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# Age effects on the perception of motion illusions

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**Abstract.** Anomalous motion illusions represent a popular class of illusions and several studies have made an effort to explain their perception. However, understanding is still inconsistent. Age-related differences in susceptibility to illusory motion may contribute to further clarification of the underlying processing mechanisms. We investigated the effect of age on the perception of four different anomalous motion illusions. The Enigma illusion, the Rotating-Snakes illusion, the Pinna illusion, and the Rotating-Tilted-Lines illusion were tested on a total of one hundred and thirty-nine participants covering an age range from 3 to 82 years. In comparison with young adults, children showed a lower likelihood of perceiving motion in all illusions with the exception of the Rotating-Tilted-Lines illusion. For adult subjects, we found significant age effects in the Rotating-Snakes illusion and the Rotating-Tilted-Lines illusion: occurrence of the illusory effect decreased with age. The other two illusions turned out to be unaffected by aging. Finally, inter-correlations between different motion illusions revealed that only the Pinna illusion and the Rotating-Tilted-Lines illusion correlated significantly with each other. The results confirm that anomalous motion illusions should not be considered as a homogeneous group. Possible links between perceptual data and neurophysiological changes related to age are discussed. Perceptual differences due to age provide the opportunity to improve our understanding of illusory motion and point to specific underlying mechanisms.

## 1 Introduction

Static images eliciting anomalous motion illusions represent a very popular class of visual illusions. The interest in anomalous motion illusions is reflected by a rising number of studies concerned with the underlying processing mechanisms which might explain their occurrence. However, our understanding of illusory-motion perception appears to be far from conclusive.

Since a variety of patterns have been observed to elicit a percept of illusory motion, it may not be possible to give an exhaustive list of the studied phenomena. Kitaoka and Ashida (2007) have provided a review of motion illusions and suggested a possible classification. A coarse distinction can be made between illusions that occur spontaneously and illusions that are triggered by real retinal motion. Examples of the former class are MacKay's Rays (MacKay 1957), the Enigma illusion (Leviant 1996), the peripheral drift illusion (Fraser and Wilcox 1979; Faubert and Herbert 1999), and repeated asymmetric patterns (Kitaoka 2003a; Kitaoka and Ashida 2003). In contrast, the Ouchi illusion (Ouchi 1977; Hine et al 1995), the Pinna illusion (Pinna and Brelstaff 2000), and the Rotating-Tilted-Lines illusion (Gori and Hamburger 2006) represent examples of illusions dependent on at least minimal retinal motion.

To gain insights into the generation of illusory motion percepts, different methodological approaches have been pursued. Brain imaging studies by fMRI and near-infrared spectroscopy have found robust activation of the V5 complex when illusory motion is perceived (Zeki et al 1993; Budnik et al 2005; Williams et al 2005; Hashimoto et al 2006). Thus, cortical processing mechanisms for the perception of illusory motion and for the perception of real motion have been assumed to be similar. However, imaging data cannot explain the origin of critical motion signals which could arise at peripheral or central stages of the visual pathway. In several studies an effort has been made to explore the sources of illusory-motion signals. Psychophysics, electrophysiology, and computational

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modeling have been used to determine specific features which convey illusory motion and to specify relevant neural mechanisms.

There has been some debate about possible low-level causes of illusory motion. Streaming motion in the MacKay's Rays and the Enigma illusions has been attributed to irregular fluctuations of accommodation, inducing temporal modulation in stimulus processing (Campbell and Robson 1958; Gregory 1993, 1995). Furthermore, the role of eye movements has been discussed in the case of the Enigma illusion as well as in motion perception of repeated asymmetric patterns (Mon-Williams and Wann 1996; Fermüller et al 1997; Faubert and Herbert 1999; Murakami et al 2006). Although peripheral mechanisms should not be neglected, there is a consensus that motion illusions primarily reflect cortical mechanisms.

Illusory motion in MacKay's Rays has been attributed earlier to a cortical antagonism by Georgeson (1976). He postulated that pattern channels selective for a given orientation are grouped together with channels selective for movement in the orthogonal direction. Motion signals could arise from an antagonism between these channels mediated by inhibitory processes. Recent studies of the Enigma illusion have also led to the conclusion that cortical mechanisms account for the illusory motion. In a computational explanation, Fermüller et al (1997) have considered eye movements and accommodation changes as triggers for motion signals that are misinterpreted by higher-level processes. However, experimental approaches have not confirmed a significant contribution of peripheral mechanisms to the generation of illusory motion (Kumar and Glaser 2006; Hamburger 2007). Findings appear to indicate that neural noise accounts for the Enigma illusion. It has been suggested that high-contrast lines abutting annuli of uniform luminance produce high activity in edge-detecting neurons. Owing to their large receptive fields, which overlap both lines and uniform regions, emanating neural signals could induce illusory motion in the empty channels. Orthogonal junctions seem to be most effective in eliciting the rotatory motion (Gori et al 2006; Kumar and Glaser 2006; Hamburger 2007).

Systematic differences in visual latencies have been considered as explanations of the peripheral drift illusion and illusory motion in repeated asymmetric patterns. Latencies have repeatedly been shown to depend on luminance and contrast (compare eg Roufs 1963; Wilson and Anstis 1969; Mansfield 1973; Lennie 1981; Rabin et al 1994; Kitaoka and Ashida 2007). Low-level motion detectors could therefore be activated by timing differences between responses to elements with different contrast or luminance. Several methodological approaches have confirmed this mechanism (Faubert and Herbert 1999; Naor-Raz and Sekuler 2000; Backus and Oruç 2005; Conway et al 2005). Again, peripheral contributions to the illusory motion appear to be of minor importance. Naor-Raz and Sekuler (2000) have found that the motion percept in the peripheral-drift illusion does not require fluctuations in accommodation. In the case of repeated asymmetric patterns there is some evidence that eye movements enhance illusory motion by retinal refreshment of the image (Murakami et al 2006).

Processing of local motion signals in V1 seems to play a critical role in motion illusions that depend on movement upon the retina. Motion detecting cells at the earliest stage of visual processing have small receptive fields and can signal only one-dimensional motion direction, orthogonal to local pattern. Because of this aperture problem, two-dimensional motion integration is assumed to be biased for motion direction orthogonal to local contours (Marr and Ullman 1981; Nakayama and Silverman 1988a, 1988b). Patterns with contrasting orientation in the Ouchi illusion might be subject to disparate biases during motion integration, which could result in illusory relative motion perception (Hine et al 1997; Khang and Essock 1977a, 1977b; Fermüller et al 2000; Mather 2000). A similar explanation has been suggested for the Pinna illusion that consists of micropatterns with differently oriented low-spatial-frequency components.

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Owing to biased motion integration, different oblique orientations give rise to either clockwise or counterclockwise rotation when the figure is moved forward and backward (Pinna and Brelstaff 2000; Gurnsey et al 2002; Gurnsey and Pagé 2006; Ichikawa et al 2006). The Rotating-Tilted-Lines illusion induces motion perception similar to the Pinna illusion, but is composed of tilted lines of a given length. Likewise, a directional bias orthogonal to line orientation has been proposed as the origin of the illusory rotatory motion (Gori and Hamburger 2006; Gori and Yazdanbakhsh 2008; Yazdanbakhsh and Gori 2008). However, recent findings have also challenged the attribution of illusory motion to the aperture problem in early visual processing. There is evidence from the analysis of the Ouchi illusion in the Fourier frequency space that it is more likely to depend on the Fourier components of its different patterns than on their local contours (Ashida 2002; Ashida et al 2005).

To summarise, studies of motion illusions have explored important aspects of possible underlying processing mechanisms. Nevertheless, our knowledge is far from conclusive. It seems necessary to differentiate explicitly between different phenomena because specific mechanisms may elicit the respective illusory motion percept. We suggest that our understanding could be improved by exploring age-related differences in susceptibility to illusory motion. Although detailed functional understanding cannot be derived from age effects, they may enable us to separate different mechanisms (compare eg Weale 1986; Habak and Faubert 2000; Page and Crognale 2005). Furthermore, consideration of known age-related changes in visual processing might allow us to evaluate the proposed underlying mechanisms.

Studies of the developing human visual system have provided some insights into immature mechanisms during the first years of childhood. Visual evoked potentials have revealed decreasing response latencies (Madrid and Crognale 2000; Crognale 2002). Responses to achromatic patterns develop early and reach adult-like latencies after the first year of age. In contrast, maturation of responses to chromatic patterns is slower, extending over approximately 12 years of postnatal development. Several neurophysiological changes in the striate cortex have been suggested. There is evidence of extended maturation of columnar connections and of the balance between excitatory and inhibitory mechanisms (Burkhalter et al 1993; Murphy et al 2005). Receptive field size decreases with age (Wilson 1988). Also, higher levels of intrinsic neural noise (Skoczenski and Norcia 1998) and broader directional tuning (Morrone and Burr 1986; Banton et al 1999) have been found to occur during the development.

At young-adult age, visual capacities can be considered as stabilised at a maximum level. It is well documented that many aspects of visual function deteriorate during the normal aging process (Weale 1986; Spear 1993; Faubert 2002; but see Enoch et al 1999). Although several optical changes during aging have been described, such as increased lenticular density, senile miosis, and yellowing of the lens, there is consensus that senescent optics of the eye cannot sufficiently explain the reported functional declines (Ball and Sekuler 1986; Weale 1987; Bennett et al 1999).

While volumetric studies confirm that the human striate cortex is subject to only a moderate volume loss (Giedd et al 1999; Raz et al 2004), it has been pointed out that functional declines during normal aging are probably due to more subtle neurophysiological changes, such as loss of myelin, degradation of synapses, decrease in neurotransmitters, or dysfunction of receptors (Wickelgren 1996). These changes could account for the finding that visually evoked potentials increase in latency with aging (Fiorentini et al 1996). There is some evidence that this latency increase may be more pronounced for chromatic patterns than for achromatic patterns (Crognale et al 2001; Page and Crognale 2005). Furthermore, neurophysiological studies on monkeys have shown that senescent V1 neurons exhibit increased latencies, decreased selectivity, and elevated spontaneous activity (Schmolesky et al 2000; Wang et al 2005; Hua et al

2006). These degraded response characteristics are thought to result from reduced GABA-mediated inhibition (Leventhal et al 2003).

Recent psychophysical studies on humans have linked these findings to perceptual changes during aging. Decline in orientation discrimination under different noise levels has been explored by Betts et al (2007). Bennett et al (2007) have considered motion detection as well as direction identification during aging and represented performance with a multichannel model of motion. Results from both studies mirror well decreased selectivity and increased spontaneous activity in senescent VI neurons. Moreover, Betts et al (2005) have demonstrated that direction discrimination improves with age when motion information is extracted from large, high-contrast patterns. They argued that this result agrees with the postulated degradation of GABA-mediated inhibition which weakens centre-surround suppression in motion-selective neurons.

Illusory motion perception has been mainly attributed to a failure of signal processing by neurons at early visual processing stages. Evidence of neurophysiological changes in the striate cortex during maturation and aging suggests that age might account for individual differences in susceptibility to illusory motion. For example, Kitaoka (2003b) reported from field studies that the Rotating-Snakes illusion, a popular example of repeated asymmetric patterns, is closely correlated with age: the older the observer, the less likely he or she perceives the illusory rotatory effect. However, this has never been investigated systematically and with standardized data acquisition. To our knowledge, studies on anomalous motion illusions, no matter which methodological approach is chosen, generally deal with 'ideal' samples, ie mostly student subjects aged 20 to 30 years, and thus ignore potential differences associated with age.

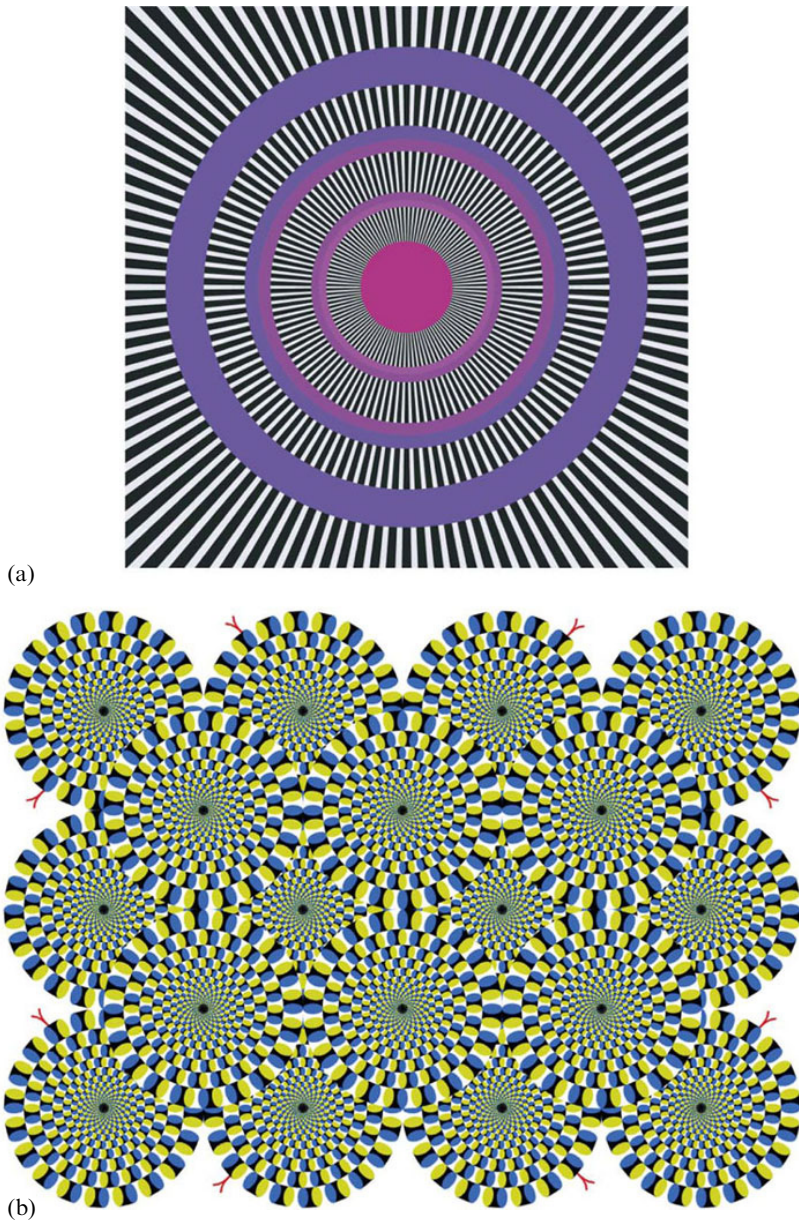
Our aim here was to investigate the effect of age on the perception of motion illusions. We explored different phenomena in a representative sample covering a wide age range. Differential age effects on the occurrence of specific motion illusions would confirm the diversity of the phenomena. We intended to gain insight into underlying processing mechanisms by relating observed age effects to known changes in the visual pathways during maturation and aging.

## 2 Methods

### 2.1 Stimuli

We chose four static motion illusions attributed to different underlying mechanisms (compare section 1). Figure 1 shows the studied illusions: the Enigma illusion (Leviant 1996) and the Rotating-Snakes illusion (Kitaoka 2003a), an example of repeated asymmetric patterns, represent illusions that occur spontaneously; the Pinna illusion (Pinna and Brelstaff 2000) and the Rotating-Tilted-Lines illusion (Gori and Hamburger 2006) require retinal motion.

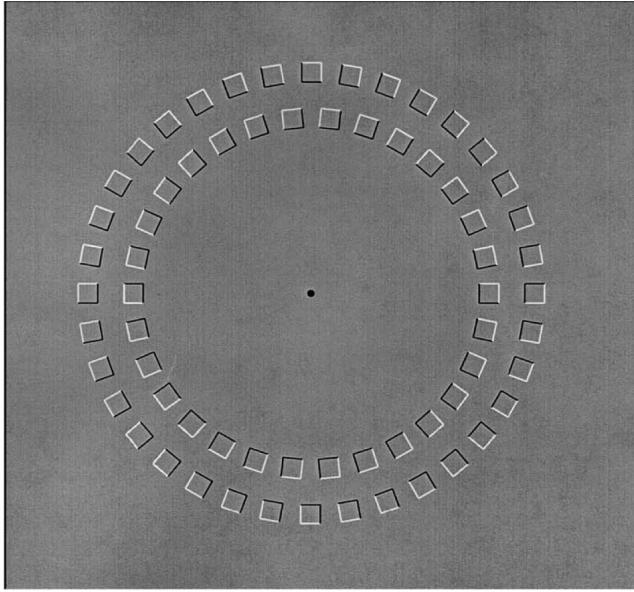
All the illusions were presented as printer-paper versions. Paper was used instead of a computer display in order to limit technical artifacts which are sometimes suspected to play a confounding role in these phenomena. In previous studies printouts as well as computer monitors have been used to display illusion stimuli. However, there is no evidence that a specific presentation form is superior to any other (compare eg Hamburger 2007). We therefore decided to keep the illusions in their original versions. No efforts were made to measure luminances or colour coordinates. It has been often shown for the two coloured illusions (the Enigma illusion and the Rotating-Snakes illusion) that it does not matter whether they are presented with different chromaticities or in achromatic form (Zeki et al 1993; Conway et al 2005; Kumar and Glaser 2006; Hamburger 2007). Informal exploration showed that an observation distance of 60 cm allowed for comfortable viewing and was appropriate to elicit motion perception reliably for all considered illusions. Stimuli (see figure 1) subtended approximately 27 deg horizontally and 19 deg vertically.



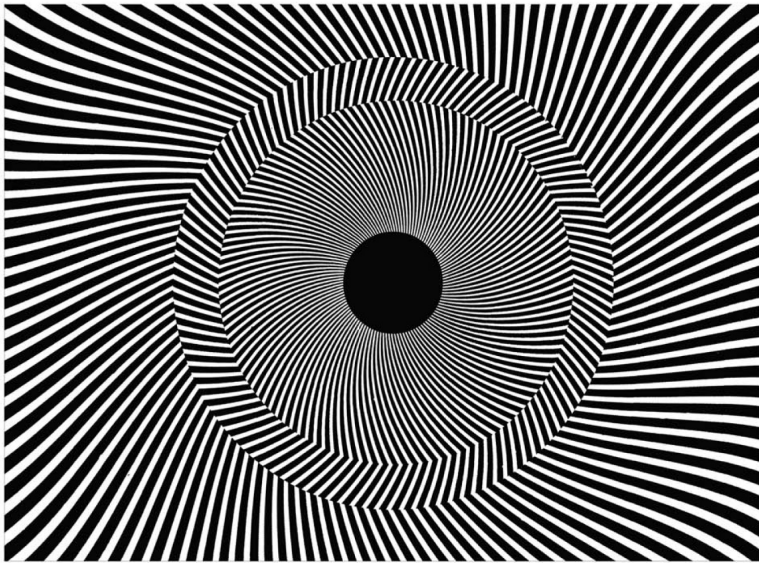
**Figure 1.** [In colour online, see <http://dx.doi.org/10.1068/p5886>] (a) Enigma illusion (Leviant 1996). (b) Rotating-Snakes illusion (Kitaoka 2003a). (c) Pinna illusion (Pinna and Brelstaff 2000). (d) Rotating-Tilted-Lines illusion (Gori and Hamburger 2006).

## 2.2 Participants

A total of one hundred and thirty-nine subjects ranging in age from 3 to 82 years participated in the study. We were able to separate the sample into different age groups: young children (3–6 years:  $M = 5.2$  years,  $SD = 1.0$  year,  $N = 24$ ), young adults (18–39 years:  $M = 25.4$  years,  $SD = 5.7$  years,  $N = 45$ ), middle-aged adults (40–64 years:  $M = 54.3$  years,  $SD = 7.8$  years,  $N = 32$ ), and senior adults (65–82 years:  $M = 73.0$  years,  $SD = 5.0$  years,  $N = 38$ ). The sample consisted of an overall balanced proportion of females and males (52.1% females). Furthermore, we confirmed a consistent distribution of gender across the different age groups ( $\chi^2_{4, N=139} = 2.34$ ,  $p = 0.673$ ). All participants



(c)



(d)

**Figure 1** (continued)

had normal or corrected-to-normal visual acuity and normal colour vision. Visual acuity was measured binocularly with a Landolt C chart constructed for near space. Colour vision was examined by Ishihara plates. Owing to organisational constraints we were not able to carry out standardised assessment of visual abilities in young children. Detailed reports of parents and carers did not provide any evidence of abnormal functions. Although visual acuity is still developing during preschool age, it can be assumed that at the age of 3 years children have attained satisfactory acuity, particularly for near space (Fern and Manny 1986; Lithander 1997). Ocular diseases, medications known to

interfere with normal visual functioning, and any history of neurological disorders were ruled out by focused interviews. Informed consent was obtained from adult participants and from parents of under-age participants. Methods and procedures were approved by the ethics committee of the German Psychological Society (DGPs).

### 2.3 Procedure

Participants were presented with each stimulus once. The experimenter held the stimuli in front of the participants at an observation distance of 60 cm. The Pinna illusion and the Rotating-Tilted-Lines illusion were moved smoothly back and forth. Presentation took place in daylight and without time constraints. Most participants were naive concerning the illusory effects and no information was given. Participants were provided with an instruction for observation (Enigma illusion: look at the centre of the image and try to focus your attention on the coloured rings; Rotating-Snakes illusion: move your gaze over the image; Pinna illusion and Rotating-Tilted-Lines illusion: look at the centre of the image) and were asked to describe what they saw in each image. Following a response scheme, the experimenter noted down all descriptions, but was mainly interested in streaming motion on the three rings changing direction periodically in the Enigma illusion, systematic rotation in the Rotating-Snakes illusion, and systematic clockwise and counterclockwise rotation of the rings in the Pinna illusion and the Rotating-Tilted-Lines illusion. If critical descriptions were not given spontaneously, the experimenter asked more specifically whether there was any perception of motion in general. Although we cannot exclude individual differences in response criteria, specific age-related biases appear rather unlikely.

A comfortable atmosphere was provided to all participants and, independently of age, most of them gave their responses spontaneously. We did not observe more indecision in any particular age group. Moreover, potential age-related response biases would uniformly affect all illusions so that they could not obscure differential age effects on specific occurrence rates. For data analysis, the experimenter rated dichotomically whether critical illusory motion occurred or not.

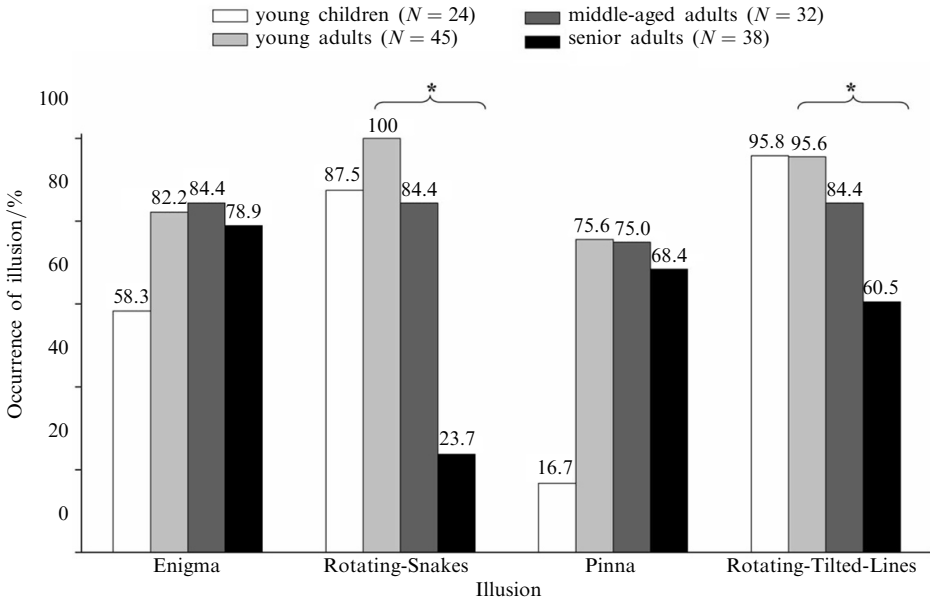
## 3 Results

Figure 2 illustrates the relative frequency of perceived illusory motion in the different age groups. Because of developmental processes, the group of young children represents a special subgroup. Therefore it was treated separately from the adult groups.

### 3.1 Perception of motion illusions in children

It is of obvious interest whether illusory-motion perception can be elicited in young children who rely on a developing visual system. Figure 2 shows that young children reported motion perception in all illusions. However, frequencies of occurrence varied between 16.7% and 95.8% for specific illusions. Comparison with young adults, who rely on an assumedly mature visual system, revealed some significant differences. Only the Rotating-Tilted-Lines illusion was perceived as often by children as by young adults ( $\chi^2_{1, N=69} < 0.01$ ,  $p = 0.957$ ). Here 95.8% of the children and 95.6% of the young adults reported illusory rotation. In contrast, children described motion in the Enigma illusion ( $\chi^2_{1, N=69} = 4.63$ ,  $p = 0.031$ ), the Rotating-Snakes illusion ( $\chi^2_{1, N=69} = 5.88$ ,  $p = 0.015$ ), and the Pinna illusion ( $\chi^2_{1, N=69} = 21.94$ ,  $p < 0.001$ ), less frequently than young adults. The Enigma illusion was described by only 58.3% of the children, whereas 82.2% of young adults perceived illusory motion. The Rotating-Snakes illusion was reported by 87.5% of the children and 100% of the young adults. The largest frequency difference was found for the Pinna illusion, which was perceived by only 16.7% of the children but by 75.6% of the young adults. In summary, perception of motion illusions in children supports the assumption that different processing mechanisms account for specific phenomena. These mechanisms seem to develop at different rates.





**Figure 2.** Relative frequency of reported illusory motion in different age groups for the four motion illusions tested. Significant frequency differences with regard to adult age groups are indicated by asterisk,  $p < 0.001$ .

### 3.2 Perception of motion illusions in adults

In considering the adult age groups, our object was to explore whether aging of the visual system affects the frequency of perceived illusory motion. Analysis of the effect of age on the frequency of perceived illusory motion yielded different results for the different illusions. We found that occurrence of the Rotating-Snakes illusion and the Rotating-Tilted-Lines illusion differed significantly between the age groups ( $\chi^2_{2, N=115} = 61.76$ ,  $p < 0.001$  and  $\chi^2_{2, N=115} = 16.69$ ,  $p < 0.001$ , respectively). The higher the age of our participants the less frequently they reported seeing motion. The effect could be considered as large for the Rotating-Snakes illusion, where the occurrence of the illusion dropped from 100% in the young adult group to 84.4% in the middle-aged adult group, and to 27.3% in the senior group. Perception of the Rotating-Tilted-Lines illusion was affected to a lesser degree. Whereas 95.6% of the young adults reported illusory motion, only 84.4% of the middle-aged adults and 60.5% of the senior adults did. In contrast, the frequency of perception of illusory motion in the Enigma illusion and the Pinna illusion turned out to be independent of age ( $\chi^2_{2, N=115} = 0.35$ ,  $p = 0.838$  and  $\chi^2_{2, N=115} = 0.62$ ,  $p = 0.734$ , respectively). For the Enigma illusion, occurrence ranged between 84.4% and 78.9%; and for the Pinna illusion it ranged between 75.6% and 68.4% in the different age groups. Data for the adult age groups confirm, in agreement with the results for children, that different processing mechanisms underly specific motion illusions. Processing mechanisms appear to be affected differentially by aging.

### 3.3 Intercorrelations between the perception of different motion illusions in adults

In order to further distinguish the aforementioned anomalous motion illusions, we investigated intercorrelations between their occurrence. We were particularly interested in separating correlations due to shared processing mechanisms from those due to the possible common effect of age. Therefore, we calculated Pearson's  $\phi$  coefficients and distinguished them with respect to age. Table 1 gives overall correlation coefficients and partial correlation coefficients controlling for age.

Only few correlations reached significance. There was a medium correlation between the Rotating-Snakes illusion and the Rotating-Tilted-Lines illusion. However, this correlation



**Table 1.** Intercorrelations between perception of different motion illusions, without and with control for age.

Motion illusion	Illusion		
	Rotating-Snakes	Pinna	Rotating-Tilted-Lines
Enigma	0.14	0.12	0.11
controlled for age	0.12	0.12	0.09
Rotating-Snakes		0.17	0.32*
controlled for age		0.18	0.10
Pinna			0.40*
controlled for age			0.41*

Note: Pearson's  $\phi$  coefficients are given. Analysis is based on data of one hundred and fifteen subjects with an age range of 18–32 years. \* $p < 0.01$ .

could be attributed mainly to the common correlation with age. When this factor was controlled, perception of the Rotating-Snakes illusion and the Rotating-Tilted-Lines illusion turned out to be independent of each other. Indeed, the only intercorrelation that reached significance and could not be attributed to the age factor was that between the Pinna illusion and the Rotating-Tilted-Lines illusion. Thus, intercorrelations provide further evidence that the investigated motion illusions should not be considered as a homogenous group and that they rely on predominantly independent mechanisms.

#### 4 Discussion and conclusion

We aimed to contribute to a better understanding of illusory-motion perception by exploring individual differences in susceptibility to illusory motion. We decided to investigate age as the critical factor for the perception of motion illusions. In contrast to some field surveys by Kitaoka (2003b) our study is the first systematic approach exploring the relationship between age and illusory-motion perception. We considered four different motion illusions and provided a representative data set of one hundred and thirty-nine participants with an age range from 3 to 82 years.

Our data support differential age effects on the perception of different motion illusions and confirm that anomalous motion illusions represent a heterogeneous group. We postulate that different phenomena rely on specific processing mechanisms which mature at different rates and are more or less prone to age-related decline. Given that the contribution of peripheral mechanisms to the generation of illusory motion perception can be considered as rather limited, our findings are primarily related to changes in the central visual pathways during maturation and aging. Neurophysiological explanations for the different motion illusions appear to be far from conclusive and are still subject to vivid debate; thus any attempt to link age-related perceptual changes to specific processing mechanisms has to remain strongly speculative. Nevertheless, this approach might provide valuable insights for identifying critical mechanisms for further investigation.

The Enigma illusion has recently been attributed to neural activity of edge-detecting neurons inducing illusory motion in a bordering uniform area (Kumar and Glaser 2006; Hamburger 2007). In our sample, occurrence of the phenomena was not correlated with any other motion illusion under consideration. This finding points to differentiated processes that give rise to the Enigma illusion. This illusion was reported less frequently by children than by young adults, but was not affected by age in adults. About 60% of young children experienced illusory rotatory motion. In our adult groups, we found a relatively stable occurrence rate of approximately 80%.

It may be assumed that the postulated mechanism of illusory motion induction in the Enigma figure depends on neural connectivity and regulatory processes in the striate cortex. Less frequent occurrence of the phenomenon in children could reflect the prolonged maturation of columnar connections and the still immature excitatory and inhibitory mechanisms (Burkhalter et al 1993; Murphy et al 2005). Although it has been reported that response characteristics of senescent neurons in the striate cortex degrade (Schmolesky et al 2000; Wang et al 2005; Hua et al 2006), these changes appear to be of minor relevance for the Enigma illusion. Perception of illusory motion was preserved in our senior adults. Indeed, connectivity per se might prove relatively robust even though senescent neurons exhibit increased latencies, decreased selectivity, and elevated spontaneous activity. To our best knowledge, neurophysiological studies have not yet explored neural connectivity in the striate cortex during healthy aging.

The Rotating-Snakes illusion is assumed to rely on timing differences between responses to different patterns of the figure (Backus and Oruç 2005; Conway et al 2005). Our data reveal that occurrence of the Rotating-Snakes illusion is not correlated with any other phenomenon in the present study. This can be considered as evidence for a specific underlying mechanism. Although illusory rotation was reported by about 90% of young children, this occurrence rate lay significantly below the rate in the young adult group where the illusion was elicited in every participant. With increasing age, occurrence rates decreased significantly. In the senior adult group, only approximately 25% of the participants experienced illusory motion.

A possible explanation for the pronounced age-related differences in the occurrence of the Rotating-Snakes illusion might be provided by developmental data on response latencies. We used the illusion in its original version consisting of chromatic and achromatic elements. There is evidence that response latencies for chromatic and achromatic elements mature and age at different rates (Madrid and Crognale 2000; Crognale et al 2001; Crognale 2002; Page and Crognale 2005). Findings indicate that achromatic responses develop early during the first months after birth and show resistance to aging. In contrast, chromatic response characteristics continue to change into early adolescence and decline with increasing age. If differences between response latencies for chromatic and achromatic patterns contribute to the Rotating-Snakes illusion, developmental discontinuities can be expected to affect occurrence. In particular, the probability that a critical latency difference is exceeded might increase in young children and in older adults. As a result, illusory-motion perception should disappear. Indeed, children described the illusion less frequently than young adults and the frequency of occurrence dropped with increasing age in adults.

It can be speculated that an achromatic version of the Rotating-Snakes illusion, which is known to elicit illusory-motion perception in young adults, should not be affected by age. Since we did not consider an achromatic version in the present study, differential age effects remain to be investigated systematically. In an informal exploration with two senior observers illusory motion was reported for the chromatic as well as for the achromatic version, but the perception was judged to be weaker for the chromatic version than for the achromatic one. This side observation certainly does not allow for any conclusions; however, it points to a promising approach.

Although it appears tempting to attribute age effects in the Rotating-Snakes illusion to age-related latency changes, peripheral changes in the optics due to aging (compare Werner et al 1990) should be considered as another possible explanation. Processing of blue and yellow patterns in Rotating-Snakes illusion relies on the  $S - (L + M)$  visual pathway. This pathway is particularly affected by age because yellowing of the lens reduces the amount of short-wavelength light that reaches the retina. Therefore, the illusion may disappear in senior adults owing to less effective processing of the coloured patterns. However, this peripheral explanation cannot be applied to

the lower occurrence rate of the illusion in children than in young adults. Again, an investigation of age effects on an achromatic version of the Rotating-Snakes illusion could contribute to clarification.

The Pinna illusion and the Rotating-Tilted-Lines illusion have been explained by the failure of the visual system to solve the aperture problem (Pinna and Brelstaff 2000; Gori and Yazdanbakhsh 2008). These phenomena can be understood in terms of a bias to perceive motion direction orthogonal to local contours. In line with the common explanation, we found occurrence of both illusions significantly correlated with each other, but not with the Enigma illusion or the Rotating-Snakes illusion. The correlation could not be attributed to a confounded age effect. Thus, our data support the view that the Pinna illusion and the Rotating-Tilted-Lines illusion share some underlying processing mechanisms. However, an analysis of age effects in the occurrence of the two illusions reveals that these conclusions should be qualified. The Pinna illusion was reported by less than 20% of young children. Significantly higher occurrence rates of about 70% to 75% were determined in adult groups and those rates did not decline with increasing age. In contrast, the Rotating-Tilted-Lines illusion was already observed by about 95% of young children. An equivalent occurrence rate was found in the young adult group, but the illusion was reported significantly less frequently by middle-aged and senior adults. In the senior adult group, only 60% of the participants could perceive the illusory rotation.

Differential age effects on the occurrence rates of the Pinna illusion and the Rotating-Tilted-Lines illusion appear puzzling if it is assumed that both illusions can be attributed to the aperture problem in early visual processing. Although previous explanations can be considered as plausible and empirically supported (Pinna and Brelstaff 2000; Gurnsey et al 2002; Gurnsey and Pagé 2006; Gori and Yazdanbakhsh 2008), there is a need for exploring alternative mechanisms or additional specific triggers for the two illusions. In the case of another well-studied illusion, the Ouchi illusion, the exclusive attribution to the aperture problem has already been challenged (Ashida 2002; Ashida et al 2005).

Current evidence leads us to assume that an orthogonal bias in motion integration at least contributes to both the Pinna illusion and the Rotating-Tilted-Lines illusion. This mechanism may be subject to age effects. The aperture problem relies on receptive field size of neurons in the striate cortex. If receptive field size is larger than the size of critical moving patterns, motion direction can be detected veridically. Thus, illusory motion should depend on a certain ratio between pattern size and receptive field size. Yazdanbakhsh and Gori (2008) have recently demonstrated such a dependence for the Rotating-Tilted-Lines illusion. Receptive field sizes have been shown to decrease during development (Wilson 1988), but there is a lack of knowledge how they are affected by aging. Hence, neurophysiological data do not allow specific age-related predictions. In the present study, we did not manipulate the size of patterns triggering the illusory motion. Insights might be gained by variation of pattern size and parallel investigation of age effects on occurrence rates.

In summary, our findings support the notion that the motion illusions considered here originate from distinct processing mechanisms. As regards internal neural noise, which increases during the development and aging, we found no evidence for its general contribution to illusory motion perception. Specific underlying mechanisms appear to mature and age differentially. We have made an attempt to link perceptual data to possible neurophysiological changes related to age. Though speculative, this approach might indicate critical parameters for further investigation. We assume that perceptual differences between the age groups primarily mirror central processes. Although we cannot exclude the possibility completely, we consider it as rather unlikely that optical parameters or oculomotor functions account for our results. It has been repeatedly

shown that optical changes during aging cannot adequately explain functional declines (Ball and Sekuler 1986; Weale 1987; Bennett et al 1999). There is no conclusive evidence of deterioration of oculomotor functions during aging (Kerber et al 2006; Yang and Kapoula 2008). A detailed investigation of peripheral contributions to illusory-motion perception lay beyond the scope of the present study.

Although our methodological approach does not allow further specification of processing mechanisms underlying illusory-motion perception, we hope that our findings will encourage research on individual differences in susceptibility to illusory motion. Investigation of individual differences might point to physiological parameters which in turn could lead to better explanations of illusory phenomena. Future studies could profit by consideration of the chromaticity of illusions and manipulation of pattern sizes. Age represents a particularly promising factor associated with potential perceptual differences due to changing neurophysiology.

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