-action provides an accurate egocentric representation of an object, based on the continually changing metrics of its position in relation to the observer. This allows for accurate and fast ‘goal-directed’ actions such as catching a ball. The internal representation required for such actions is based on visual information processing which might by-pass conscious experience.³ The ventral processing of vision-for-perception, on the other hand, allows the identification of an object within the visual scene regardless of its distance from the observer or the context in which it is situated. The internal representation required for ventral stream purposes must be scene-based, allocentric, detailed and long-lasting, thus enabling object recognition in any situation and over any time-frame. Thus ventral stream processing allows conscious identification of the approaching object as a particular ball (e.g. a baseball vs. a cricket ball), based on previous knowledge and experience.

The TVSH relies significantly on evidence from humans with damage to either the dorsal or ventral stream. Dorsal stream damage results in impaired hand-eye coordination when reaching for, or grasping, a visual target;⁴ this is known as ‘optic ataxia’.^{5,6} Patients with optic ataxia can describe the location of a visual target and its orientation but when asked to reach towards and grasp the target they cannot do so accurately, particularly if the object is positioned peripherally.⁷ Ventral stream lesions can cause visual form agnosia, a condition

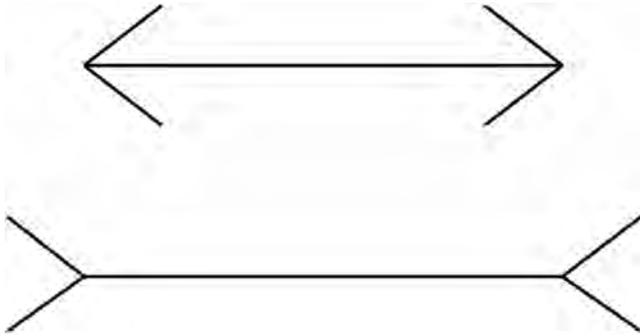


Fig. 1. The Müller-Lyer (ML) illusion. The principle of the illusion is that two lines of equal length are perceived to be of relatively shorter and longer lengths when flanked by inwardly and outwardly pointing arrowheads, respectively. To those affected by the illusion, the line joining the arrowheads in the upper image will appear shorter than the line in the lower image, when in fact they are of equal length. The arrowheads of the ML and related illusions are commonly referred to as 'wings' and the line connecting them as the 'shaft'. The upper figure has been referred to as the compressing ML illusion and the lower figure as the expanding ML illusion.

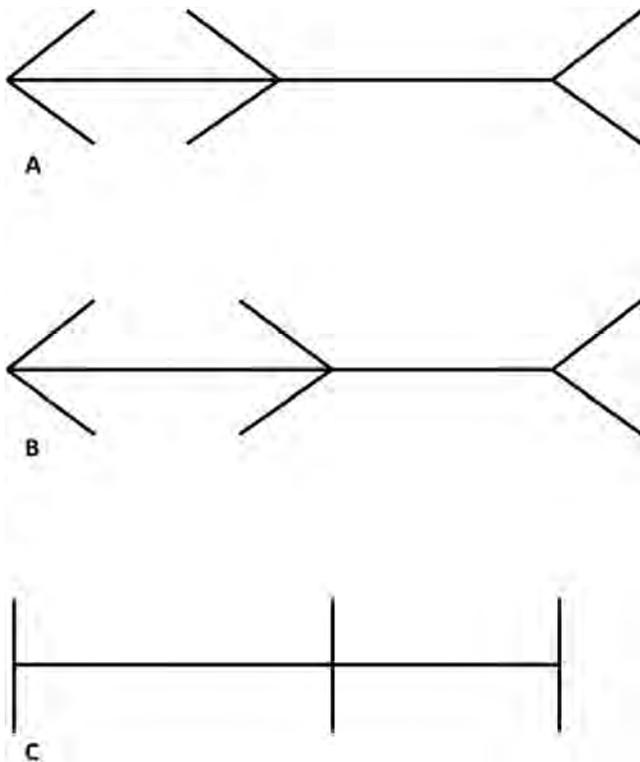


Fig. 2. (A) The Brentano version of the ML illusion. The vertex of the central arrowhead is precisely in the centre but appears to be skewed towards the left. (B) In this figure the vertex of the middle arrowhead appears to be in the centre of the shaft but in fact it is closer to the right. This is similar to the figure used in 'Experiment 1' by McCarley *et al.* 2003,²⁶ for which the stimulus dimensions were chosen so that the expanding and compressing sections of the figure were of equal apparent lengths and therefore different physical lengths (C) Example of a control figure similar to that used by McCarley *et al.* 2003.²⁶ The dimensions are the same as in (B) but vertical lines replace the illusion-inducing wings.

characterised by defects in visual shape perception.⁸ A particular patient with visual form agnosia, 'DF', was the subject of a multitude of experiments by the authors of the TVSH.⁹ The results of such experiments formed a

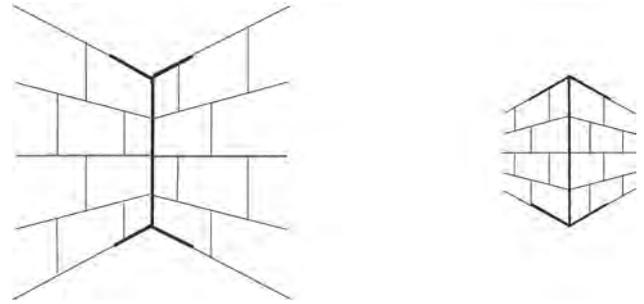


Fig. 3. Illustration of Gregory's¹⁷ popular explanation in which the ML figures were regarded as flat perspective drawings of three-dimensional corners. The expanding ML illusion can be thought of as a perspective drawing of the corner of a room and the compressing ML illusion as the outside corner of a house or a box. These perspective drawings allegedly provide depth-cues, which in turn trigger constancy scaling and an illusion of length. The constancy scaling would be appropriate if the figure were three-dimensional, but because it is two-dimensional the constancy scaling is inappropriate and has an illusory effect: things which appear further away seem bigger (*right*) and things which appear closer seem smaller (*left*).

critical part of the evidence upon which the TVSH rested and, in fact, DF's unusual visual behaviour was the inspiration for Milner and Goodale's re-interpretation of the dorsal/ventral split.¹⁰ DF was unable to recognise or describe simple line drawings of shapes or familiar visual objects but she could accurately reach towards and grasp objects.

It would be problematic if such perception/action dissociations had only been demonstrated in subjects with damaged brains. However, actions, such as grasping and pointing, in normal healthy subjects, were shown to resist the effects of illusions which by definition caused misperceptions.¹¹ This result proved controversial and was criticised on methodological grounds.¹² Other studies investigated the effect of illusions on a different type of action: fast eye movements (saccades). Again there was considerable apparent variability in the results observed. If saccades were affected by illusions, then the TVSH would be undermined because it would demonstrate that a perceptual illusion also has an effect on visuomotor action; there would be no perception/action dissociation as predicted by the TVSH.

One of the most frequently used illusions in the literature is the Müller-Lyer¹³ (ML) illusion, in which line length or the separation of vertices is perceptually distorted by the presence of inwardly or outwardly directed wings (Figs. 1, 2). Although there is no universally accepted explanation for the perceptual effects of the ML illusion, its effects tend to be large and robust and it has been shown that higher cognitive areas are involved in generating the illusion effect^{14,15} (see Fig. 3 for a popular explanation for the illusion effect).

The magnitude of the illusory effect on perception can be modified by altering the physical attributes of the ML figure,^{15,16} with practice¹⁷ or prolonged viewing time,¹⁶ and by instructing observers to selectively attend to particular components of the figure.¹⁸ Presumably the saccadic effects of the illusion might similarly depend on both the attributes of the stimulus and other methodological issues specific to experiments involving eye movements.

Table 1. This table includes data from 10 recent papers (comprising 30 experiments) which assessed the effect of the ML illusion on saccades. Experimental conditions are shown, including attributes of the ML figure and viewing conditions

Experiment no.	Reference	Mean shaft length (°)	Wing angle (°)	Wing as % of shaft	Display time (ms)	Preview period (ms)	Orientation	No. of trials per block	Illusion effect (%)	
1	Bernardis, Knox and Bruno 2005 ¹⁹	6.00	45	16.5	200	–	Horizontal	270	24.8	
2		6.00	45	16.5	200	–	Horizontal	270	20.20	
3	Binsted and Elliott 1999 ²⁰	15.50	45	7.07	Throughout	n/a	Horizontal	72	13.38	
4		23.30	45	7.07	Throughout	n/a	Horizontal	72	6.82	
5	de Grave, Franz and Gegenfurtner 2006 ²¹	31.00	45	7.07	Throughout	n/a	Horizontal	72	3.01	
6		6.77	30	29.42	200	–	Vertical	72	22.18	
7		6.77	30	29.42	200	–	Horizontal	72	29.88	
8		6.77	30	29.42	200	–	Vertical	72	26.49	
9		6.77	30	29.42	200	–	Horizontal	72	33.33	
10		6.77	30	29.42	200	–	Vertical	72	24.71	
11		6.77	30	29.42	200	–	Horizontal	72	36.76	
12		5.40	30	24.06	Throughout	n/a	Vertical	89	10.50	
13		DiGirolamo <i>et al.</i> 2008 ²³	8.10	30	22.45	490+59+?*	490	Horizontal	48	6.10
14			8.10	30	22.45	490+59+?*	490	Horizontal	48	18.52
15	Knox and Bruno 2007 ²⁴	8.25	30	22.45	490+59+?*	490	Horizontal	40	6.36	
16		8.25	30	22.45	490+59+?*	490	Horizontal	40	18.09	
17		6.00	45	16.5	200	–	Horizontal	288	22.0	
18	Lavrysen <i>et al.</i> 2006 ²⁵	6.00	45	16.5	200	–	Horizontal	288	17.0	
19		6.00	45	16.5	1000	–	Horizontal	288	11.0	
20	McCarley, Kramer and DiGirolamo 2003 ²⁶	21.08	45	14.14	Throughout	n/a	Horizontal	?	11.57	
21		21.08	45	14.14	?	?	Horizontal	?	30.94	
22	McCarley and Grant 2008 ²⁷	8.25	30	22.04	506+59+?*	506	Horizontal	100	3.44	
23		8.25	30	22.04	506+59+?*	506	Horizontal	100	20.74	
24		8.25	30	22.04	506+59+?*	506	Horizontal	100	4.85	
25	Tegetmeyer and Wenger 2004 ²⁸	7.20	30	18.04	500+50+500*	500	Horizontal	132	7.55	
26		7.20	30	18.04	500+200+500*	500	Horizontal	132	15.58	
27	Tegetmeyer and Wenger 2004 ²⁸	15.00	65	11.75	Throughout	n/a	Horizontal	80	2.55	
28		15.00	65	11.75	Throughout	n/a	Vertical	80	2.72	
29		15.00	65	11.75	Throughout	n/a	Horizontal	80	2.13	
30		15.00	65	11.75	Throughout	n/a	Vertical	80	2.97	

* Preview + go-signal + remaining display time.

?, Unspecified by authors.

This review aims to determine whether saccades are affected by the ML illusion and what factors influence the magnitude of the illusion effect and thus might explain the variability in existing results.

Methods

Experiments included in the analysis (Table 1)

Ten recent papers were identified which measured the effect of the ML illusion on saccade amplitude.^{19–28} Each included multiple experiments between which the authors altered experimental conditions. The results from each experiment were therefore considered independently. Table 1 is a collation of data from these experiments and includes 30 results for the illusion effect on saccade amplitude along with information regarding experimental methods.

The illusion effect converted to a percentage

Several studies reported the illusion effect on saccadic amplitude as a percentage effect size.^{19,21,22,24} Where this was not provided (e.g. Binsted and Elliott²⁰) results were converted into a percentage using the following formula:

$$\% \text{ effect} = \left[\frac{(\text{expanding} - \text{compressing})}{\text{baseline}} \right] \times 100.$$

This formula was adapted from a study which reviewed

the effect of the ML illusion on visually guided pointing.²⁹ *Expanding* and *compressing* refer to the reported mean result for saccadic amplitude between the vertices of the ML figure with *inwardly* and *outwardly* pointing wings, respectively (see Fig. 1 for illustration of expanding and compressing illusions). *Baseline* refers to control data for saccadic amplitude between two vertices the same distance apart but without ML wings.

For example, in Binsted and Elliott²⁰ the authors reported the following results for their figure with a shaft length of 15.5°:

Expanding = 15.8°, Compressing = 13.7°,
Baseline = 15.7°.

Baseline in this case referred to saccades between two ‘plus’ symbols. The following percentage effect was obtained:

$$\left(\frac{15.8 - 13.7}{15.7} \right) \times 100 = 13.38\%.$$

Exceptions

The above formula was inappropriate for results from ‘Experiment 1’ in McCarley *et al.*²⁶ and ‘Experiment 3’ in DiGirolamo *et al.*,²³ in which the segments of the Brentano version of the ML illusion were of the same ‘apparent length’ (i.e. they were perceived to be the

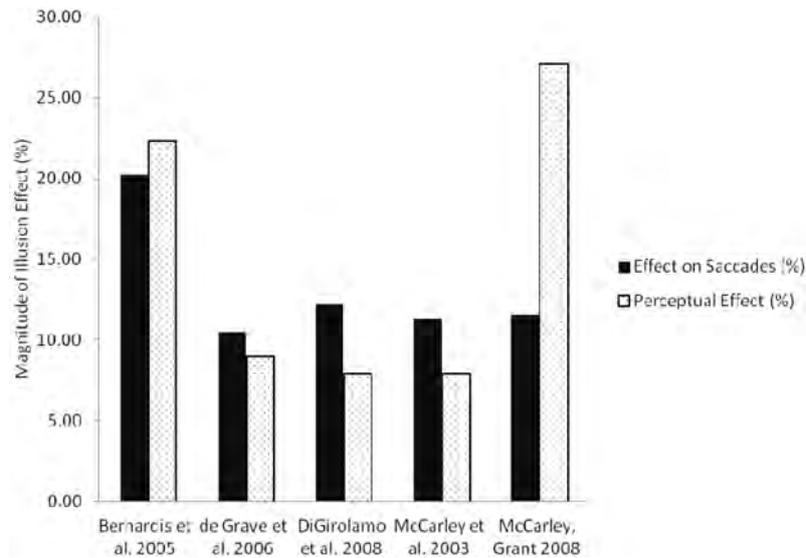


Fig. 4. Bar chart comparing the magnitude of the Müller-Lyer illusion effect (%) on saccades and perception. Only the studies which included data for perceptual effect are shown.

same) and therefore different physical lengths (Fig. 2B). In these cases the following formula was used instead:

$$\% \text{ effect} = \left[\frac{(\text{expanding} - \text{control 1})}{\text{control 1}} + \frac{(\text{control 2} - \text{compressing})}{\text{control 2}} \right] \times 100.$$

Expanding and *compressing* refer to the mean saccadic amplitude between the sections of the figure flanked by inwardly and outwardly pointing wings respectively. *Control 1* and *control 2* refer to data obtained from the authors' control experiments which measured saccadic amplitude to a figure of the same dimensions but with bisecting lines instead of ML wings (Fig. 2C). *Control 1* was the physically shorter of the two lengths and *control 2* the physically longer.

For example, for 'Experiment 3' in DiGirolamo *et al.*,²³ the longer section of the figure was 8.9° and the shorter section was 7.6°. Their results (for the reflexive saccade condition) were as follows:

Shorter section: Expanding = 7.7, Actual length = 7.6, Control 1 = 7.4.
 Longer section: Compressing = 8.5, Actual length = 8.9, Control 2 = 8.7.

To calculate the expanding illusion effect as a percentage, first the difference in length between the shorter control result and the expanding illusion result is calculated (i.e. 7.4 subtracted from 7.7). This difference (0.3) is then divided by the control result (7.4) and multiplied by 100 (4.05%). To calculate the compressing illusion effect as a percentage, the difference in length between longer control result and the compressing result is calculated (8.5 subtracted from 8.7) then divided by this control result (8.7) and multiplied by 100 (2.30%).

The formula below combines the expanding and compressing result to give a single illusion effect as a percentage:

$$\% \text{ effect} = \left[\frac{(\text{Expanding} - \text{control 1})}{\text{control 1}} + \frac{(\text{control 2} - \text{compressing})}{\text{control 2}} \right] \times 100.$$

$$\% \text{ effect} = \left[\frac{(7.7^\circ - 7.4^\circ)}{7.4^\circ} + \frac{(8.7^\circ - 8.5^\circ)}{8.7^\circ} \right] \times 100 = 6.36\%.$$

Results

Illusion magnitude

An illusion effect was found in all the experiments reviewed but the effect size was markedly variable, ranging from approximately 2% to 38% (Table 1). The mean (\pm SD) effect size was 15.37% \pm 10.21%, which differed significantly from zero according to a one-sample *t*-test ($t(29) = 8.2$; $p < 0.001$).

Comparison with perceptual effects

Five of the 10 papers included a measure of the illusion effect on perception^{19,22,23,26,27} (Fig. 4). The mean perceptual effect from these five papers was 13.65% \pm 8.46%. The mean illusion effect on saccades from the 12 saccade experiments in the same five papers was 13.48 \pm 6.34%. These means were not statistically different according to a paired-sample *t*-test ($t(11) = 0.065$; $p = 0.949$).

Proportions of the ML figure

There was significant negative correlation (Spearman's $r = -0.431$; $p < 0.05$) between wing angle and illusion effect. There was significant correlation between the wing length (as a percentage of the shaft) and the illusion effect on saccades ($r = 0.58$; $p < 0.01$). There was also significant negative correlation between shaft length and illusion effect ($r = -0.51$; $p < 0.01$).

Thus the illusory effect was increased by reducing the length of the shaft, reducing the angle between the shaft and the wings, and increasing the proportion of the shaft taken up by the wings. This is consistent with previous findings for perception.^{15,30}

Viewing conditions

Viewing conditions varied considerably between studies. One striking difference was whether the ML figure was continuously visible throughout a block of trials or whether it was only visible for a discrete length of time during each trial. Four of the 10 papers opted for the former approach^{20,22,25,28} and the remaining six for the latter. There was a significant difference between the means of those experiments which used a continuously visible figure and those which did not ($t(26) = 3.84$, $p < 0.05$). This suggests that continuous visibility of the figure reduces the illusion effect on saccades. Likewise, Festinger *et al.*³¹ found that the illusion magnitude on saccades, and on perception, decreased following continuous inspection of the figure with 'free eye-movements'.

In experiments which used a discrete display time, this varied from 200 ms to 1000 ms. There was significant negative correlation between the display time and the illusion effect on saccades (Spearman's $r = -0.72$; $p < 0.01$).

Additionally, three papers (nine experiments) which used a discrete display time also included a preview period before the saccade 'go-signal' of approximately 500 ms.^{23,26,27} The mean illusion effect sizes for those experiments which did and did not include a preview period were $24.4\% \pm 7.3\%$ and $11.8\% \pm 6.3\%$, respectively. The means were significantly different ($t(18) = 4.1$, $p < 0.001$).

Thus continuous viewing of the ML figure decreased its illusion effect on saccades and longer display times and a preview period weakened the illusion effect. An explanation for the first two of these findings is that longer display times or continuous viewing of the stimulus could allow for saccade adaptation.³² If the ML stimulus remained present after the saccade had landed, a retinal error signal would have been generated based on the difference between the intended landing position (i.e. vertex) and actual landing position. Knox³² demonstrated that the ML illusion could indeed induce saccade adaptation of a type very similar to that observed with classic adaptive techniques (e.g. double-step adaptation^{33,34}) when display time was long enough to allow for retinal error signals.

Factors which did not influence illusion effect

The mean illusion effect for horizontally positioned

ML figures was $15.48\% \pm 10.27\%$. The mean illusion effect for vertically positioned ML figures was $14.93\% \pm 10.89\%$. There was no significant difference between them ($t(28) = 0.117$, $p = 0.91$). The style of ML figure used (i.e. Brentano, 'no-shaft' or traditional ML) had no bearing on the illusion effect according to a one-way ANOVA ($F_{2,25} = 2.25$, $p = 0.126$). There was also no correlation between the number of trials per block and the illusion effect (Spearman's $r = -0.041$; $p = 0.835$).

The effect of the ML illusion on reflexive versus voluntary saccades

Saccades are considered to be voluntary when they employ inhibition, working memory or other processes that require attendance to contextual cues or instructions.³⁵ Saccades are 'reflexive' when they are generated towards novel stimuli that suddenly appear in the environment.³⁶ Wong and Mack³⁷ reported that reflexive saccades were immune to the 'dot in frame' illusion whereas memory-guided saccades were not. The results of this experiment led to the hypothesis that the use of perceptual coordinates in the programming of saccades was restricted to situations requiring information stored in memory. In an experiment by Binsted and Elliot²⁰ in which participants saccaded between the vertices of a permanently visible ML figure, an illusion effect was found. Although the saccades used by Binsted and Elliot were not memory guided, they were voluntary and not reflexive. Goodale and Westwood³⁸ proposed that this apparent difference in illusion effect between reflexive and voluntary saccades was consistent with the predictions of the TVSH: voluntary saccades may be perceptually driven relying on ventrally processed information, whereas reflexive saccades are more 'automatic' and thus solely dependent on dorsal mechanisms.

Four of the studies under review compared the effects of illusions on voluntary and reflexive saccades.^{23,24,26,27} Three of the four studies found that voluntary saccades were affected more than reflexive saccades; one found the opposite.²⁴ The biggest anomaly was the difference in the reflexive result found by Knox and Bruno²⁴ compared with the other three.

There were notable differences in the methods used in the reflexive condition by Knox and Bruno²⁴ compared with the remaining studies. The analysis in the previous section found that a preview period resulted in a weaker illusion effect. The preview period used by DiGirolamo *et al.*,²³ McCarley *et al.*²⁶ and McCarley and Grant²⁷ may explain their smaller results for reflexive saccades. Furthermore, the stimulus was visible throughout each saccade in all except the Knox and Bruno²⁴ study, in which it disappeared after 200 ms. Therefore retinal error feedback, and saccade adaptation, was not possible in Knox and Bruno's experiment. Interestingly, it was Knox and Bruno's²⁴ results which corresponded with the data from all 30 experiments. In order to enable this comparison, the saccade types used in each of the 30 experiments under review were classified as either reflexive or voluntary. There was no significant difference between the two groups ($t(28) = 2.01$, $p > 0.05$).

Reflexive versus voluntary saccades: implications of results

The above analysis suggests that both reflexive and voluntary saccades are affected by the ML illusion. The cortical areas which control reflexive and voluntary saccades are located in the parietal and frontal lobes.³⁵ Reflexive saccades have little or no ventral input.³⁵ However, both voluntary and reflexive saccades are affected by the ML illusion, and to about the same extent. This demonstrates that a dorsally controlled action is subject to the same illusion effects as conscious perception without the engagement of ventral stream mechanisms. This does not support the notion of separate internal representations underlying vision-for-action and vision-for-perception.

Discussion

Overall the analysis suggests that both perception and saccades are affected by the ML illusion and that the magnitude of the illusion effect is equivalent, particularly when saccade-specific issues (such as avoiding saccade adaptation) are given appropriate consideration. This is consistent with a shared internal representation underlying both perception and saccades. The physical attributes of the ML figure and the conditions in which it is viewed alter the magnitude of the illusory effect and this may account for the variability found between studies. Recent studies have shown that other variables, not covered in the present analysis, also influence illusion magnitude. De Grave and Bruno³⁹ and Van Zoest and Hunt⁴⁰ demonstrated that saccades with shorter latencies were more affected by the ML illusion than saccades with longer latencies. Additionally, saccades performed in an unpredictable direction were also more affected by the illusion.³⁹ This suggests that the more information the saccadic system has about the stimulus (either from memory or adaptation or time to plan) the less the saccadic amplitude is affected.

Space-perception was described as a dorsal function by Ungerleider and Mishkin,¹ who studied the brain of the monkey. Advances in human neuro-imaging techniques have since provided further clues about the role of the human parietal lobe. It appears to serve multiple visual functions, including the type of visuomotor processing defined as vision-for-action in the TVSH. However, as proposed by Ungerleider and Mishkin,¹ the parietal lobe may also contribute to the perception of spatial relationships.⁴¹ Rizzolatti and Matelli⁴² proposed that there were two distinct functional systems within the dorsal stream: the dorso-dorsal stream serving the online control of action, and the ventro-dorsal stream, serving action organisation, space perception and action understanding. Other authors have suggested differences in function between the right and the left inferior parietal lobe (IPL).⁴³ There is also evidence linking the precuneus to both visuospatial processing and aspects of memory and consciousness.^{44,45} The precise visual function of each parietal area is a matter of continuing debate.

According to the TVSH² the dorsal stream processes vision for the purpose of generating actions; it

specifically does not generate visual percepts. The critical point above is that mounting evidence suggests that dorsal processes contribute to conscious visual perception; this is incompatible with the TVSH.

Conclusion

This review aimed to determine whether evidence from experiments which have investigated the effect of the ML illusion on saccade amplitude supports or contradicts the TVSH, one of the most important and productive hypotheses in visual neuroscience. The evidence demonstrates that saccades are affected by the ML illusion. The illusion magnitude is similar for both perception and saccades. Furthermore, the illusion affects both voluntary and reflexive saccades. Reflexive saccades do not receive ventral input. This suggests that a single representation underlies perception and at least one type of dorsally controlled action.

Competing interests: The authors declare they have no competing interests.

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